Ecosystem Assessment: Developing Environmental and Intrinsic Recruitment Indicators for Cod (*Gadus morhua* L.), Herring (*Clupea harengus* L.) and Sprat (*Sprattus sprattus* L.) in the Baltic and beyond

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ZUSAMMENFASSUNG

Marine Ökosysteme sind weltweit schweren Zeiten ausgesetzt, denn durch klimatische Veränderungen und übermäßige Ausbeute kommt es allerorts zur Verringerung der Artenvielfalt, und die Notwenigkeit für sorgfältig durchdachte Ökosystemleistungen und Nahrungsproduktionen wird dringender. Einer der global bedeutendsten Nahrungsfische stellt der Dorsch/Kabeljau (*Gadus morhua L.*) dar, welcher zusammen mit Hering (*Clupea harengus L.*) und Sprotte (*Sprattus sprattus L.*) im Fokus der vorliegenden Arbeit steht, da der Erfolg der Anzahl der Nachkommen als Antwort auf Umweltveränderungen verstanden werden kann.

Die vorliegende Arbeit besteht aus drei Kapiteln, welche sich mit der Frage nach den inneren und äußeren Einflüssen beschäftigt, welche im Zusammenhang mit dem Rekrutierungserfolg mariner Fischpopulationen beschäftigt. Äußere Einflüsse sind durch die Umwelt bedingt und können biotischer (z.B. Nahrungsverfügbarkeit, Räuberaufkommen) oder abiotischer (z.B. Salzgehalt, Temperatur) Natur sein. Innere Faktoren beziehen sich auf die Gesundheit und die genetischen Voraussetzungen der Population oder, im kleineren Zusammenhang, der Elterntiere. Diese Einflüsse werden dann ‚Indikatoren‘ genannt, da sie einen Zusammenhang aufzeigen (to indicate = engl. aufzeigen, abbilden). Besonders der Gadidae Dorsch/Kabeljau (*Gadus morhua L.*) (Kapitel II und IV) steht im Fokus dieser Studie, da die Bestände im Atlantik und der Ostsee in den letzten Jahrzehnten vielen Herausforderungen gegenüberstanden, was die Populationsgröße drastisch reduzierte und die Bestandsabschätzungen und Managementstrategien erschwerten. Als weitere Arten wurden Hering (*Clupea harengus L.*) und Sprotte (*Sprattus sprattus L.*) (Kapitel III) behandelt und die Frage nach den Stressoren, die neben der Fischerei den Rekrutierungserfolg beeinflussen, erörtert.

In den **Kapiteln II und III,** umweltbedingte Indikatoren, welche in unmittelbaren Zusammenhang mit dem Rekrutierungserfolg stehen, wurden anhand von einfachen linearen Modellen erster und zweiter Ordnung berechnet. Diese Methode kann sehr einfach und zeitsparend in anderen Zusammenhängen mit entsprechenden Daten angewandt werden. Von den gefundenen Indikatoren wurden mit Hilfe einer fünffachen Vergleichsprüfung konnten Grenzwerte berechnet werden, welche die „gute“ und die „schlechte“ Seite der Rekrutierungsvoraussetzungen der untersuchten

Arten definieren. Als Resonanzgröße auf die Rekrutierung wurden die Residuen aus dem Verhältnis von Rekruten- und Laicherbiomasse genutzt und als RecRes bezeichnet. Durch die Subtraktion der Grenzwerte von den identifizierten Indikatoren, wurde der jährliche Wert der „guten“ oder „schlechten“ Rekrutierungsvoraussetzung ermittelt. Die Standardabweichung der Vergleichsprüfung definiert einen Raum, in welchem „gut“ und „schlecht“ neutralisiert werden und so Möglichkeit für natürliche Schwankungen im Rekrutierungserfolg bieten.

Die Hauptindikatoren für den Dorsch in **Kapitel II** waren sowohl die Tiefe der 11 psu Isohaline, als auch die Größe des ‚Reproduktiven Volumen‘ (Wasserkörper [km^3], welcher eine höhere Salzkonzentration als 11 psu aufweist und eine Sauerstoffkonzentration von über 2 ml / l misst. Diese Bedingungen sind ideal für die Entwicklung von Dorscheiern in der zentralen Ostsee und im Gotland Becken, welches durch Plikshs et al. 1993 definiert wurde. Die Tiefe der Isohaline war hier jedoch der essentiellere Indikator, da er im größten Zusammenhang mit der Rekrutierung des Ostseedorsches stand. Dieser Indikator wurde auch für die Evaluation der RecRes genutzt, um zu prüfen, ob sich die RecRes als Resonanzgröße für mögliche Vorhersagen eignen.

Die in diesem Kapitel abgeleiteten Indikatoren und ihre entsprechenden Schwellenwerte für EB Dorsch weisen darauf hin, dass abiotische Faktoren die Hauptfaktoren für den Rekrutierungserfolg von Dorsch im Baltikum zu sein scheinen, da ideale Bedingungen für eine erfolgreiche Entwicklung und das Überleben der Eier die wichtigsten Mechanismen sind, die die Stärke der Jahresklasse beeinflussen.

Das **Kapitel III** kann als Methodenevaluation des ersten Kapitels verstanden werden. Sowohl für die Indikatoren als auch für die Grenzwertbestimmung wurden die gleichen Methoden angewendet. Allerdings unterschieden sich hier die Arten, denn es wurde nun der Rekrutierungserfolg von Hering und Sprotte untersucht. Die Hauptindikatoren für die Sprottenpopulation waren hier ebenfalls die Tiefe der 11 psu Isohalinen im Bornholm und im Gotland Becken, die Größe des Rekrutierungserfolges des Dorsches, die Temperatur im ‚Reproductive Volume‘ und die Nahrungsabundanz von Bosmina spec. im Sommer. Für die Evaluierung der RecRes wurde der stärkste Indikator, die Tiefe der 11 psu Isohalinen (Bornholm

Becken) genutzt. Die Hauptindikatoren die das Rekruitment der Heringspopulation in der Zentralen Ostsee beeinflussen waren die Nahrungsabundanz (*Acartia spec.)* im Sommer, die Tiefe der 11 psu Isohalinen (Bornholm Becken) sowie die die Größe der geschlechtsreifen Dorschpopulation. Weitere Indikatoren wie beispielsweise die Abundanz von *Pseudocalanus* spec. als weitere Nahrungsquelle und die Tiefe der 11 psu Isohalinen in der zentralen Ostsee wurden ebenfalls als Indikatoren identifiziert aber nicht für weitere Analysen genutzt, da die Standardabweichungen hoch waren und womit annähernd genaue Ergebnisse nicht möglich sind.

Im Gegensatz zu Kapitel II zeigten sich hier auch biotische Faktoren, die den Rekrutierungserfolg der Bestände der Clupeiden beeinflussten. Da Hering und Sprotte pelagische Fische sind und sowohl durch ‚Bottom-Up' (Salzgehalt, Temperatur, Beutetiere) als auch von ‚Top-Down' (Raubdruck durch z.B. Dorsch) Mechanismen kontrolliert werden, scheinen die Ergebnisse nicht überraschend zu sein, da die Arten ein Mittelglied von z.B. die Nahrungskette in der Ostsee darstellen.

Die angewendete Methode zur Identifikation geeigneter Umweltindikatoren und ihrer entsprechenden Grenzwerte pro Art in beiden Kapiteln bietet die Möglichkeit, Indikatoren zu verwenden, die für Vorhersageszenarien (z.B. künftige Rekrutierungserfolge) ausgewählt wurden können, wenn die zugrunde liegenden Dynamiken gut verstanden und stets im Auge behalten wird, dass sich Systeme stetig wandeln. Außerdem kann die hier verwendete Testvariabel (Residuen der Laicherbestand / Rekrutierungsbeziehung) aufgrund der mangelnden Unabhängigkeit zwischen Laicherbestand (SSB) und Rekrutierungsabschätzung durch z.B. Autokorrelation verfälscht sein und muss daher sehr sorgfältig gehandhabt werden, wenn sie in einem Managementkontext implementiert werden soll.

In **Kapitel IV** wurde der Fokus auf die intrinsischen Indikatoren gelegt, also auf die physiologischen Einflüsse, die zu einem erfolgreichen Rekruitment führen. In diesem Kapitel wurde der elterliche Beitrag zu einer erfolgreichen Nachkommenschaft in einem umfangreichen laboratorischen Experiment erforscht. Die intrinsischen Indikatoren, die den Rekrutierungserfolg des atlantischen Kabeljaus am meisten beeinflussen waren in dieser Studie Eiergröße und somit der Gehalt an Dotter, sowie die Gesundheit der Mutter (definiert als Fulton's Konditionsfaktor K). Diese

Indikatoren haben im Experiment signifikant zu der Mortalitätsrate der frühen Lebensstadien im atlantischen Dorsch beigetragen.

Die Ergebnisse aus Kapitel IV zeigen, dass es neben Feld- und Abschätzungsdaten aus Bewertungsmodellen weitere Mechanismen gibt, die den Rekrutierungserfolg beeinflussen, da die gefundenen Indikatoren intrinsischer und genetischer Natur sind (d. H. Dotterversorgung, Körpergröße, Fitness). Hier liegt der Rückschluss nahe, dass für die Abschätzung des Rekrutierungserfolges auch die Längen-Gewichtsbeziehungen der Weibchen in Betracht gezogen werden sollten, da diese Merkmale maßgeblich zu dem Rekrutierungserfolg beitragen. Die Ergebnisse dienen als Erweiterung der Indikatoren aus den vorherigen Kapiteln und sollen daran erinnern, dass Daten jeglicher Art mit Vorsicht bearbeitet werden sollen, um nicht voreilige Rückschlüssen (z.B. Vorhersagen) zu ziehen, da nicht jede Dynamik der natürlichen Umstände in jedem Datensatz wiedergegeben ist.

Die Arbeit schlägt eine Analyseabfolge bestehend aus 6 Schritten vor (Diagramm 1) für die Analysen im zweiten und dritten Kapitel vor, mit dessen Hilfe die Methode auf entsprechende Daten und andere Arten angewendet werde kann. Im **1. Schritt** werden die besten Schätzwerte / Resonanzgrößen bezogen auf den Rekrutierungserfolg anhand verschiedener (möglichen) statistischer Modelle berechnet. Der **2. Schritt** befasst sich mit der Identifikation und Auswahl von abiotischen und biotischen Umweltparametern, welche als Rekruitmentindikatoren genutzt werden können. Diese Indikatoren werden durch lineare Regressionsmodelle erster und zweiter Ordnung bestimmt sowie durch eine Vergleichsprüfung eines Testdatensatzes geprüft. Im **3. Schritt** werden für die ausgewählten Indikatoren Grenzwerte berechnet, welche als Maß für mögliche Vorhersagen genutzt werden können. **Schritt 4** befasst sich mit der Evaluation des genutzten Modells durch einen Trainingsdatensatz. Um die Sinnhaftigkeit der RecRes im Zusammenhang mit den identifizierten Indikatoren für den Rekrutierungserfolg verschiedener Arten zu bestimmen, werden die Indikatoren im **5. Schritt** mit Hilfe des gesamten Datensatzes evaluiert. Abschließend können die Ergebnisse im **6. Schritt** für mögliche Vorhersageszenarien bezüglich der äußerlichen (Umwelt) Rekrutierungsvoraussetzungen genutzt werden.

Neben der Identifizierung von umwelt- und ökophysiologischer Schlüsselindikatoren für den Rekrutierungserfolg mariner Fische, bietet die Arbeit einen Überblick über den historischen Hintergrund der analysierten Gebiete (zentrale Ostsee und Ostküste Kanada) und zeigt die Schwierigkeiten auf, deren Fischpopulationen in den letzten Jahrzehnten ausgesetzt waren. Darüber hinaus werden in der vorliegenden Arbeit weitere mögliche Maßnahmen, z.B. Risikoanalysen der verschiedenen Managementansätze sowie die festere Einbeziehung der Interessengruppen diskutiert.

SUMMARY

Marine ecosystems are facing difficult times as climate change and heavy exploitation lead to biodiversity loss, the need of advanced ecosystem services, and deliberate adjustments especially in the food production industry. Cod (*Gadus morhua L.*), as one of the most important species for human consumption worldwide, is the focus of the presented study along with herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*) in the Baltic, as the species' recruitment success oscillate according to environmental changes.

The present study consists of three chapters that deal with the question of environmental and intrinsic indicators underlying recruitment success in marine fish species. The primary focus of this approach is the gadoid cod (*Gadus morhua L.*), as stock assessment (in the Baltic) has been error-prone throughout the last decade, leaving possible management strategies in question. Apart from Eastern Baltic (EB) (Chapter II) and Atlantic cod (Chapter IV), Baltic herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus* L.) (Chapter III) were species examined in this study. The overall idea of the presented approach is to find, besides fishing pressure, key indicators per species, area and period of factors, that fundamentally affect recruitment success. In **Chapters II and III,** environmental indicators connected with recruitment success were obtained through a simple linear regression approach that can be applied in an easy and timesaving manner in other contexts. From these indicators, individual threshold values are derived by means of a 5-fold cross-validation approach, that define the barrier between a "good" and "bad" recruitment environment for the analyzed species. As the response variable to recruitment success, the recruitment residuals (RecRes) gained from the recruitment – spawning stock biomass (SSB) relationship were used. By subtracting the threshold value of an environmental indicator, the degree of how "good" and how "bad" recruitment environment was in certain years was assessed. The standard deviation of the cross-validation method serves as a range of uncertainty, where "good" and "bad" becomes neutral and hence gives more space for natural variability regarding recruitment success.

In **Chapter II, “Anticipating “good” or “bad” prospects for offspring of commercially important fish populations – objectively identifying indicators and thresholds for Eastern Baltic cod (*Gadus morhua L.*) recruitment environment”,** the main indicators found for EB cod were the depth of the 11 psu isohaline as well as the reproductive volume (RV) (water body [km^3], that measures more than 11 psu and oxygen content exceeds 2 ml / l and therefore provides optimal condition for cod egg development) in the central Baltic and in the Gotland Basin. Derived indicators and their correspondent thresholds for EB cod indicate, that abiotic factors seem to be the main drivers affecting Baltic cod recruitment success, as ideal conditions for successful egg development and survival are the most important mechanisms influencing year class strength. The depth of the isohaline was considered to be the most important indicator as it showed the strongest correlation with recruitment. Therefore, it was used for the evaluation of the RecRes as a good measure of response to recruitment and for possible forecast scenarios.

Chapter III, “Identifying recruitment indicators and thresholds for Baltic herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*) by using a single-species approach developed for their top predator, Eastern Baltic Cod (*Gadus morhua L.*)” is an evaluation paper of the method applied in Chapter II. Here, the same approach was conducted within the same area (Subdivisions of Central Baltic) but for different species (sprat and herring). Key indicators for sprat were found to be the depth at 11 psu isohaline in the Bornholm and Gotland Basin, cod recruitment, as well as temperature in the reproductive volume of the Bornholm Basin and prey abundance (*Bosmina* spp.) in summer. For the evaluation of the RecRes, depth of the 11 psu isohaline (Bornholm Basin) was used. For herring, the main indicators affecting recruitment were found to be *Acartia* spp. abundance in summer, the depth of the 11 psu isohaline in the Bornholm Basin, as well as cod SSB. Prey abundance (*Pseudocalanus* spp.) as well as the depth of the 11 psu isohaline in the central Baltic also showed a correlation with herring recruitment but were not used for further analysis as the standard deviation was high.

In contrast to Chapter II, biotic factors were also found to affect recruitment success of the clupeid stocks in the Baltic. As herring and sprat are pelagic fish and are controlled both, bottom-up (salinity, temperature, prey organisms) and top-down (predation pressure by cod), the results do not seem to be surprising as the species represent a middle link, e.g., of the food chain, in the Baltic.

The method used to derive a suitable set of environmental indicators and their corresponding thresholds per species in both chapters generates the opportunity to use indicators selected for predictive scenarios (i.e. future recruitment success) if underlying mechanisms are well understood and always with the understanding in mind, that systems are continuously changing. Also, revealed recruitment mechanisms could be falsified due to the lack of independence between SSB and recruitment data (i.e. autocorrelation) and therefore must be handled very carefully if implemented in a management context.

In **Chapter IV, "Parental effects on early life history traits in Northwest Atlantic cod, *Gadus morhua L.*."**, the focus was put on physiological, and therefore, intrinsic indicators responsible for recruitment success. Here, the parental contribution to the successful offspring was investigated in an extensive laboratory set up. Intrinsic indicators affecting Atlantic cod recruitment success were found to be egg size (amount of yolk) and fitness of mothers (Fulton's condition factor K) that contributed significantly to decreasing mortality rate in the early life stage of Atlantic cod.

The results of Chapter IV indicate that there are more mechanisms driving recruitment success other than field observations and data gained from assessment-models, as the indicators found are of intrinsic and genetic nature (i.e. yolk supply, body size, fitness). An obvious conclusion could be stated, that it may be better to estimate recruitment success using length-/weight-at age data of females as female size and fitness contribute significantly to recruitment success. Findings serve as an enhancement to the indicators found in the previous chapters, as well as a cautionary reminder to handle data holistically, if predictions derived from this are to be reliable.

This study proposes a 6-step framework (Diagram 1) for Chapters II and III, that can help the reader understand and apply the method to other appropriate data and species. In **step 1**, the estimation of unbiased response variables (RecRes) is the focus using different statistical approaches. **Step 2** deals with the selection of abiotic and biotic environmental indicators by applying linear regression models and cross-validation to a training data set. Thresholds to the identified indicators are obtained in **step 3**. In **step 4**, the model performance is tested based on a training data set. The full data set is used for the evaluation of the identified indicators according to the RecRes in regard to recruitment success in **step 5**. And finally, **step 6** proposes how results can be applied to a forecast scenario as ideas for future usage of results.

Beyond the identification of environmental and intrinsic key indicators and thresholds or fish recruitment, the present study provides an insight into the historical background of the investigated sites (Eastern Baltic and eastern coast of Canada) and describes the difficulties of the fish stocks in the last decades. The study also discusses further steps that need to be taken within a successful management framework such as risk analysis and stakeholder involvement.

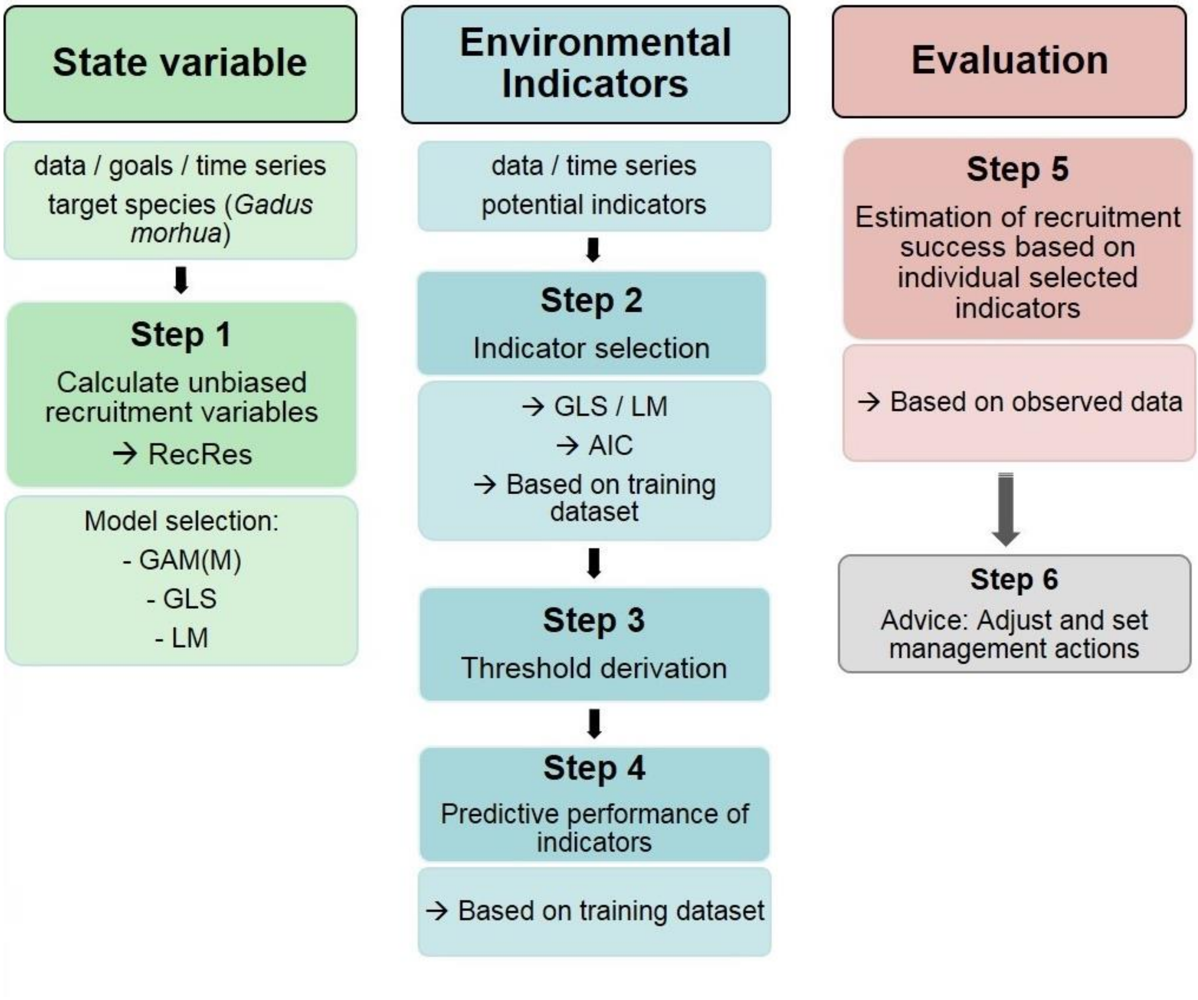

Diagram 1: Steps of our applied method. **Step 1**: estimation of unbiased state variables (RecRes) of Eastern Baltic cod (*Gadus morhua L.*) using different statistical approaches. **Step 2:** Selection of environmental indicators by conducting multiple sound statistical and validation methods on a training dataset (1965 – 2003). **Step 3**: derivation of individual thresholds per selected indicator. **Step 4**: model performance based on a training dataset. **Step 5**: Evaluation of recruitment success of target species based on selected environmental indicators by using the fully-observed dataset (1965 – 2009). **Step 6**: future usage of presented approach that was not subject to this study.

Chapter I

GENERAL INTRODUCTION

1. GENERAL INTRODUCTION

The awareness for changing (eco)systems becomes more and more evident globally, as anthropogenic interests and doubts are widely discussed and accessible to everybody. With the current open pool of knowledge, science has to provide even more accurate and well-defined results and statements, that can be implemented and worked with to hold up against outside scrutiny, e.g., 'Fake News', that is influencing humanity more and more every day.

In the last decades, the call for useful indicators has risen and various studies (e.g., Rice & Rochet, 2005; Samhouri et al., 2009; Levin et al., 2010; Gårdmark et al., 2011; Otto et al., 2018) set their aim to find (environmental) indicators that can be used for achieving management goals. Indicators can help to explain mechanisms behind biological and physical correlations, and therefore serve as a good proxy for ecosystem dynamics (Rice & Rochet, 2005).

Indicators, and their respective threshold per species, defined in the present study were derived from the residuals (RecRes) of the spawning stock biomass (SSB) to recruitment success relationship and can serve as an estimation tool for spawning stock biomass strength per year and / or the setting of fishing quotas.

In order to get an idea on how to implement indicator-based (fisheries) management successfully, indicators are generally developed in the context of case studies in defined areas. That way, selected indicators can be tested and adjusted as needed. The present study uses the Baltic Sea as the study area for developing recruitment indicators for its main fish species cod (Chapter II), herring and sprat (Chapter III). The developed method in Chapter II of how to define recruitment indicators for cod is reapplied in Chapter III for clupeids and adjusted accordingly. Chapter III provides an experimental insight to another case study conducted in a laboratory on Atlantic cod regarding intrinsic recruitment indicators and discussed possible mechanisms of recruitment on a genetic level.

One of the top predators of the Baltic, the eastern Baltic cod (*Gadus morhua L.*) is representative of a species that had to react to new environmental conditions within a changing world after the reorganization. After the 'cod collapse' at the beginning of the 1990's (e.g. Köster et al., 2005), the population struggled until a mysterious recent recovery (Eero et al., 2011), leaving the dynamics and stressors of the comeback unclear (Eero et al., 2015). Hence, we have taken a closer look into the possible factors influencing cod recruitment, hoping to find indicators that can serve as early warnings in order to prevent population breakdowns in the future.

1.1 History of the Baltic Sea Region

The semi-enclosed and reasonably shallow Baltic Sea has a relatively young history of development and is about 10,000 years old. The area underwent some major changes in its formation: from presenting a freshwater Baltic ice lake (appr. 13,000 years ago) to a marine system with the biodiversity in flora and fauna as we know it today (appr. 4,000 years ago). Not only the geological and biological development, but also the history of human-kind, has made it a unique area of trade and shared interests. After the Vikings had their peak around 1,000 AD, the Baltic region has always been split between many countries sharing the same anthroposphere and interests. Moving to more recent times, in the last century until the early 1990's, the Iron Curtain separated the Baltic Sea region for almost 50 years into socioeconomically underprivileged eastern Baltic countries dominated by the Soviet Union and the richer counties to the west. After the downturn of the dominant regime in the east, major political changes resulted in the following nine coastal Baltic Sea countries: Russia, Poland, Estonia, Latvia, Lithuania, Germany, Denmark, Finland and Sweden. With Russia being the only country outside the European Union (EU), it should be relatively easy to follow political and scientific guidelines as a joint goal regarding the management and the protection of the common source: the Baltic Sea. Nevertheless, different starting conditions regarding politics and socioeconomic interests make the collaboration and communication between the countries a barrier to achieving a common target, especially in the fields of agriculture, transport, environment, fisheries, water resources and scientific research. The growing population on the coast of the Baltic region has resulted in the deterioration and degradation of the area, pushing exploitation further towards its limits since the early 1940s, when industrialization began to rise. Today, more than 85 million people inhabit the Baltic Sea drainage basin that obtain a multitude of resources and trade channels from it; their activities would be able to change and impact the future of the Baltic environment for the better if clear frameworks of management actions were laid out and being implemented (Thulin & Andrushaitis, 2003).

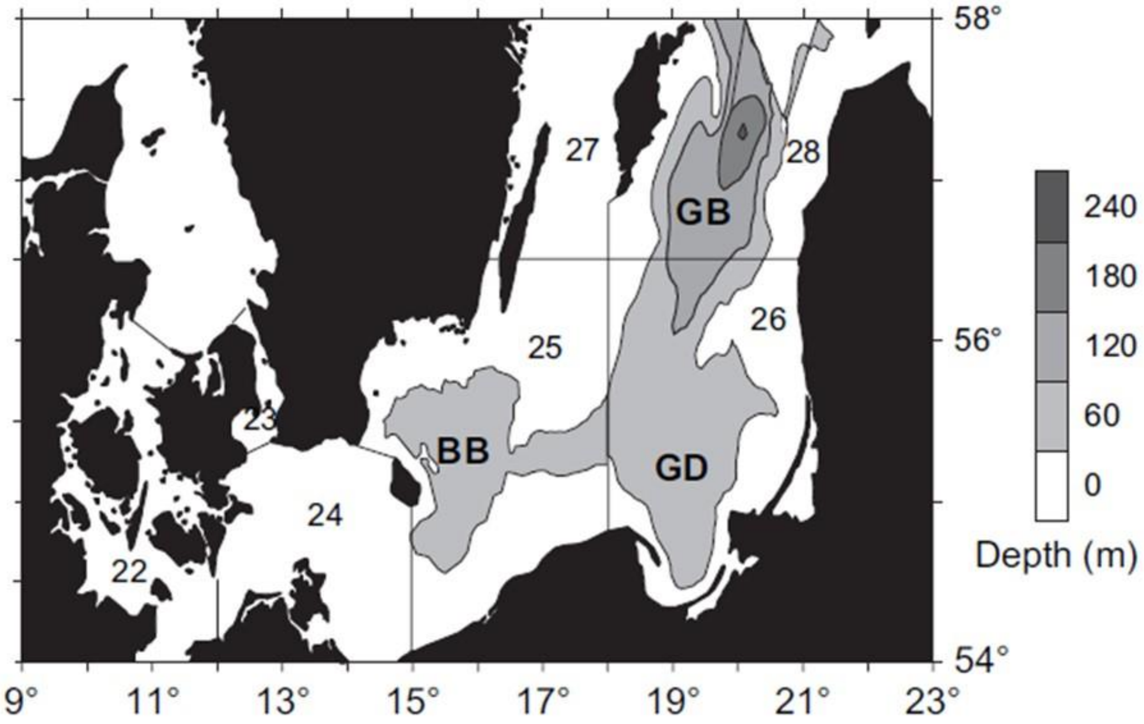

Figure 1: The southern and central Baltic with spawning areas of the eastern Baltic cod stock in ICES Subdivisions 25 (BB: Bornholm Basin), 26 (GD: Gdansk Deep), and 28 (GB: Gotland Basin) from Köster et al., 2005.

The Baltic Sea is divided into various sections that each have special attributes and characteristics. Three deep basins, namely the Arkona, Bornholm and Gotland Basin, are located inside the entrance towards the central Baltic proper, filled with saltier, heavier water that sinks down after entering the narrow and shallow passage through Skagerrak/Kattegat and the Øresund channel from the North Sea. River run-off and rain water form a steady current of freshwater at the surface, which results in, for most parts of the Baltic Sea, a strong vertical stratification of fresh water at the surface and saltwater at the bottom that rarely mix. Due to these layered water masses, the oxygen passage from the surface into deep water masses is limited, causing some severe oxygen depletion zones in the deep (Sandberg, 1994). Inflows of oxygen-rich water from the North Sea occur on a regular basis, but it is the major ones that are washed in by land-based run-off which increase the oxygen level in the whole water column, ease the stratification and dilute the concentration of pollutants. Unfortunately, those essential major inflows are very infrequent and occur roughly every 10 years as they are highly connected to climate events such as the North Atlantic Oscillation (NAO). Moving further to the North or the East of the Baltic Sea in the direction of Finland or Russia/ Estonia, the water becomes fresher and it is not as influenced by salty inflows anymore. Species inhabiting the Bothnian Bay on the coast of Sweden and Finland or the Gulf of Finland shared by Finland, Russia and Estonia have to be adapted to less salty water with no halocline as well as high nutrient loadings from the coastal drainage areas (HELCOM 1993).

Areas of low salinity or oxygen, high nutrient loadings and therefore areas of increasing eutrophication, ice coverage in winter and changing temperatures makes the Baltic Sea a harsh environment to live in. For most freshwater species, the Baltic is too saline and for most marine species, the water is too fresh, leaving the Baltic ecosystem with fewer species than other marine habitats. The biodiversity of the Baltic Sea successively declines along the salinity gradient in this unique environment, harbouring roughly 1,500 species along Sweden's west coast and leaving the Archipelago Sea to the north with about 20 species (Thulin & Andrushaitis, 2003). But even though the Baltic seems like a system with few interactions due to a limited number of species, the BSLME is not as simple as it seems. Besides the typical grazing food chain, where energy fluxes from primary producers (phytoplankton) are carried up to higher trophic levels via grazing by herbivorous animals such as zooplankton and then are passed on to higher level predators like fish, birds and marine mammals, another circle of energy flow exists. The long microbial food chain displays an important but less efficient part of the Baltic ecosystem and is tightly coupled with multi-species interactions (i.e. predator-prey relationships) and interlinks the diverse energy pathways in a complex food web. The whole Baltic ecosystem undergoes regular variabilities in species abundance and abiotic factors such as salinity and temperature, which changes the structure and function of the food webs (Thulin & Andrushaitis, 2003). These changes result from temporal shifts in climate and environmental conditions as well as from human induced pressures (Folke et al., 2004).

1.2 Cod (*Gadus morhua L.*)

Cod (*Gadus morhua L.*) is widely distributed along shelf sea areas and coasts of the northern hemisphere. Cod is a demersal fish that contains many populations that differ in their spawning grounds, migration patterns and genetic composition.

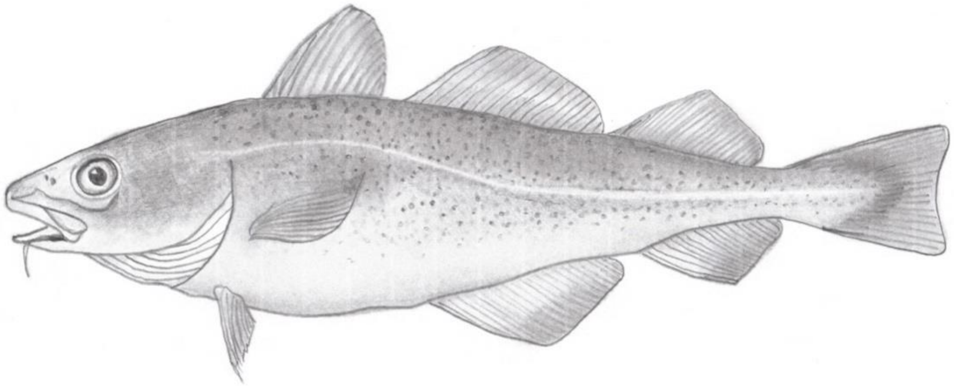

Figure 2: Drawing of *Gadus morhua L.* (Atlantic Cod).

The eggs and larvae of cod are pelagic and can experience a wide variability in environmental factors as they develop, including differences in hydrography (temperature, water currents) and predation pressure (Buch et al., 1994). Cod has not only been an important species in the history of fisheries (Innis, 1978; Kurlansky, 1997), but also plays an important role in the trophodynamics of marine communities, for example in the Baltic Sea (Köster & Möllmann, 2000) and on the eastern Scotian Shelf (Bundy et al., 2005).

Eastern Baltic cod is of considerable importance as it is commercially the most important fish stock in the Baltic Sea, and dominant top-predator in the food web (Casini et al., 2008, Möllmann et al., 2008). Climate driven hydrographic changes and extensive fishing forced the collapse of the population at the beginning of the 1990s (Köster et al., 2005, Eero et al., 2012, Köster et al., 2016). The new millennium started out promising, as signs of recovery were evident, but assessment has been difficult due to failing analytical assessments caused by data uncertainty and unanticipated growth problems (Eero et al., 2012, Casini et al., 2016).

The Atlantic cod stocks that inhabit the eastern coastline of Canada have always been one of the world's richest and most important fishery sources, as it advanced the settlement of Europeans in North America (Innis, 1978; Kurlansky, 1997). After World War II, the Northern cod stocks were under severe pressure from industrialized trawler fleets and cod biomass fell to minimum levels on a historically unprecedented scale. It became apparent that this collapse, today known as the “the cod collapse” did not only affect the Northern cod. Also stocks off Nova Scotia, New England, Greenland and the Gulf of St. Lawrence were dangerously depleted by the early 1990s (Boreman et al., 1997).

Not only overfishing led to the decrease in cod biomass: since every cod stock responds differently to environmental factors such as prey density and temperature (Puvanendran & Brown, 1999; Brander, 1995). Climate driven events, such as the NAO winter index, strongly affects recruitment of the European Shelf cod stocks, as the study of Ottersen & Stenseth (2001) showed. This has consequences for their management, and for models that are used to carry out short- and long-term projections. In the case of Europe, the management of cod stocks must take into account, that there is a higher vulnerability to environmental variability, when SSB is low (Ottersen & Stenseth, 2001; Brander & Mohn, 2004; Stige et al., 2006). The reason why every stock responds differently to given environmental situations is the fact that every population has slightly different genetic constellations as reported by Møller (1968) for the Norwegian stocks and more recently for stocks in the Northwest Atlantic (reviewed in Ruzzante et al., 1999). Genetic differences in growth have been found for larval, juvenile and adult stages in Norway (Van der Meeren et al., 1994; Suthers & Sundby, 1996; Svåsand et al., 1996; Otterlei et al., 1999) and for larvae and juveniles in the North West Atlantic (Van der Meeren & Jorstad, 2001) regarding temperature, Hunt von Herbing et al. (1996) looked at feeding behavior and Purchase & Brown (2000, 2001) studied prey densities for cod larvae considering their genetic differences. Cod, like most other marine animals with pelagic eggs or larvae are highly fecund and an abundant species that exhibit large variations in recruitment. These large recruitment fluctuations, frequently observed among such species, are generally attributed to factors affecting early life stages (Hjort, 1914; Cushing, 1972; Houde, 1987; Peterman et al., 1988; Taggart & Frank, 1990).

1.3 Herring (*Clupea harengus L.*)

The Atlantic herring (*Clupea harengus L.*) populations inhabiting the Baltic display one of the most economically relevant clupeid fish stocks in the Baltic that are able to handle low salinity gradients as well as changes in temperature quite well (Cardinale et al., 2009). Their resilience totters if humans continue destroying coastal spawning grounds, as herring lay their eggs on plants and rocks near the shoreline (Aneer, 1989). Different populations are characterized by their different spawning times, starting in January in the western regions (ICES SD 24) and ending in July in Finnish waters (SD 31) (Parmanne et al., 1994; Aro, 1989). Herring has a predator- prey interaction with the Baltic's top predator cod (*Gadus morhua*) and plays an important role in the smaller pelagic fish community within a food web.

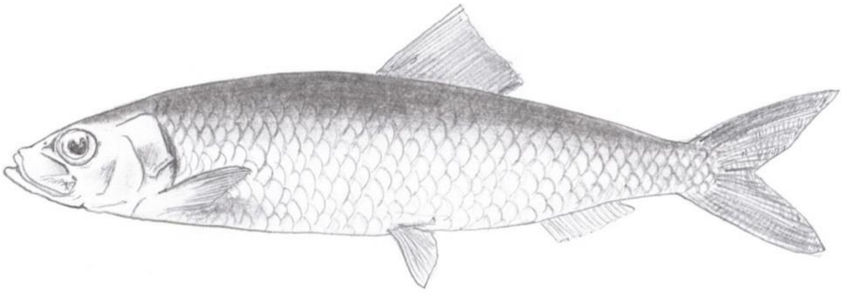

Figure 3: Drawing of *Clupea harengus L.* (Herring).

1.4 Sprat (*Sprattus sprattus* L.)

Along with herring, sprat (*Sprattus sprattus L.*), is also an important commercial clupeid fish species in the Baltic (ICES, 2010). The deep basins of the Baltic Sea (Bornholm Basin, Gdansk Deep and Gotland Basin) mark the northern distribution boundary of sprat (MacKenzie & Köster, 2004), that spawn asynchronous in these basins, making it challenging for the detection of the seasonal recruitment success (Voss et al., 2012). Unlike herring, sprat have difficulties adjusting to rapid changes in environmental stressors, which was evident in fluctuations in recruitment success in the last century, as environmental drivers and large-scale changes in the Baltic ecosystem such as regime shifts were perceivable in sprat biomass (Alheit et al., 2005;

Möllmann et al., 2009). Specifically, the cod collapse at the beginning of the 90s showed a direct response in sprat biomass as it increased distinctly in correlation with the cod stock's decrease (Bagge et al., 1994; Parmanne et al, 1994; Köster et al., 2001). The oscillating biomasses of cod and sprat also stem from the profound predator-prey relationship of the two species, as sprat represents a major food source for adult cod, as well as the most important predator of cod eggs (Bagge et al., 1994, Köster & Schnack, 1994).

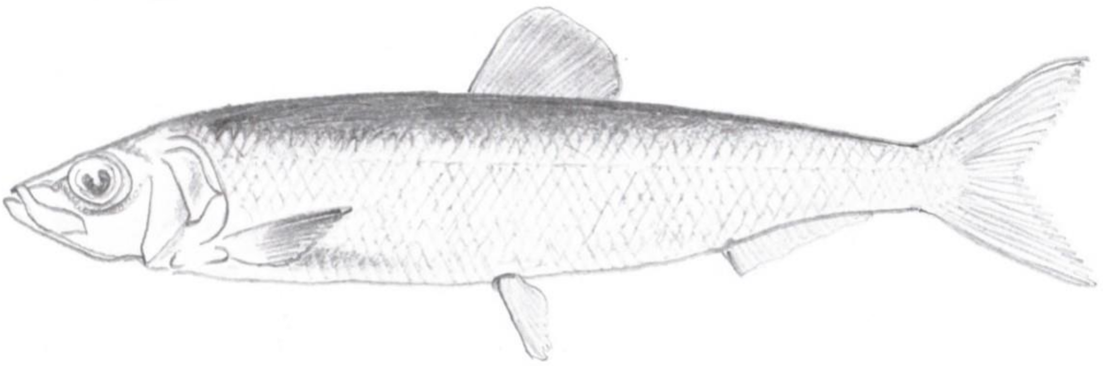

Figure 4: Drawing of *Sprattus sprattus L.* (Sprat).

1.5 Fish in a Changing Environment

The commercially important species in the Baltic, cod (*Gadus moruha L.*), herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*), have displayed an example of major changes and shifts in abundance and biomass during the last century (Köster & Möllmann, 2000) that were the result of excessive fishing in the eighties and changes in hydrographic conditions.

Several regime shifts due to climatic variations in the Baltic Sea regions led to an increase in temperature during winter and spring, a decrease in salinity in the central Baltic proper, and a lack of major Baltic inflows (decrease in oxygen). Consequently, unfavourable conditions for the cod stocks rose, presenting another drop for the already diminished populations of the formerly dominating species. The increasing temperatures led to a shift in zooplankton composition, which resulted in major changes in the food-web by shifting the system from a gadoid-dominant to a clupeid-dominant state (Matthäus & Schinke, 1994; Köster & Möllmann, 2000; Köster et al., 2003). This occurred successively when the main prey item for larval and juvenile cod, the copepod *Pseudocalanus elongatus,* (Ojaveer et al., 1998; Vuorinen et al., 1998; Möllmann et al., 2000; Hinrichsen et al., 2002) decreased while the clupeids' diet (copepods: *Temora longicornis* and *Acartia* spp.) increased (Grauman & Yula, 1989; Kalejs & Ojaveer, 1989). The predation of clupeids on cod eggs (Köster & Möllmann, 2000), the decreasing salinity and therefore, the dispersing halocline that is essential for the cod eggs to float in, (Thorsen et al., 1996; Wieland & Jarre 1997), as well as low oxygen concentrations that disadvantage the egg survival, and therefore the recruitment success (e.g. Kosior & Netzel, 1989; Lablaika et al., 1989; Nissling & Vallin 1996), presented large impacts and nearly insuperable barriers on the cod stock's success of recovery.

The decrease in top predators like cod, not only leads to economic losses for the fishing industry, it primarily results in a loss of biodiversity that can eventualize in a loss of ecosystem resilience (Elmqvist et al., 2003; Bellwood et al., 2004). Loss of resilience makes it harder for managers and scientists to return the system to a desirable state (Österblom et al., 2007).

The consideration of environmental factors affecting recruitment success longs for a more holistic view of recruitment dynamics as the individual response to environmental stressors goes hand in hand with the intrinsic set up of the individual. Therefore, understanding early life history traits of fish is requisite knowledge for any further investigations of recruitment dynamics or natural responses to environmental stressors.

1.6 Understanding Early Life History Traits of Fish

In marine fish, rates of natural mortality (M) are highest during early life and are negatively correlated with rates of growth and body size. In these early life stages (eggs, larvae, young juveniles), subtle differences in M can cause large differences in recruitment and year-class success (Houde, 1987). Therefore, it is particularly critical to understand factors that contribute to variability in M during early life. In order to understand variability among laboratory-reared cohorts, previous studies have mostly examined maternal effects, assuming that egg quality and lipid reserves are obviously provided by the mother (Chambers & Leggett, 1996). Parental effects on offspring can be separated in maternal and paternal influences (Bernardo, 1996). In maternal effects, female age, size, condition and spawning experience have a great influence on egg size and quality (Chambers & Leggett, 1996). Egg size has been found to correlate positively with larval size, yolk-sac volume and time of metamorphosis (Baroudy & Elliot, 1994; Cunningham & Russell, 2000). The influence of the father on his offspring was often considered as synonymous with genetic effects, since the only significant contribution of sperm is DNA. Understanding the factors underlying larval morphology and metabolism can help us to improve our knowledge regarding recruitment success. In early fish development, high mortality rates occur in different phases of development, since the embryos and larvae are sensitive to environmental conditions. After hatching, larval stages of marine fish are considered to be a bottleneck, since high rates of mortality are evident (Gulland, 1965; Hjort, 1914). Laboratory results show that depending on temperature and egg size rates (Steinarsson & Björnsson, 1999), and therefore mortality rates of early life stages of cod, are genetically and environmentally driven. The survival success of each individual larvae is strongly influenced by its morphological traits, namely body size, which is assumed to influence the magnitude of predation pressure in the wild (Houde, 1987; Pepin & Myers, 1991), yolk reserves, which determine the amount of energy available for growth and metabolism in the first days post hatch (Theilacker, 1981; Rana, 1985), growth efficiency and rapidity of development. The latter affects duration of life history stages, during which larvae are particularly vulnerable to a wide variety of predators (Leggett & Deblois, 1994). The sooner a larva becomes bigger, the better its chances to survive and grow out of the critical situation of being a prey item for many predators (bigger – is – better hypothesis, Houde, 1987).

Differences in egg quality are apparent among batches and females (Rideout et al., 2005) and, it is clear that “good” eggs result in “good” larvae. Many studies mention that egg size is a good metric for egg quality because more lipid reserves are available for the larvae until first feeding in larger compared to smaller eggs (Blaxter, 1988). This is partly the case since lipids, whether aggregated in oil globules or dispersed throughout the yolk, supply larvae with energy directly after hatch (Blaxter, 1969; Lloret et al., 2008). Therefore, low energy reserves may lower the chances of survival, leading to an increase of natural mortality (Cunjak, 1988; Griffiths & Kirkwood, 1995; Sogard & Olla, 2000). Chambers et al. (1989), however, found no correlation between initial egg size, yolk volume, length at hatch and post hatching lifespan in capelin (*Mallotus villosus*), which clearly stands in contrast to the assumption that large eggs favor better survival of larvae after hatch. That means that even though the eggs were of good quality and were big, the fitness of the larvae also depends on the length of the embryonic stage. If daily mortality rates are greater in the embryonic period than in the larval period, an extended embryonic period is seen as a cost of being large at hatch. Which also means that the larvae itself is bigger, has better chances to find prey items due to further developed mouth and jaw, may be more locomotive, but also has less yolk to feed from at the start (Chambers et al., 1989).

For management applications and the setting of new fishing quotas per year, environmental and physiological interactions and pressure as described above need to be recognized per species, as they may influence the population and an ecosystem fundamentally (Rudstam et al., 1994).

1.7 Marine Ecosystem Management

From an ecosystem-based-(fisheries)-management (EB(F)M) perspective, understanding the dynamics underlying a shift is of great importance to become active and prevent or avert greater ecological and economic damages. Therefore, the identification of key drivers in the system as well as appropriate collaboration between stakeholders and the courage to discuss different possible scenario outcomes after a reorganization has happened is essential (Scheffer & Carpenter, 2003). Sadly, the communication and cooperation between science and management authorities is thus far mostly lacking and driven by conflicting goals; but regardless of the intention, an axiom everybody should aim for is the implementation of ecological, social-culture and economic objectives that are beneficial to the system as a whole.

Since abrupt changes are quite uncertain and highly complex, identifying the key attributes and objectives remains challenging. Nevertheless, various studies (e.g. Link 2005; Kershner et al., 2011; James et al., 2013; Riche & Rochet 2005; Shin & Shannon 2010) have ventured to quantify indicators that could serve as possible early warning units for approaching regime shifts. Identified variables include general factors that relate to resilience and variability (e.g. Scheffer et al., 2009; Dakos et al., 2010) as well as spatial and dynamic attributes of an ecosystem (Carpenter & Brock, 2006; Carpenter et al., 2008; Carpenter et al., 2011; Dakos et al., 2012).

The increasing importance of incorporating ecosystem principles in ocean and coastal resource management is inevitable. Several reports of commissions (e.g. U.S. Oceans Commission on Ocean Policy (2004), Pew Oceans Commission (2003), and Ocean Action Plan (2004)) and other organizations call attention to the rising concern regarding the health and state of marine and other aquatic ecosystems. Therefore, ecosystem approaches to management (EAM) frameworks are established and developed to guide the management decision making process. The EAM framework is highly dependent on scientific- based integrated ecosystem assessments (IEAs) which support the realisation of the EAM action plan by providing formal synthesis and quantitative analysis of biological, physical or socioeconomic data that are relevant to accomplish the set goals for a specific ecosystem. The approaches implemented in an IEA are chosen to determine if the biological or socioeconomic components of a system will stay or if they have the ability to return to a favourable state as defined by the management goals. The synthesis not only includes the scientific world, but is strongly supported by a variety of stakeholders, such as the industry, policy makers, resource managers and citizens in order to attain the goals of the EAM. To meet the requirements of a successful management action, and in order to define clear, well-understood ecosystem targets built on scientific research, the IEA must be evaluated carefully. Special attention must be laid on the scale over which ecosystem dynamics and management issues occur. Space and time are extremely important when it comes to potential threats of an ecosystem since those habitats are not defined by exact borders but rather blend into each other, especially in the Baltic Sea. Borders itself are a human construct and so it is up to us to define the ecosystems boundaries by looking into ecological, geological and oceanographical ranges, as well as the scales and scopes of management actions and government structures. There are at least five steps that should be followed and must be critically considered before the decision-making process that are described by Levin et al. 2010.

1.8 Indicators

In order to sustainably and successfully manage an ecosystem with all its components, useful indicators need to be assembled. Depending on management goals, the set of indicators must cover all basic principles of the ecosystems' structure and function regarding "ecosystem health". Useful measures for supporting the ideal goal are diversity, resilience, primary and/or secondary productivity, energy recycling and mean trophic level (Samhouri et al., 2009). Rice and Rochet (2005) provided a framework of attributes that indicators need in order to be useful markers for ecosystem-based management. Hence, indicators must be directly observable and cost effective to measure, based on well-defined theory and are ideally supported by historical time series, as well as sensitive and responsive to changes in ecosystem state and specific to properties theory that they are intended to measure. Considering these guidelines, useful indicators for a holistic management approach of the Baltic are needed. In the following, the steps that need to be taken to accomplish a set of indicators and thresholds for the central Baltic Sea region will be explained.

Many indicators seem useful for a lot of reasons, but the difficulties lie in the definition of a limited number of key indicators with which we can detect changes within the ecosystem and its many interactions. With a well-defined catalogue of candidate indicators, scientists and managers can gain valuable information for the evaluation of future scenarios and relevant management and policy decisions.

Defining a suitable set of indicators for the goal that is to be achieved, general principles should be considered in that indicator identification process: besides being coherent with the management objectives, an indicator should be easily understood and measured, justifiable regarding acceptance and verifiability, as well as cost effective (Degnbol & Jarre, 2004; Rice & Rochet, 2005). A framework drafted by the Organisation for Economic Cooperation and Development (OECD, 1993) and refined by the European Environment Agency (EEA, 1999) highlights the need of indicators related to **D**riving forces (economic sectors, human activities), **P**ressures (pollution, emissions), **S**tates (biological, chemical, physical), **I**mpacts (on ecosystems' and human's health) and (political) **R**esponses (DPSIR) of the system of interest. Identifying such indicators is a crucial process in assuring their utility to and acceptance by managers, stakeholders and scientists. Environmental indicators can be of biotic, abiotic or socio-economic nature and are diverging depending on the dynamics and attributes of the system. The challenge lies in identifying a useful set of indicators that help implement the determined management objectives and goals.

In EB(F)M the desire to develop indicators that can be used to understand the complexity and dynamics of a system and therefore help measure the progress of management actions and needs is still rising. Many different types and sets of indicators already exist that are widely used in management contexts and are termed by Degnbol & Jarre (2004). 'Descriptive' or 'contextual' indicators mostly refer to abiotic conditions such as climatic and physical attributes that are not alterable by humans in contrast to 'control' indicators which compile information on conditions that are controllable by humans within the management cycle. 'Performance' indicators can act as a tool to compare the current state of management actions and the desired goal. Other indicators, such as 'efficiency' or 'total welfare' indicators are useful if economic, social or sustainability questions are processed (Perry et al., 2010). If key aspects of an (eco)system are not well understood or (anthropogenic) pressures are more assumed than studied, 'surveillance' indicators are used to monitor and track the dynamics of the system at hand and give further information supporting the goal-fulfilling process (Shephard et al., 2015). Ecological indicators (e.g. size distributions, aggregate community, energy flows) have been proposed as a tool to classify ecosystem state and functions (Large et al., 2013) in order to understand pressure-response relationships within a system (Link et al. 2010, Blanchard et al., 2010).

Depending on the (management) goal that is to be achieved using a recruitment relationship, different methods have been and can be applied to estimate recruitment variability (as shown in e.g. Needle, 2002) using a set of (environmental) indicators. In any case, data must be handled with care since estimates of recruitment are generally difficult to obtain as the success of offspring is highly linked to climatic forces and multiple biotic pressures, and data is mostly autocorrelated with spawning stock biomass data, from which the recruitment estimates are usually derived. Working with muddled data such as this, stock-recruitment relationships can easily be falsified which makes predictions of possible stock status difficult. Nevertheless, due to the aforementioned problems working with stock-recruitment relationships, it is even more important to find multiple methods of defining indicators that can be used to measure the impacts and pressures on recruitment variability. Recruitment indicators can be anything that influences the success of a population to reproduce, such as temperature, salinity, oxygen levels of ambient water, climatic events such as storms, inflows and oscillations (abiotic) as well as predation pressure, prey availability, parental fitness and egg quality (biotic) and can be defined in a single-pressure approach as shown in this study, or as a merged recruitment indicator that combines all factors influencing cod recruitment (age structures in EB cod, *Pseudocalanus acuspes* biomass, spawning stock of sprat, cod reproductive volume, depth of 11 psu isohaline in Gotland Basin) using a fuzzy logic model approach as an example of how indicators can support model-based stock estimates, and to demonstrate how deterministic approaches commonly used for assessment of fish stocks can lead to false assumptions regarding mechanisms that drive recruitment success if results are based on noisy data (Gårdmark et al., 2011).

Whether estimated indicators are useful or not is contingent on factors such as data structure, length of time-series used (Needle, 2002), knowledge and understanding of biological and physiological factors affecting investigated species, as well as aim for indicator application etc. Conclusions or mechanisms drawn from output of applied indicator approach must be dealt with very cautiously, since results oftentimes stem from recruitment correlations that are based on impure data from the start, as mentioned above. Therefore, mechanisms assumed from correlations can include errors of great magnitude and need to be evaluated using expert knowledge and biological understanding of the correlation and the species of interest.

1.9 Thresholds

After the development of indicators, individual thresholds can be defined for each one of them. An ecological threshold is defined as a point where small changes in the system can have large changes in the ecosystems' dynamic or state. Therefore, it is essential to have the knowledge about the function of the system of concern (Samhouri et al., 2010). In this step, the indicator magnitude is evaluated in order to answer questions such as "how much is enough" or "how little is too little" for the ecosystem to take on its way to a "healthy" and/or desired state. The thresholds are often simulated and set using models like EwE (Ecopath with Ecosim) or Atlantis but since there are multiple criteria working together simultaneously, these models must be coupled and expanded with the help of other models to achieve a holistic picture of the ecosystem dynamics. Depending on the data situation and the management goals, thresholds can be defined in various ways such as analysis of ecosystem trends in data poor situations or quantitative estimates using only a small portion of the system. Single-species models can also guide and highlight trends towards a set of thresholds (Tallis et al., 2010). Along with the environmental thresholds, there are so-called 'utility thresholds' which are defined as "a point at which small changes in environmental conditions produce substantial improvements in the management outcome" (Martin et al., 2009). Samhouri and his colleagues (2010) give a detailed description of how to define and set utility thresholds mathematically.

In the present study, we used the recruitment residuals (RecRes) in Chapters II and III obtained from the recruitment – spawning stock biomass (SSB) relationship as response variables representing recruitment unaffected by parental influence. This approach represents a simple method for the detection of trends over time and can be applied when adequate data is available in any context with any species. RecRes were then used to identify key indicators by running simple linear (L) and polynominal (P) models. If environmental pressures showed significant correlations with RecRes, indicator specific thresholds were obtained. As the mean of the RecRes is per definition 0, the intercept of the identified indicator with the RecRes mean is the defined threshold that divides the "good" side from the "bad" side. Both, linear (L) and polynominal (P) models appeared to be a suitable tool for deriving indicator per species. The threshold derivation process is described in Diagram 1.

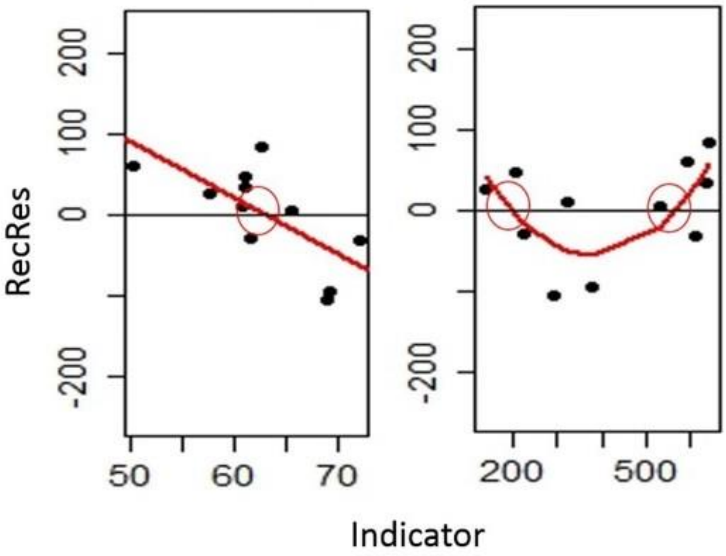

Figure 5: Possible Thresholds derived as intercept of RecRes and respective environmental indicator. Left: linear model (L), right: polynominal model (P). Circles show possibilities in threshold value within the approach.

In Chapter VI, recruitment indicators and thresholds were derived in the laboratory and defined as the early life history traits (indicators) that made life possible for the longest time (threshold). Here, twelve different males were used for crossing experiments to analyse the parental contributions to early life survival of Atlantic cod. This chapter serves as a strong support for recruitment mechanisms discussed in Chapters II and III of present study, as results are derived from an extensive experimental and naturalistic set up.

1.10 Aim of the Study

The present study focuses on the first two steps of a management plan as suggested by Levin et al. (2010): the scoping of goals and the identification of suitable indicators. The following three chapters deal with the search for suitable recruitment indicators of cod (*Gadus morhua L.*), herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*). For the Baltic ecosystem, environmental recruitment indicators were found that stand in close connection with the recruitment success of the three species. For cod in an Atlantic aquaculture system, intrinsic recruitment indicators such as egg quality and parental condition were analyzed and discussed as important factors influencing recruitment success.

The aim of the study was to identify a set of useful indicators by implementing simple mathematical models (linear regression) that are easily understood and recreated. The assumption, that complicated relationships can be straightforward and do not require high-end modelling, is tested by fitting time-series and developing a set of indicators and respective thresholds per species for possible forecast scenarios, and discussed in the following. From the selected (Baltic Sea) indicators, thresholds could be derived that determine ‘favorable’ and ‘unfavorable’ recruitment success of the species. The question, if the RecRes can be used as a suitable response variable for recruitment success, was discussed and evaluated.

The outcome of the study can be used to understand underlying factors that play an important role in recruitment success in the different species and areas and points out the importance of recruitment indicators to be recognized in assessment models for management purposes. With this simple method, (recruitment) indicators can be easily identified in other species, areas and contexts.

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CHAPTER II

Anticipating “good” or “bad” prospects for offspring of commercially important fish populations – objectively identifying indicators and thresholds for Eastern Baltic cod recruitment environment

Anticipating “good” or “bad” prospects for offspring of commercially important fish populations – objectively identifying indicators and thresholds for Eastern Baltic cod recruitment environment

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ABSTRACT

Supplementing fish stock assessment with environmental indicators is the core of ecosystem-based fisheries management. Indicator based approaches are important for fish populations that are strongly affected by climate-induced changes in the environment, such as Baltic cod (*Gadus morhua callarias L.*). Besides the effects of over-fishing, reproductive success is a crucial phase in cod population dynamics; hence, indicators that reliably contribute to predict recruitment are candidates for integrated advice. Our study focuses on the identification of potential environmental indicators for cod recruitment success, including the setting of thresholds discriminating between good and bad environmental conditions for recruitment. The present study shows that (i) only abiotic indicators explain variation in recruitment success of Eastern Baltic (EB) cod after accounting for the effect of spawning stock size, and that for this case study (ii) spatially explicit indicators and thresholds must be considered. Here we show that depending on stock and environmental conditions, thresholds are inevitable and essential tools in supporting assessment-model based stock advice for predicting recruitment success and providing first steps towards ecosystem-based fisheries management.

Keywords: Environmental indicators, threshold, Baltic cod, management advice, recruitment success, Ecosystem Approach to Fisheries (EAF)

2.1 INTRODUCTION

Today’s environment is influenced by anthropogenic use more than ever before and calls for sustainable resource management actions that maintain the ecosystems´ productivity for the future, especially in the fisheries sector, as seafood currently accounts for up to 17 % of the global protein sources (Porritt & McCarthy, 2016). An Ecosystem Approach to Fisheries (EAF) was defined by the FAO in 2003 in order to develop a sustainable fisheries management that considers the miscellaneous impacts that an ecosystem has to bear. EAF is now established as a paradigm for the sustainable living resource management applying a holistic approach that considers the whole ecosystem as well as socio-ecological linkages (Kempf, 2010).

An essential step in an EAF is the identification and selection of indicators that represent key characteristics (e.g. drivers, pressures, responses) of a system in order to monitor, preserve and manage an ecosystem (Slocombe, 1998, Rice & Rochet, 2005, Levin et al., 2009). A framework drafted by the OECD (1993) and refined by the EEA (2003) enables a comprehensive causal analytical representation of relevant processes relating to biodiversity. The framework highlights the need for indicators related to Driving forces (economic sectors, human activities), Pressures (pollution, emissions), States (biological, chemical, physical), Impacts (on ecosystems’ and human’s health) and (political) Responses (DPSIR) of the system of interest. Identifying such indicators is a crucial process to assure their utility to and acceptance by managers, stakeholders and scientists. Environmental indicators diverge depending on the dynamics and attributes of the system and can be of biotic, abiotic or socio-economic nature. Applicable indicators have the qualities of being easy to measure, understand and communicate, are comprehensive in their data structure and are sensitive to anthropogenic forces (Greenstreet et al., 2011; Rice & Rochet, 2005). Hence, the challenge lies in objectively identifying the right set of indicators depending on the management objectives and goals set.

For selected indicators, thresholds or limits are needed that allow for an evaluation if the ecosystem attribute, represented by the indicator, is in a favourable or unfavourable state (Samhouri et al., 2010). Historically, thresholds have been set and used in many anthropogenic contexts, for example in poverty evaluation. A poverty threshold (PTH) was defined by Charles Booth in London (UK) in the 20th century and developed by Mollie Orshansky in 1963/64 (US) (Fisher, 1992; Gillie, 1996) as the mean of the annual costs for essential resources such as shelter, food, health care and clothing per person. In most countries, rent is the most dominant expense, which means that the PTH is mostly driven by the real estate market and housing prices and therefore varies depending on economic situations per country (Ravallion, 1992). These essential resources can be seen as indicators for the quality of life being “good” above the threshold and “poor” below the threshold.

In fisheries, recruitment defines the strength of a year-class and is the most important process in the dynamics of fish populations and crucially dependent on the physical and biological environment encountered by their early-life history stages (Houde, 1987, Westin & Nissling, 1991; Wieland et al., 1994; Hutchings, 2000; Hutchings & Reynolds, 2004). We use the Eastern Baltic (EB) cod (*Gadus morhua callarias L.*) for our analysis because estimates of recruitment are generally difficult to obtain and therefore lead to false stock-recruitment relationships that make predictions of a possible stock status difficult. However, reliable predictions are desperately needed, hence environmental indicators are required to countenance the estimates from the current stock assessments. The environmental indicators identified in this study give insight into how abiotic characteristics can be used to underpin the recruitment dynamics for EB cod and can be used as thresholds that serve as a guide for more precise predictions of recruitment success. Especially for species with precarious stock sizes and recruitment success, thresholds based on environmental indicators are an essential tool for the stock assessment and applied management actions.

Eastern Baltic (EB) cod is commercially the most important fish stock in the Baltic Sea, and of considerable importance as the dominant top-predator in the food web (Casini et al., 2008; Möllmann et al., 2008). Not only its position in the ecosystem, also its history and development leveraged EB cod to an exciting study object: through over-fishing and climate driven hydrographic changes, the population collapsed at the beginning of the 1990s (Köster et al., 2005; Eero et al., 2012; Köster et al., 2016). After signs of recovery at the beginning of the new millennium, the state of the stock is now unclear due to failing analytical assessments caused by data uncertainty and unanticipated growth problems (Eero et al., 2012, Casini et al., 2016).

Recruitment processes of EB cod have been extensively investigated (Köster et al., 2003; Köster et al., 2005; Köster et al., 2016) and a number of potential recruitment indicators such as weight-at-age, sprat spawner biomass and reproductive volume (see below) have been proposed by Gårdmark et al. (2011) and Eero et al. (2012). In addition to defining a suitable set of recruitment indicators for EB cod, the present study estimates respective thresholds for each indicator (Tab. 1), presenting a clear changepoint for cod recruitment success. Thresholds can be measured relatively quickly with simple regression methods, keeping possible sources of error low. Another novel aspect of this study is the evaluation of the response variable (RecRes) as i) a suitable measure of recruitment correlation with the environment, and ii), as suitable response variables for recruitment predictions (Tab. 2).

In general, cod recruitment success is believed to be largely dependent on hydrographic conditions, especially combinations of high salinity and oxygen conditions that are necessary for egg survival (Wieland et al., 1994; Nissling & Vallin, 1996; Nissling & Westin, 1997). Particularly in the eastern Baltic, the cod population face harsh abiotic conditions for egg and larval survival as the ideal water masses for successful cod spawning defined as the 'reproductive volume' by Plikishs et al. (1993), in which the salinity measures more than 11 psu and the oxygen content exceeds 2 ml / l depend on the depth of the halocline layer. Since the upper layer of the Baltic is characterized by low salinity, water layers suitable for egg development are found deeper with the tendency to sink down where the danger of anoxic conditions is high until an inflow event from the North Sea brings fresh oxygenated waters into the Baltic (HELCOM, 1996; MacKenzie et al., 2000). A further source of Baltic cod egg mortality is predation by clupeid, planktivorous fish, mainly sprat (*Sprattus sprattus L.*) and herring (*Clupea harengus L.*) (Köster & Möllmann, 2000; Neumann et al., 2014). Biotic factors mostly affect larval survival, i.e. availability of zooplankton prey, such as the calanoid copepod *Pseudocalanus acuspes* (Hinrichsen et al., 2002, Köster et al., 2005, Möllmann et al., 2008).

This The present study presents a new approach to deriving recruitment indicators and focuses not only on the identification of environmental indicators and respective thresholds useful for anticipating recruitment success potentially useful for assessment and management of EB cod, but also evaluates if the used response variable (RecRes) can serve as a suitable proxy for recruitment relationships. Our results show the importance of physical oceanographic variables for evaluating the quality of the recruitment environment of this important fish population. Furthermore, we present a routine for selecting indicators of recruitment environment using modern regression techniques, an approach that can be easily transferred to other fish species and areas as a prompt assessment for recruitment success to help overcome uncertainties associated with recruitment predictions and therefore push management in fisheries to a new level.

2.2 MATERIALS & METHODS

2.2.1 State variable

The first step in our analysis was the computation of a stock – recruitment model of which the residuals serve as a state variable for identifying indicators for the quality of the EB cod recruitment environment. Stock size, represented by spawning stock biomass (SSB), and recruitment (numbers at age 2) values were derived from stock assessments of EB cod (Subdivisions 25, 26 & 28) conducted by the International Council for the Exploitation of the Sea (ICES, 2013) (see map, Fig. 1, Chapter I).

Then we identified the suitability of our candidate indicators by evaluating their relationship to recruitment success, represented as the residual variation around the relationship between spawning stock (i.e. parent) biomass (SSB) and recruitment (R), the so-called stock-recruitment (SSB – R) relationship. This procedure accounts for the effect of the parental stock on recruitment and assumes that the residual variation is due to biotic and abiotic influences on early life-stage survival (Pauly, 1984). The response variables obtained From the SSB – R relationship, the recruitment residuals, are referred to as RecRes from hereafter.

In order to gain robust RecRes, we selected a general least square (GLS) model with no autocorrelation or heterogeneity structure in the process of deriving the RecRes of the respective time periods using the packages {nlme} in R (Pinheiro et al., 2013). This approach is known to be a simple but less error-prone statistical method.

2.2.2 Environmental Indicators

We used an initial set of 28 biotic and abiotic variables (Appendix, Table A1) in Step 2 of our analysis as candidate indicators to be tested in pressure – state relationships with RecRes.

Here, we modelled RecRes as a function of each of the 28 candidate indicators by fitting linear (i) or polynomial (ii) models. In order to account for possible autocorrelation within the data, we tested for peculiar variance structures using the (corAR(1)) as well as the auto.arima command in the forecast package in R. Also, an auto-regressive moving average ((corARMA(p,q) in the R package{nlme}) correction was applied:

i) $$y = b \cdot x + a$$

ii) $$y = b + a \cdot x + c \cdot x^2$$

with a being the intercept, b the slope, c being the degree of the curve and x being the observed value of the individual indicator suited to the accordant value of y.

Variables that showed a significant relationship with RecRes based on the p-value and biological plausibility were considered to be useful indicators and used in the next step which quantifies thresholds for the selected indicators with respect to good and bad recruitment.

In step 3, thresholds per indicator were assessed in a single approach depending on a linear (iii) or polynomial (vi) relationship as follows:

iii) $$x = \frac{(y - a)}{b}$$

vi) $$x = \frac{-b}{(2 \cdot c)} \pm \sqrt{\left(\frac{b^2}{(2 \cdot c)}\right)^2 - \frac{(a - y)}{c}}$$

where a represents the intercept of model outcome shown above, b is the slope of model, c shows the degree of the curve and y is the RecRes mean which is per definition 0.

The state or quality of the recruitment environment of EB cod is then indicated by the deviation of the observed indicator from its threshold value. Hence, positive deviations from the threshold indicate “good” and negative deviations indicate “bad” recruitment environment for EB cod.

In order to test for the robustness of the analysis applied, we incorporated a 5-fold cross-validation within the step of finding suitable thresholds per indicator, as well as its standard deviation and mean square error (MSE) (for more detailed description of method see James et al., 2013). Cross-validation was conducted on the long time period only.

2.2.3 Time periods and Training dataset

A common phenomenon in ecological systems is non-stationarity in the existence or strength of relationships, which is especially true for SSB – R relationships. Relationships may especially depend on an ecosystem state that is known to have changed between distinct regimes in the Baltic Sea (Möllmann et al., 2009). We accounted for this by conducting our analysis over different time periods (Fig. 3, Table 1): i) a standard period (S) 1975 – 2003 representing the period of best data availability and covering boom and bust periods of EB cod, ii) a time period (R1) before 1975 – 1986 and iii) after 1987 – 2003 (R2) the regime shift in the mid-eighties, and finally (iv) a long period (L) 1965 -2003 representing the full EB cod stock assessment period.

Studies of Eero et al. (2015) and Gårdmark et al. (2011) point out the particular development of the stock dynamics and allude to the fact that the estimation for the SSB – R relationship shows divergent trends starting in the year 2006. Having this valuable information in mind, we ran our analysis only until the year 2003 as a training dataset and evaluated our results with the remaining years until 2006 because up to that point the assessment seemed robust.

We then predicted the SSB – R relationship for the remaining years (until 2009) and compared them to existing results in the last step of our analysis to obtain a possible future outlook.

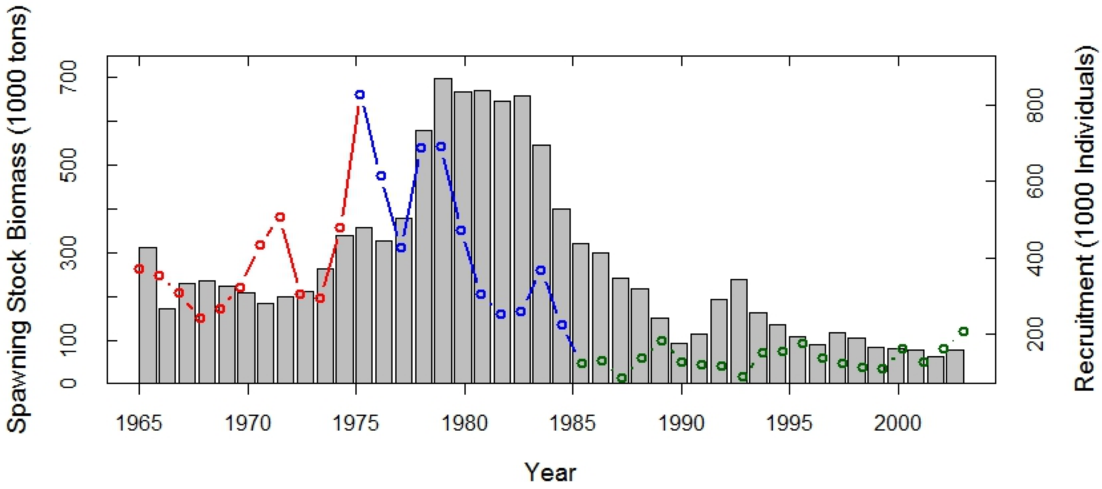


Figure 1: Spawning stock biomass (grey bars) on y-axis and Recruitment (dotted line) on secondary axis of BE cod (*Gadus morhua L.*). Different colours indicate different time periods used in the analysis. Red until end: Long period L (1965 - 2003), blue until end: Standard period S (1975 – 2003), blue: regime shift period R1 (1975 – 1986), and green: regime shift period R2 (1987 – 2003).

2.2.4 Evaluation

In our prediction trial in step 5, we used the RecRes for the years 1965 – 2009 and derived thresholds from individual indicators that showed a significant relationship with the response variables (Tab. 1). With the derived threshold value based on respective time length, predictions of potential recruitment environments were calculated by subtracting the threshold from continuing data until present (2003 - 2009). Results were then compared annually to RecRes to assess if our response variable can serve as a suitable measure for the estimation of recruitment success. The possible validity [%] of recruitment environment per year was calculated by ranking each indicator based on their performance in the analysis (low standard deviation, biological relevance based on expert knowledge). Therefore, as the depth of 11 psu isohaline showed the best and most accurate fit in the analysis, we ranked it as the most important indicator with 60 %. Further, the reproductive volume in the central Baltic was ranked as the second-best indicator for cod recruitment success and got 30 % validity. As the reproductive volume in the Gotland Basin only revealed clear results in some time periods tested and showed a relatively high standard deviation within the threshold derivation process, we ranked it with 10 % expressiveness. As trends of some years could not be clearly identified where the value was in the range of SD, only 0.5 % of full rank was given (Table 2).

2.3 RESULTS

2.3.1 State variable

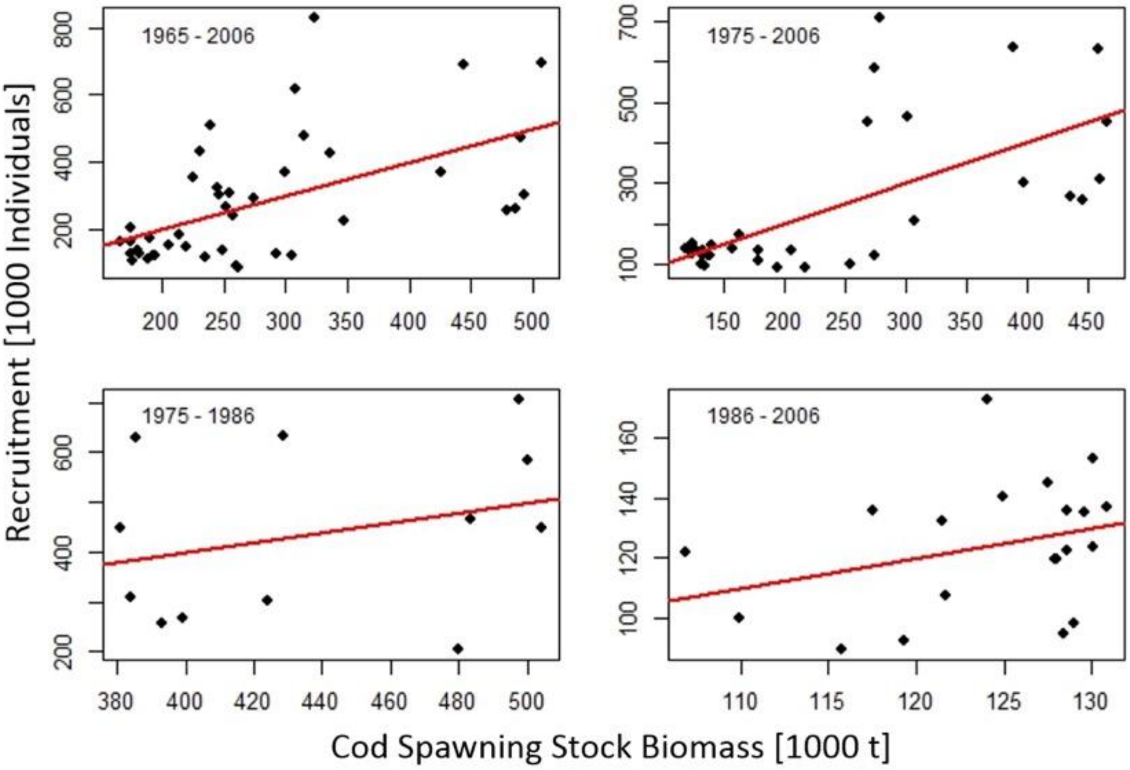


Figure 2: GLS models of SSB- Recruitment relationship of BE cod (Gadus morhua L.) for all time periods tested.

All RecRes of the respective time periods selected by applying GLS models are shown in Figure 3.

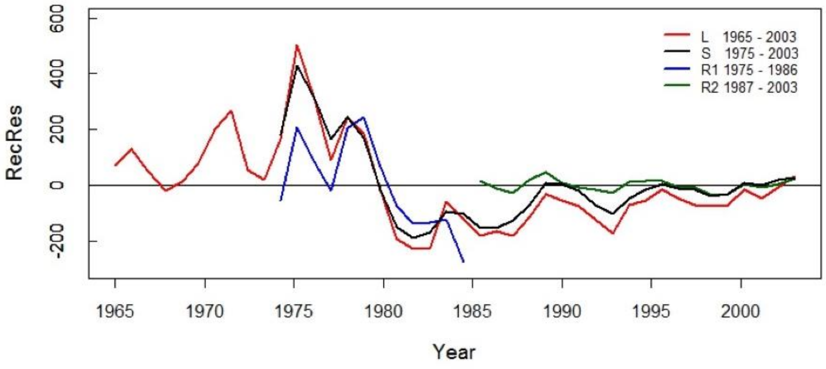


Figure 3: Recruitment residuals (RecRes) of the different time periods used for the indicator selection.

2.3.2 Environmental Indicators

The results of our indicator selection routine show that only abiotic variables showed significant relationships with the recruitment residuals (RecRes) in every time period tested (Table 1, Appendix Table A1). None of the indicators turned out to be suitable when only considering the R2 (1987-2003) time period. The cross-validation process revealed indicator thresholds of similar value to what was found in previous analysis. The respective standard deviations (SD) fitted the range of the derived thresholds and the MSE of the training set was lower than the one of the test datasets (Tab. 1.).

Table 1: Results of the threshold derivation of the identified indicators per time period (L= long (1965-2003), S= Standard (1975 – 2003) and R1 (1975 – 1986), respectively. Model types are L (linear) or (P) polynomial. Thresholds are shown in the unit of the corresponding indicator. Mean threshold values from the 5-fold cross-validation (CV) process are shown as well as ± standard deviation and the MSE values for the training (MSECV) and test (MSEtest) data set

Indicator	**Period**	**Model type**	**p – value**	**Explained variance [%]**	**Threshold value**	**Mean Threshold value $_{CV}$**	**Standard Deviation $_{CV}$**	**Mean Square Error**	
								CV	**Test**
Depth [m] 11psu $_{GB}$	L	P	< 0.001	48	110	**110**	**1.27**	**12593.7**	**18627.5**
	S	P	< 0.001	63	115				
	R1	L	0.002	66	109				
RV $_{total}$ [km^3]	L	P	0.04	46	289	**291**	**19.5**	**14541.3**	**1425180**
	S	P	0.02	51	272				
	R1	L	0.05	32	225				
RV $_{GB}$ [km^3]	L	P	< 0.001	38	68	**91**	**43.02**	**12593.7**	**14880.7**
	S	L	< 0.001	42	44				

2.3.2.1 Indicators

Depth of the 11 psu isohaline in the Gotland Basin was the most obvious indicator to have a significant relationship with the RecRes of all tested periods as it explained 48 – 66 % of the variance in BE cod recruitment success.

The reproductive volume of the combined central Baltic Basins also showed coherence results in all tested periods, explaining 32 – 51 % of variance. Reproductive volume of the Gotland Basin showed significant results in the long and standard time period (explained variance 68 and 44 % respectively), revealing a spatially important area for EB cod recruitment success.

2.3.2.2 Model selection

Both, linear (L) and polynominal (P) models appeared to be a suitable tool for deriving possible thresholds per indicator at hand, depending on the data structure of the respective indicator. Models were selected by the better p-value (Tab. 1).

2.3.2.3 Thresholds

Calculated thresholds were similar for the same indicators despite differences in time length of used data: thresholds for the depth of 11 psu isohaline gave values between 109 (R1) and 115 (S). The mean threshold CV matched the findings as it was 110 ± 1.27. The threshold of the combined reproductive volume (RVtotal) ranged from 225 (R1) to 289 (L) km3 (CV = 291 ± 14.5), and RV Gotland Basin thresholds showed values of 68 (L) and 44 (S) km^3 and explained 38 and 42 % of recruitment success. This indicator was the only one with a relatively high standard deviation and a CV threshold outside the range of the previous step, showing values of 91 ± 43.02 (Tab.1).

2.3.2.4 Time periods and Training dataset

Conducting the analysis over different time periods revealed, that in most cases the same indicators showed a significant relationship with cod recruitment success independent of time period. Therefore, the applied method was considered as a robust approach of identifying reliable environmental indicators and their respective thresholds of the tested time periods. Especially the 5-fold cross-validation of the longest data series proved that the applied method seems suitable for EB cod in the training as well as in the full data set.

2.3.2.5 Evaluation of trends in recruitment environment

Based on the selected indicators and their respective thresholds, we were able to describe changes in the EB cod recruitment environment (Fig. 4 a-c). All indicators showed that the physical oceanographic conditions of the cod recruitment environment started to become detrimental ("bad conditions") at the beginning of the 1980s, irrespective of the length of the period used. Only single years revealed positive deviations ("good conditions") from the threshold, i.e. in the Gotland Basin. Conducting the analysis for the depth of the 11 psu isohaline, a similar pattern became evident: a 20-year detrimental phase (~ 1982 - ~ 2002) for all time periods tested. Figure 5 displays the three indicators found to be most important for EB cod recruitment and their respective threshold ± SD derived from the cross-validation.

2.3.2.6 Evaluation

The last step of our analysis addressed evaluating the use of RecRes based on individual selected indicators. We compared the RecRes from the long time period (1965 – 2009) to the results of the respective indicators to find evidence, that the residuals are a good measure for the applied method. We found that in the depth of 11 psu isohaline only six years diverged in the results (meaning that a positive (green) year in the indicator showed a negative value of RecRes) in the 44 years tested. With this primary result we, once again, recognize this indicator as the most important environmental force for EB cod recruitment success. The two indicators related to the reproductive volume showed nine divergent years, with some years being on the fence as they were in the limits of the respective SD (orange colored in Table 2) and could not be assigned absolutely.

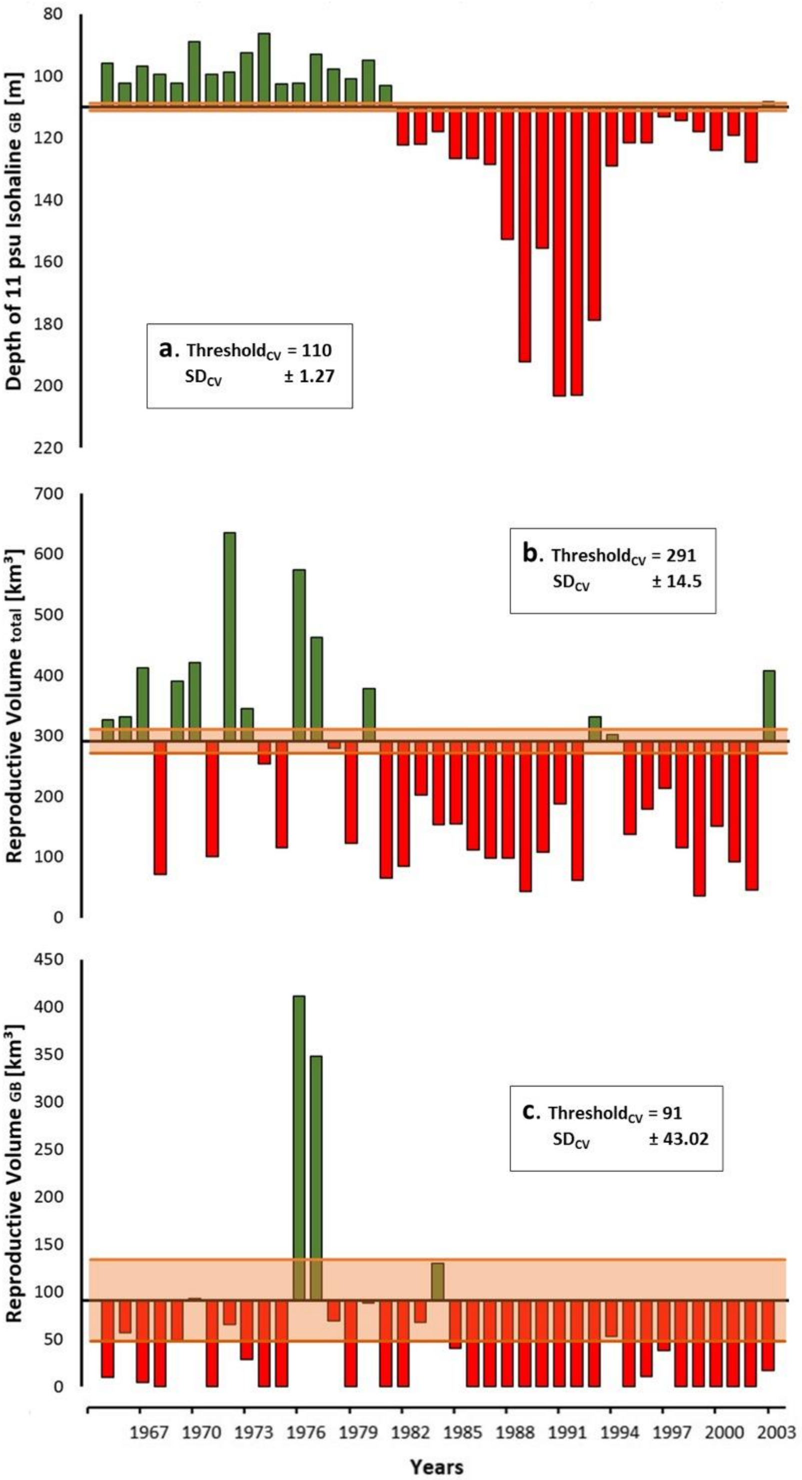
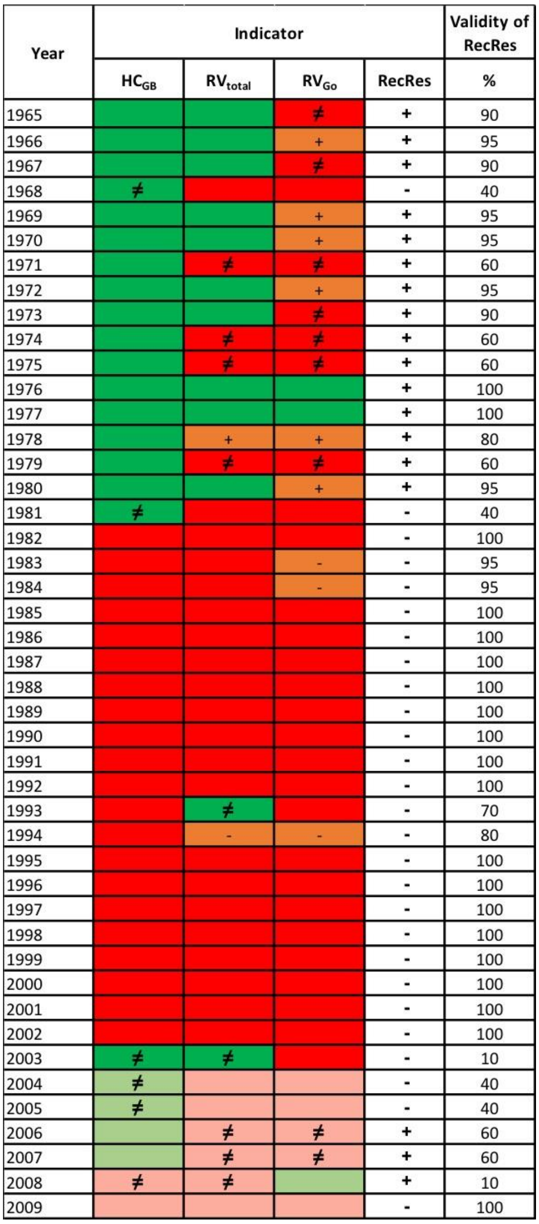


Figure 4: Potential ‚good‘ and ‚bad‘ recruitment environments based on thresholds ± SD derived from 5-fold cross-validation analysis over time per indicator of the long time period, respectively. Red= ‘bad’ = below threshold, green= ‘good’ = above threshold, orange = ± Standard Deviation of respective threshold of the three environmental indicators (a. Depth at 11 psu [m], b. reproductive volume total and c. reproductive volume in the Gotland Basin [km^3]) identified as relevant to BE cod recruitment success. Respective threshold value and ± SD are shown in boxes.

Table 2: Color code of potential ‚good‘ and ‚bad‘ recruitment environments based on thresholds of depth of 11 psu halocline (HCGB), reproductive volume total (RVtotal) and reproductive volume Gotland Basin (RVGB) derived from cross-validation analysis in the years 1965 to 2009, respectively. Red= ‘bad’ = below threshold, green= ‘good’ = above threshold, orange = ± Standard Deviation (SD) of respective threshold. Unequal symbols indicate contrary RecRes values of the particular year when compared with the respective threshold value. Light red and green boxes (2003- 2009) show potential recruitment environment after comparing results of test dataset to the observations until 2009. Percentages display possible validity of result with respect to recruitment success. Ranking of indicators: HCGB = 60 %, RVtotal = 30 %, RVGB = 10 %. If threshold value was found to be in the range of the SD, 0.5 % of original ranking was given.



Year	Indicator				Validity of RecRes
	HC_{GB}	RV_{total}	RV_{Go}	RecRes	%
1965	🟩	🟩	🟥 ≠	+	90
1966	🟩	🟩	🟧 +	+	95
1967	🟩	🟩	🟥 ≠	+	90
1968	🟩 ≠	🟥	🟥	-	40
1969	🟩	🟩	🟧 +	+	95
1970	🟩	🟩	🟧 +	+	95
1971	🟩	🟥 ≠	🟥 ≠	+	60
1972	🟩	🟩	🟧 +	+	95
1973	🟩	🟩	🟥 ≠	+	90
1974	🟩	🟥 ≠	🟥 ≠	+	60
1975	🟩	🟥 ≠	🟥 ≠	+	60
1976	🟩	🟩	🟩	+	100
1977	🟩	🟩	🟩	+	100
1978	🟩	🟧 +	🟧 +	+	80
1979	🟩	🟥 ≠	🟥 ≠	+	60
1980	🟩	🟩	🟧 +	+	95
1981	🟩 ≠	🟥	🟥	-	40
1982	🟥	🟥	🟥	-	100
1983	🟥	🟥	🟧 -	-	95
1984	🟥	🟥	🟧 -	-	95
1985	🟥	🟥	🟥	-	100
1986	🟥	🟥	🟥	-	100
1987	🟥	🟥	🟥	-	100
1988	🟥	🟥	🟥	-	100
1989	🟥	🟥	🟥	-	100
1990	🟥	🟥	🟥	-	100
1991	🟥	🟥	🟥	-	100
1992	🟥	🟥	🟥	-	100
1993	🟥	🟩 ≠	🟥	-	70
1994	🟥	🟧 -	🟧 -	-	80
1995	🟥	🟥	🟥	-	100
1996	🟥	🟥	🟥	-	100
1997	🟥	🟥	🟥	-	100
1998	🟥	🟥	🟥	-	100
1999	🟥	🟥	🟥	-	100
2000	🟥	🟥	🟥	-	100
2001	🟥	🟥	🟥	-	100
2002	🟥	🟥	🟥	-	100
2003	🟩 ≠	🟩 ≠	🟥	-	10
2004	🟢 ≠	🔴	🔴	-	40
2005	🟢 ≠	🔴	🔴	-	40
2006	🟢	🔴 ≠	🔴 ≠	+	60
2007	🟢	🔴 ≠	🔴 ≠	+	60
2008	🔴 ≠	🔴 ≠	🟢	+	10
2009	🔴	🔴	🔴	-	100

2.4 DISCUSSION

Understanding recruitment dynamics and mechanisms that drive variability in recruitment is crucial for any management context. Even though a variety of approaches exist that derive environmental indicators to support ecosystem-based fisheries management for well-studied and poorly studied systems (see e.g. Cury & Christensen, 2005; Trenkel et al., 2007; Petitgas et al., 2009), the challenge of predicting recruitment variability is still ongoing. To this day, stock assessments models are often not run holistically, as environmental variables affecting recruitment and stock size in perpetuating systems are not considered adequately (Gårdmark et al., 2011; Möllmann et al., 2009) and hence lead to false reference points (ICES, 2008; Collie & Gislason, 2001) that are based on stock size.

Gårdmark et al. stated in their study in 2011 that depending on the model used (deterministic vs stochastic models), different results lead to varying assumptions due to uncertainties in the input data. Their results strongly suggest additional information, i.e., environmental indicators explaining the dynamics of recruitment variability, as stock assessment based solely on single approaches do not mirror a realistic stock size (i.e., years of high stock size are often overestimated). Also, the neglection of inherit variability of recruitment from abiotic (physical environmental dynamics) and biotic (competition, predation) factors can hide signals from spawning stock size (Walters & Korman, 1999), resulting in strongly correlated and hence highly dependent SSB – recruitment relationships that make the analysis even more difficult. In order to converge a realistic stock size and hence recruitment success, more information is needed to explain stock dynamics based on (ecological) indicators.

As abiotic factors are easier to measure than biotic pressures, several physical mechanisms influencing (EB) cod recruitment success have been proposed by a number of studies (see below), that are also found to be relevant for recruitment variability in the present study.

The present study defines environmental indicators and sets thresholds as a tool for implementing successful management actions and also found a depth of 11 psu isocline in the Gotland Basin to be the most important indicator for reproduction success for the EB cod stock. Even after testing different data series regarding time length, we always returned to the same conclusion: the salinity layer is the outstanding indicator in our analysis. As expected, recruitment success (RS) increased with increasing reproductive volumes and decreased, the deeper the halocline was observed in all periods tested.

In our example, depth at 11 psu is equivalent to the housing prices in the PTH calculation as it is a fundamental indicator that influences the living conditions significantly and therefore represents a different, not less important issue that we need to think about as it is of great ecological and economic importance for the Baltic ecosystem and community.
Studies (e.g. Plikshs et al., 1999) have shown that this hydrographic variable, which serves as an all-encompassing inflow indicator, can be related to cod's life history and represents one of the most essential abiotic factors influencing the BE cod stock since a relative shallow halocline is needed for the effective development of cod eggs as it provides buoyancy and therefore avoids down-welling towards lethal oxygen conditions in deeper waters (Wieland et al., 1994; Nissling & Westin, 1997; Nissling & Vallin, 1996). The results of the predicted scenario show that, regarding the 11 psu halocline, the EB cod stock underwent a favorable time period between 2003 and 2009. Findings of Eero et al. (2015) also indicate that the cod biomass increased during that time, providing possibilities for the cod stocks to reach sustainable levels again.

Another important abiotic factor influencing BE cod is the reproductive volume of the different basins, which is the water volume that contains at least 11 psu salinity and 2 mL·L-1 oxygen, both of which represent limiting conditions for cod egg survival (Plikshs et al., 1999). For its importance to BE cod recruitment, it seems obvious that the reproductive volume became evident as an indicator in this study. Nevertheless, we have to keep in mind that this indicator is based on a calculation of different abiotic components and therefore can obtain various error sources. A simple measurement such as oxygen or salinity alone might give more precise results in this approach.

By defining the recruitment threshold as the mean of the recruitment residuals, we can calculate the possible impact on cod recruitment success in an easy and understandable way if data is available. Further investigations might show the need for other settings of thresholds, such as quintiles or derivations of the mean. In our approach the mean of the residuals serves as a good proxy for a possible environmental threshold and can be used widely. The overestimation of high years in 1975 – 1985, which result in high residuals, need to be dealt with whenever high values such as these occur, as these high values drive the whole model and therefore dictate the results to a certain degree. We accounted for autocorrelation within the indicator selection process in order to limit the magnitude of this influence. Also, the choice of time frame within the analysis needs to be chosen with care as the regime shift periods R1 and R2 show.

Using RecRes as the response variable for defining environmental indicators seemed to be a relatively good choice depending on the indicator tested. The most prominent indicator (depth of 11 psu isohaline, Gotland Basin) proved to be a very strong driver explaining recruitment variability, as only three years differed in outcome over a time period of 38 years, indicating that correlation between recruitment and depth of saline waters are significant. Also, the second-best indicator, the reproductive volume in the Central Baltic, showed differences in only six years of the time series tested. Both indicators seem robust measures and could be used together in a set of indicators to approximate recruitment success of EB cod. For recruitment predictions, all indicators showed 50 % or better accordance to respective thresholds, and can therefore serve as a guide along with other environmental information or model results to predict trends in recruitment if environmental drivers are changing.

Difficulties lie in the choice and availability of appropriate indicators that represent the ecosystem in hand. Indicators are widely used in management contexts as tools for evaluating the status of marine environments (CEC, 2008; USCOP, 2004) and are sometimes not easy to assess. Rice & Rochet (2005) provided a framework on how to select and derive appropriate indicators, which is a helpful tool but cannot be applied in every study or with every question at hand since sometimes there are only a few variables that can be used as available indicators such as in the present case. An appropriate indicator selection can only take place if applicable and fundamental research has been conducted regarding the history and biology of the studied species. External circumstances like size-selectivity in commercial fisheries or high predator populations (Eero et al., 2015) may also cause misleading assumptions regarding the indicator selection for recruitment success as mechanisms concluded from recruitment correlations, based on error prone data can be fatal (Kraak et al., 2010).

2.4.1 Conclusions

The present study provides a simple approach on how to define favorable and non-favorable recruitment environments for fish stocks by applying a hands-on statistical approach (Diagram 1). Here, we used the BE cod as an example to derive environmental indicators and calculate associated thresholds that can be used to understand stocks' dynamics and assess possible future scenarios for the recruitment success. The study shows how important different environmental indicators become, depending on the regime that is evident in a system at the time: If data is dominated by high variance, abiotic indicators seem to be the driving factors that might overlap the biotic variables. With this method we can push EAF towards desirable goals and help understand the uniqueness of every ecosystem and its inhabitants.

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CHAPTER III

Identifying recruitment indicators and thresholds for Baltic herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*) by using a single-species approach developed for their top predator, Eastern Baltic Cod (*Gadus morhua L.*)

Identifying recruitment indicators and thresholds for Baltic herring (*Clupea harengus L.*) and sprat (*Sprattus sprattus L.*) by using a single-species approach developed for their top predator, Eastern Baltic Cod (*Gadus morhua L.*)

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ABSTRACT

In a single approach to assess the possible status of the recruitment based on an indicator threshold, we used the recruitment residuals (RecRes) of the relationship between spawning stock (i.e. parent) biomass and recruitment as response variable in statistical models to identify indicators that relate to recruitment success of Central Baltic herring and sprat stocks. Thresholds for the indicators can then be defined as the intersection of the selected indicator and RecRes to identify favourable and unfavourable years for the species recruitment. Our analysis revealed the depth of the 11 psu isohaline in the Bornholm Basin to be the most influential indicator for EB herring and sprat recruitment success in all tested periods, as well as prey and predator abundance. The correlations found can serve as primary or secondary mechanisms underlying recruitment dynamics of Baltic clupeids stocks and therefore contribute to a more holistic understanding of species' interactions and influences. Even after implementing different statistical approaches regarding the accuracy of scaling, i.e., looking at separate basins relevant to the fish stocks, as well as different time scales and ages of fish, the results remained similar. Results from the present approach can be used to inform and adjust management actions (i.e., setting of Total Allowable Catches – TACs) accustomed to any target species (Diagram 1).

Keywords: Environmental indicators, Baltic, threshold, herring, sprat, management advice, recruitment success, Ecosystem Approach to Fisheries (EAF)

3.1 INTRODUCTION

Wherever there are (eco)systems used by humans, the demand for regulatory policies becomes obvious as resources should be used sustainably. For the definition and implementation of such policies, mechanisms driving the system need to be well-understood and monitored constantly, as changes in these drivers (indicators) most likely change the whole dynamic of the system and therefore the potential yield that is achieved by humans. In marine systems, environmental pressures underlying recruitment of fish stocks are a hot topic in both scientific and economic contexts.

In the central Baltic Sea ecosystem, the clupeids sprat (*Sprattus sprattus L.*) and herring (*Clupea harengus L.*) serve as a commercially important pelagic species whose well-being has strongly depended on environmental changes in the past decades: Not only did they have to face shifts in their main pray organisms within the mesozooplankton community (Möllmann & Köster, 1999; Alheit et al., 2005), but also variations in abiotic environmental attributes, such as temperature and salinity, represented major challenges for clupeids (Alheit et al., 2009).

Sprat and herring are widely used for human consumption and fish meal and are therefore of economic importance. Variation in biomass of clupeids can lead to changes within the whole Baltic food web, as it controls the biomass of lower trophic levels such as mesozooplankton as well as higher trophic levels such as cod and whiting (Ross et al., 2013). In general, clupeids are the 'middle class' of an ecosystem, as the species represent the connection between top predators (bigger fish, seals, birds) and lower tropic levels such as zooplankton. Abolition events due to heavy exploitation or climatic variability can cause severe changes in the entire ecosystem, because predator prey relationships fall out of balance and the system may shift into states that lose a) their resilience to pressures, and b) their economic relevance and hence lead to decreasing employment and living standards. An example of that phenomenon is shown in the Benguela ecosystem which highly depends on its clupeid productivity for human and animal consumption. Heavy fishing pressure reduced the stocks of sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolis*) opening a free niche for jellyfishes and pelagic goby (*Sufflogobius bibarbatus*) that had been alien to the system in this magnitude to this point and changed the system drastically (Roux et al., 2013). Examples like this show that we need knowledge on dependencies and possible consequences if systems shift from one state to another due to changes in ‘middle class’ abundance. Therefore, we need every puzzle piece that can help us understand a dynamic system in order to apply possible management scenarios.

The early life history of fish is known to be the most vulnerable phase in their life cycle (Hjort, 1914) as the fragile organisms are exposed to a multitude of external pressures, such as changes in temperature, salinity, wind stress or prey availability (Voss et al., 2012). Unfavourable environmental conditions as well as a weak spawning stock biomass (SSB) during this critical period can lead to poor recruitment success of a species and hence to severe changes in the entire ecosystem (Fey et al., 2014).

One possible theory for recruitment success is the match/mismatch hypothesis (Cushing, 1974): As larval fish survival highly depends on prey availability, especially during the time of first feeding, temporal shifted peaks of prey organisms and larval occurrence due to environmental variability may lead to severe consequences in recruitment success for the given year. Since it is not possible to foresee or even control possible climatic events, and larvae are not faced with an ‘optimal environmental window’ (Cury & Roy, 1989; Roy et al., 1992) when needed, we have to step back and focus on the information that we can use as valuable information for possible recruitment dynamics and therefore find potential environmental indicators that are linked to early life history traits of a species at hand. MacPherson et al. (this study, Chapter II & IV) found abiotic (favorable physical environments for egg survival and prey abundance) and biotic (female size, yolk amount in eggs) mechanisms to be highly linked to cod recruitment variability in the Baltic and in the lab. For clupeids, other environmental pressures become relevant, as their physiology and life cycle differ to their gadoid predator. Abiotic pressures, such as depth of saline water in the Baltic (Voss et al., 2012) or water temperature (Nissing et al. in 2003, Mohrholz et al., 2006) affect both, sprat and herring, as well as biotic drivers such as (zooplanktonic) prey abundance (e.g., *A. tonsa*) for herring (Cardinale et al., 2009) and predator (*G. morhua*) biomass for cod (Parmanne et al., 1994; Köster et al., 2001) were found to be correlated to recruitment.

In this study, we venture to identify a set of suitable environmental indicators connected to recruitment success for the Baltic clupeids sprat and herring, respectively. The approach is based on simple linear regression models and easy to follow steps in order to implement the method introduced by MacPherson e al. (this study, Chapter II) to every species and ecosystem possible if data is available (Diagram 1). Results can be used to diagnose possible recruitment dynamics within a system that can be used in an Ecosystem Based Fisheries Management (EBFM) context.

3.2 MATERIALS & METHODS

3.2.1 Case study description

3.2.1.1 Sprat (*Sprattus sprattus L.*)

In the Baltic Sea, sprat (*Sprattus sprattus L.*) is not only the most abundant and commercially important fish species (ICES, 2010), but it is also prey for the top predators cod (*Gadus morhua L.*) and harbor porpoise (*Phocoena phocoena*) as well as predator of fish eggs and zooplankton (Arrhenius & Hansson, 1993; Bagge et al., 1994; Köster et al., 2003). The Baltic Sea represents the northern boundary of the species distribution (MacKenzie & Köster, 2004), where spawning (in the Bornholm Basin, Gdansk Deep and Gotland Basin) is characterized by an asynchronous strategy which makes it difficult to detect the dimension of seasonal variability in their early life survival (Voss et al., 2012). Fluctuations in recruitment success are believed mainly to be influenced by environmental drivers and large-scale changes in the Baltic ecosystem, such as regime shifts (Alheit et al., 2005; Möllmann et al., 2009). In particular, sprat biomass was influenced by the cod collapse in the early 90s, as the drop in cod biomass due to high fishing mortality and low recruitment success (Bagge et al., 1994) increased the sprat biomass distinctly (Parmanne et al., 1994; Köster et al., 2001). Within their life cycle, cod and sprat have a profound dependency as sprat not only serve as the major prey item for adult cod, the species also represents the most important predator of cod eggs (Bagge et al., 1994, Köster & Schnack, 1994). When looking at possible management applications and setting fishing quotas, biological interactions, such as those described above, need to be considered as they may fundamentally stabilize the ecosystem (Rudstam et al., 1994).

3.2.1.2 Herring (*Clupea harengus L.*)

The Atlantic herring (*Clupea harengus L.*) represents another important link between top predators, such as cod, (*Gadus morhua L.*) and the smaller pelagic community within a food web. Herring live in big schools and lay eggs on plants and rocks in coastal areas. Unfortunately, the spawning grounds are being increasingly destroyed by humans and climatic changes (Fey et al., 2014). Different populations are characterized by their different spawning times. In the Baltic for instance, spawning starts in January in the western regions (ICES SD 24) and ends in July in Finnish waters (SD 31) (Parmanne et al., 1994; Aro, 1989). Overall, the resilient species have the ability to adapt to varying environmental conditions such as changes in temperature and salinity as shown in the Baltic herring populations (Cardinale et al., 2009). As herring is an ecologically important clupeid and domestic fisheries depend on profitable catches every year, approximately 700 000 tons per year according to HELCOM, the need for reliable management tools is clear.

3.2.2 Data

3.2.2.1 Time periods and Training dataset

In order to account for non-stationarity in Spawning Stock Biomass – Recruitment relationships (SSB – R), we analysed different training data sets representing time series depending on the SSB – R trend for herring and sprat (Fig. 1). Time periods chosen for herring where 1975 – 2003 (L), 1984 – 1994 (P1), 1993 – 2003) (P2). Time periods chosen for sprat where 1975 – 2003 (L), 1975 – 1985 (P1), 1981 – 1991), (P2) and 1992 – 2003 (P3), where the L time series represents the full EB herring and sprat assessment covering ups and downs of the stocks. Data were available after 2003 (until 2009) which were used for the evaluation process of the recruitment residuals (RecRes). We then predicted the SSB – R relationship for the remaining years (until 2009) and compared them to existing results in the last step of our analysis.

3.2.3 Modelling approach

3.2.3.1 State variable

As previously explained in Chapter 1, the first step in our analysis was the computation of a stock – recruitment model, of which the residuals serve as a state variable for identifying indicators for the quality of the herring and sprat recruitment environment. Stock size, represented by spawning stock biomass (SSB), and recruitment (numbers at age 1) values were derived from stock assessments of herring and sprat (Subdivisions 25, 26 & 28) conducted by the International Council for the Exploitation of the Sea (ICES 2013) ((see map for ICES subdivisions, Fig. 1, Chapter I and Fig. 1 this Chapter).

Candidate indicators that relate to recruitment success were identified based on the explanatory power of certain environmental variables (Table 1, Table 2). Here, the residual variation around the relationship between spawning stock (i.e. parent) biomass (SSB) and recruitment (R) is considered to be recruitment success. As we assume that the residual variation is due to biotic and abiotic influences on early life history development and hence survival (Pauly, 1984), the parental effect on recruitment success is marginal. The derived state variable (recruitment residuals) are referred to as RecRes from hereafter.

In order to gain robust RecRes, we selected a general least square (GLS) model with no autocorrelation or heterogeneity structure in the process of deriving the RecRes of the respective time periods using the packages {nlme} in R (Pinheiro et al., 2013). This approach is known to be a simple but less error-prone statistical method.

3.2.3.2 Environmental Indicators

We used an initial set of 32 biotic and abiotic variables (Appendix, Table A2 & A3) in Step 2 of our analysis as candidate indicators to be tested in pressure – state relationships with RecRes. Here, we modelled RecRes as a function of each of the candidate indicators by fitting linear regression models with or without second-order polynomials. In order to account for temporal autocorrelation found for some indicators, we applied Generalized Least-Squares (GLS) regression including autoregressive error structures of order 1 [AR(1)] as follows:

(i) $yy=b \cdot xy+a+\varepsilon y$ where $\varepsilon y= \rho \cdot \varepsilon y-1+\eta y$

with b being the slope, a the intercept, and x being the observed value of the individual indicator suited to the accordant value of y (Year). Ɛ is the autoregressive error term of residuals at time y that are a function of time y – 1 along with noise (ɳ) that follow a normal distribution. Alternatively, an auto-regressive moving average structures of order 1,1 [ARMA1,1] (Pinheiro & Bates, 2000) was applied. The best error structure was chosen based on the AIC. The model was applied to the years 1975 – 2003 (Long, herring and sprat, respectively) as well as for the time periods P1 (herring: 1981 – 1991, sprat: 1975 – 1985), P2 (herring. 1992 – 2003, sprat: 1984 – 1994) and P3 (sprat: 1993 – 2003). Variables that showed a significant relationship with RecRes based on the p-value and biological plausibility were considered to be useful indicators and used in the next step which quantifies thresholds for the selected indicators with respect to good and bad recruitment. In step 3 thresholds per indicator were assessed in a single approach depending on a linear (ii) or second-order polynomial (iii) relationship as follows:

ii) $$x = \frac{(y-a)}{b}$$

iii) $$x = \frac{-b}{(2\cdot c)} \pm \sqrt{\left(\frac{b^2}{(2\cdot c)}\right)^2 - \frac{(a-y)}{c}}$$

where a represents the intercept of model outcome shown above, b is the slope of model, c shows the degree of the curve and y is the RecRes mean which is per definition 0. The state or quality of the recruitment environment of EB herring and sprat is then indicated by the direction of deviation of the observed indicator from its threshold value. Hence, positive deviations from the threshold indicate “good” and negative deviations indicate “bad” recruitment environment for EB herring and sprat. In order to test for the robustness of the derived thresholds, we incorporated a 5-fold cross-validation within the step of finding suitable thresholds per indicator, as well as its standard deviation and mean square error (MSE) (for more detailed description of method see James at al., 2013). Cross-validation was conducted on the longtime period only.

3.2.4 Evaluation

In the prediction trial in step 5, the RecRes for the years 1975 – 2009 were used along with the derived thresholds from derived key indicators that showed a significant relationship with the response variables for herring and sprat (Fig. 3, Fig. 4). With the derived threshold value based on respective time length, predictions of potential recruitment environments were calculated by subtracting the threshold from the time series from 2003 to 2009. Results were then compared annually to RecRes to asses if our response variable is a suitable measure for the estimation of recruitment success. The possible validity [%] of recruitment environment per year was calculated by ranking each indicator based on their performance in the analysis (low standard deviation, biological relevance based on expert knowledge). For herring, biomass of Acartia sp. was ranked 50 %, depth of 11 psu isohaline (Bornholm Basin) was ranked 30 % and cod (SSB) we ranked with 20 % expressiveness. For sprat, the only key indicator (depth of 11 psu isohaline) was used for the evaluation of the RecRes and therefore ranked 100 % expressiveness. In the case of the indicator values being located within the SD range of any indicator, only 0.5 % of full rank was given (Table 3).

3.3 RESULTS

3.3.1 State variable

All RecRes of the respective time periods selected by applying GLS models are shown in Figure 2.

3.3.2 Environmental Indicators

The results of the indicator selection routine of sprat and herring showed that both abiotic and biotic variables showed significant relationships with the recruitment residuals (RecRes) in almost every time period tested (Table 1, Table 2). In both cases, one time period tested did not show any relationship with RecRes and any indicator: for sprat, the long time period (PL = 1975 – 2003) and for herring a 10-year period (P1 = 1975 – 1985), respectively.

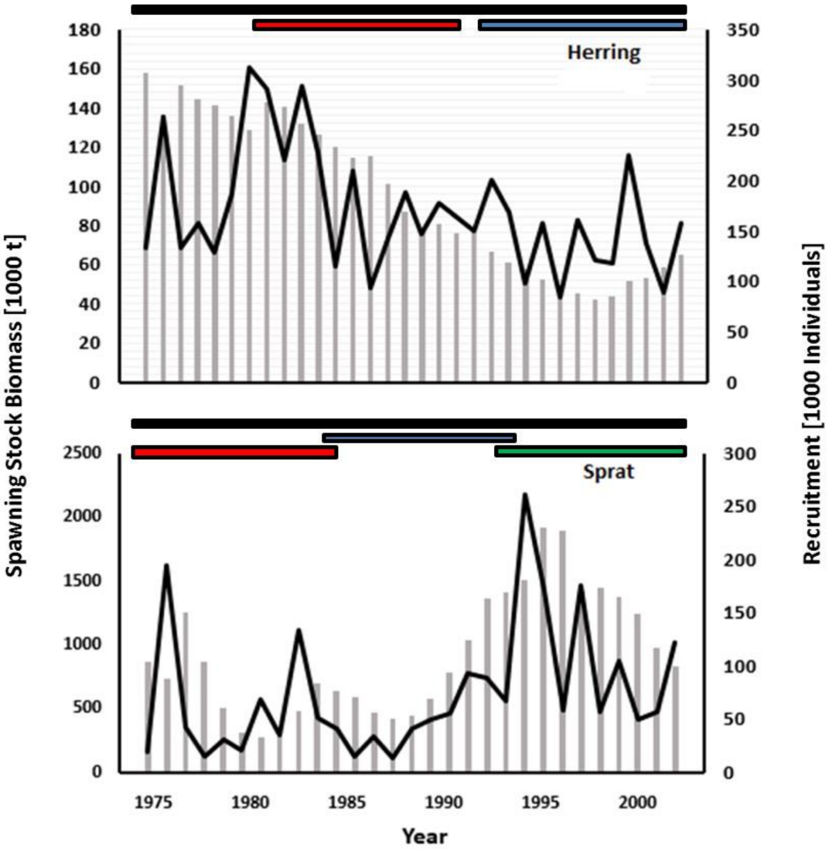


Figure 1: Spawning stock biomass (grey bars) on y-axis and recruitment (black line) on secondary axis of Central Baltic herring (Clupea harengus L.) top, and sprat (Sprattus sprattus L.), bottom. Colored bars mark the time periods analysed. Top: herring. L (black) = 1975 – 2003, P1 (red) = 1981 – 1991, P2 (blue) = 1992 – 2003. Bottom: sprat. L (black) = 1975 – 2003, P1 (red) 1975 – 1985, P2 (blue) = 1984 – 1994, P3 (green) = 1993 – 2003

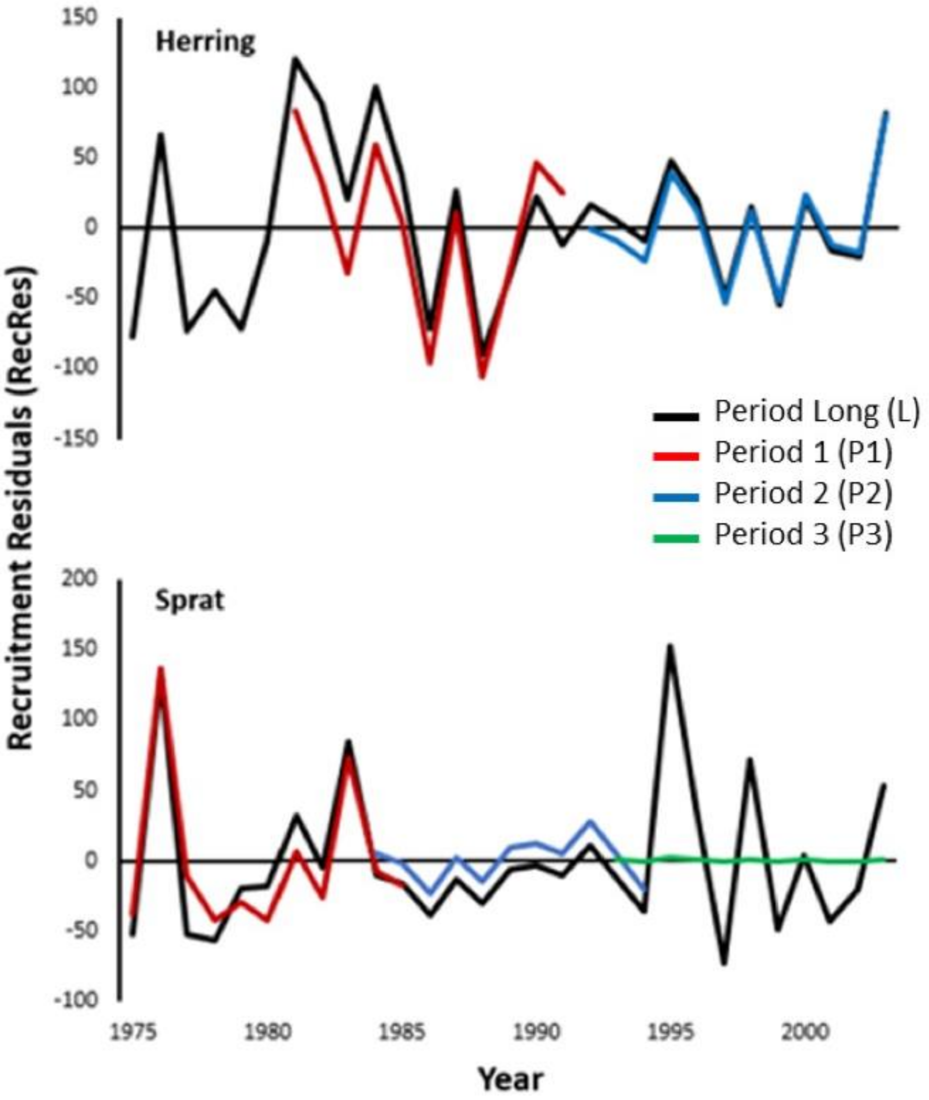
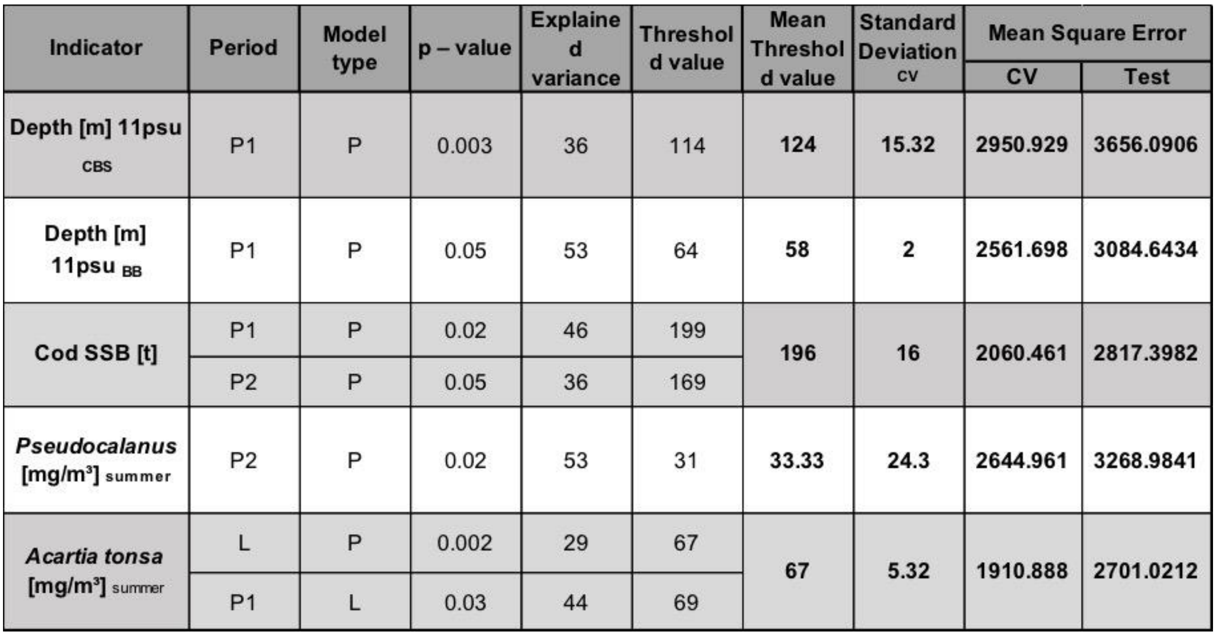


Figure 2: Recruitment residuals (RecRes) of the different periods used for the indicator selection. Top: herring. L (black) = 1975 – 2003, P1 (red) = 1981 – 1991, P2 (blue) = 1992 – 2003. Bottom: sprat. L (black) = 1975 – 2003, P1 (red) 1975 – 1985, P2 (blue) = 1984 – 1994, P3 (green) = 1993 – 2003.

3.3.2.1 Herring (*Clupea harengus L.*)

Herring recruitment success showed significant relationships with the depths of the 11 psu isohaline in the central Baltic and the Bornholm Basin, explaining variations of 36 and 53 %. For biotic factors, the annual cod spawning stock biomass explained a variance of 36 and 46 % in the RecRes. The abundance of two zooplankton species in summer also showed significant relationships and are believed to influence herring recruitment success: *Pseudocalanus sp*. and *Acartia tonsa*, explaining between 29 and 62 % of the variance in herring recruitment success in different time periods (Table 1).

Table 1: Results of the threshold derivation of the identified indicators per time period for Baltic herring stock (*Clupea harengus L.).* RecRes of time periods L, P1 and P2 showed relationships with different indicators affecting recruitment. Model types are L (linear) or (P) polynomial. Thresholds are shown in the unit of the corresponding indicator. Mean threshold values from the 5-fold cross-validation (CV) process are shown as well as ± standard deviation (SD) and the MSE values for the training (MSECV) and test (MSEtest) data set.



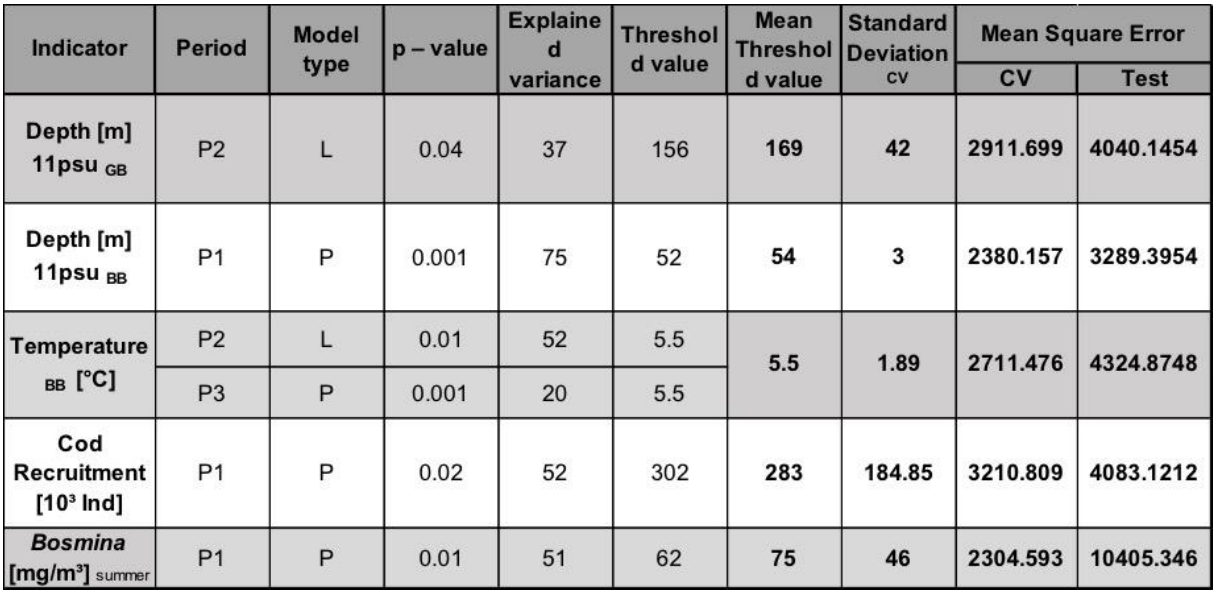
Indicator	Period	Model type	p – value	Explained variance	Threshold value	Mean Threshold value	Standard Deviation $_{\text{CV}}$	Mean Square Error	
								CV	Test
Depth [m] 11psu $_{\text{CBS}}$	P1	P	0.003	36	114	**124**	**15.32**	**2950.929**	**3656.0906**
Depth [m] 11psu $_{\text{BB}}$	P1	P	0.05	53	64	**58**	**2**	**2561.698**	**3084.6434**
Cod SSB [t]	P1	P	0.02	46	199	**196**	**16**	**2060.461**	**2817.3982**
	P2	P	0.05	36	169				
***Pseudocalanus* $[mg/m^3]$ summer**	P2	P	0.02	53	31	**33.33**	**24.3**	**2644.961**	**3268.9841**
***Acartia tonsa* $[mg/m^3]$ summer**	L	P	0.002	29	67	**67**	**5.32**	**1910.888**	**2701.0212**
	P1	L	0.03	44	69				

3.3.2.2 Sprat (*Sprattus sprattus L.)*

For abiotic variables, the depth of 11 psu isohaline in the Gotland Basin and Bornholm Basin showed a clear signal with the RecRes and explained between 75 % of variance in BE sprat recruitment success.

Further indicators, such as temperature in the reproductive volume (RV) (Plikshs et al., 1999), and biotic factors, such as the strength of cod recruitment success in the Central Baltic and abundance of cladocerans (*Bosmina sp.*) in summer, explained around 50 % of variance in the RecRes but standard deviations (SD) were relatively high. All results are shown in Table 2.

Table 2: Results of the threshold derivation of the identified indicators per time period for Baltic sprat stock (*Sprattus sprattus L.*). RecRes of time periods P1, P2 and P3 showed relationships with different indicators affecting recruitment. Model types are L (linear) or (P) polynomial. Thresholds are shown in the unit of the corresponding indicator. Mean threshold values from the 5-fold cross-validation (CV) process are shown as well as ± standard deviation (SD) and the MSE values for the training (MSECV) and test (MSEtest) data set.



Indicator	Period	Model type	p – value	Explained variance	Threshold value	Mean Threshold value	Standard Deviation CV	Mean Square Error	
								CV	Test
Depth [m] 11psu $_{GB}$	P2	L	0.04	37	156	**169**	**42**	**2911.699**	**4040.1454**
Depth [m] 11psu $_{BB}$	P1	P	0.001	75	52	**54**	**3**	**2380.157**	**3289.3954**
Temperature $_{BB}$ [°C]	P2	L	0.01	52	5.5	**5.5**	**1.89**	**2711.476**	**4324.8748**
	P3	P	0.001	20	5.5				
Cod Recruitment [10^3 Ind]	P1	P	0.02	52	302	**283**	**184.85**	**3210.809**	**4083.1212**
Bosmina **[mg/m³]** summer	P1	P	0.01	51	62	**75**	**46**	**2304.593**	**10405.346**

3.3.2.3 Model selection and Threshold derivation

Both, linear (L) and polynomial (P) models appeared to be a suitable tool for deriving indicators per species. Depending on the data, a variance structure was applied in the indicator derivation process. Thresholds conveyed from the respective indicators with the RecRes per time period are shown in Table 1 and Table 2, threshold derivation process is described in Diagram 1.

3.3.2.4 Time periods and Training dataset

The comparison of the training data set RecRes (until 2003) to the RecRes until 2006 revealed similar trends in the respective recruitment, hence the applied method was considered as a robust approach of identifying reliable environmental indicators of the tested time periods for sprat and herring.

3.3.2.5 Evaluation of trends in recruitment environment

3.3.2.6 Herring (*Clupea harengus L.*)

The zooplankton species Acartia sp. showed the strongest correlations with the RecRes of Baltic herring. Spawning stock biomass (SSB) of EB cod seems to be a highly influential factor as, together with the depth [m] of the 11 psu isohaline in the Central Baltic, both factors alternate in negative effect on herring recruitment. Once the cod SSB decreases in the late 80’s, the depth of the halocline becomes an influential factor (Fig. 3). The time period 1981 – 1991 shows that the abundance of the prey organism *Acartia sp*. mirrors the negative effect of the descending saline layer as zooplankton accumulate below it, making it hard for predators to prey on the essential food items. In the last time period (1992 – 2003), overall positive results with a few exceptions show that the recruitment environment for Baltic herring seemed to be improving after a poor phase in the previous decade.

3.3.2.7 Sprat (*Sprattus sprattus L.*)

Based on the selected indicators and their respective thresholds, we were able to describe changes in the clupeid recruitment environment (Fig. 4). For sprat, the depth of the 11 psu isohaline and the powerful recruitment success of the cod stock during the mid-70's to mid-80's had negative effects on the recruitment success. Favorable food conditions at the same time (caldoceran abundance) did not seem to benefit the sprat stock. In the following time period (1984 – 1994), the depth of the 11 psu isohaline in the Gotland Basin as well as the temperature within the reproductive volume (RV) in the Bornholm Basin showed matching results, showing positive deviations ("good conditions") from the RecRes until 1988 and "bad" environmental conditions for sprat recruitment success until 1993. The indicator showing the strongest relationship (75% variance, SD ± 3.00) with the RecRes was identified as the depth at 11 psu isohaline in the Bornholm Basin and was therefore considered as the key indicator in this analysis for sprat recruitment (Fig. 4).

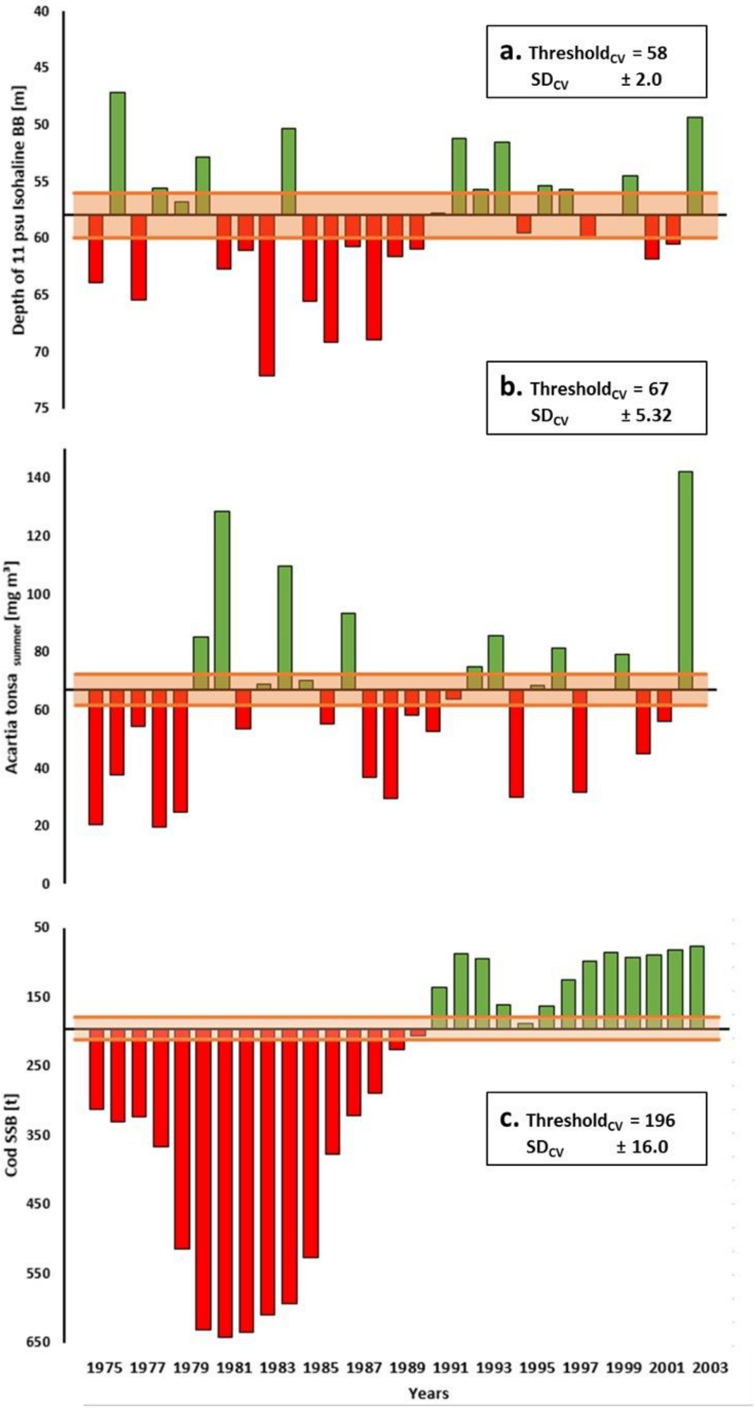


Figure 3: Potential ‚good‘ and ‚bad‘ recruitment environments for Baltic herring based on thresholds derived from analysis per indicator and time period 1975 – 2003, respectively. Red= ‘bad’ = below threshold, green= ‘good’ = above threshold of the environmental indicators identified as relevant to BE herring recruitment success. Top (a.): Depth [m] of 11 psu Isohaline in the Bornholm Basin, Threshold value = 58 ± 2.0; Middle (b.): *Acartia tonsa* abundance [mg m^3], Theshold value = 67 ± 5.32; Bottom (c.): Cod SSB [t], Threshold value = 196 ± 16.0. All Threshold values and standard deviations (SD) are in respective unit of indicator.

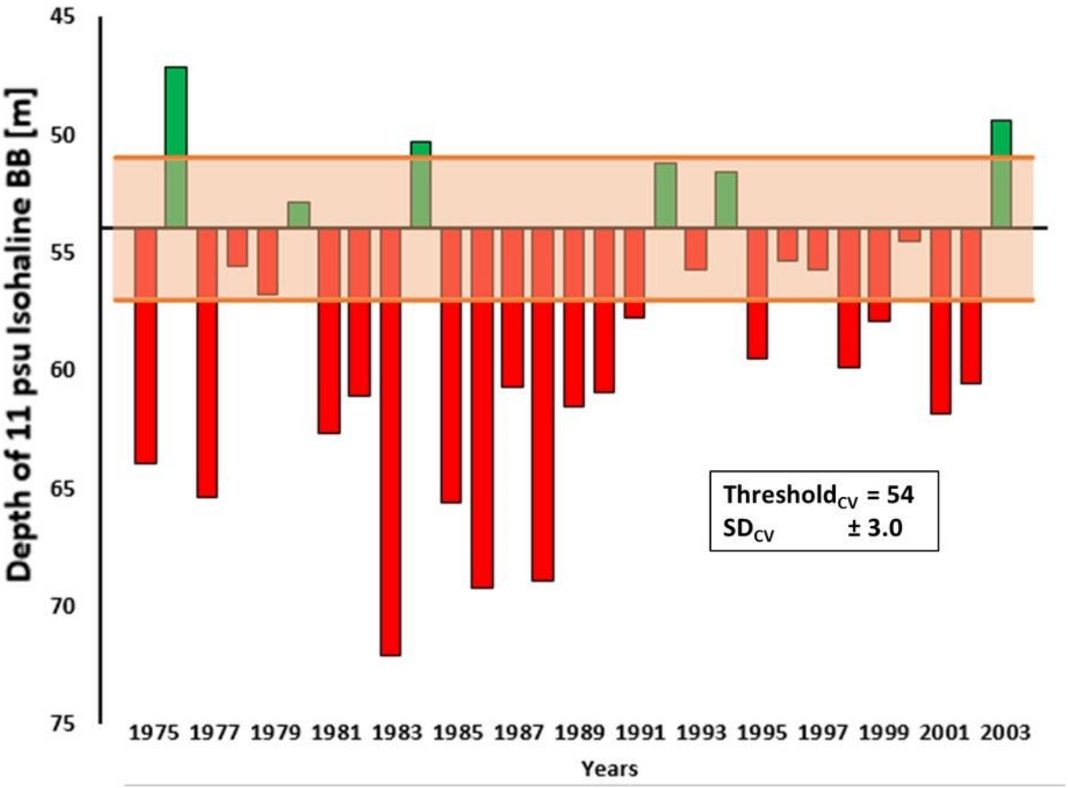
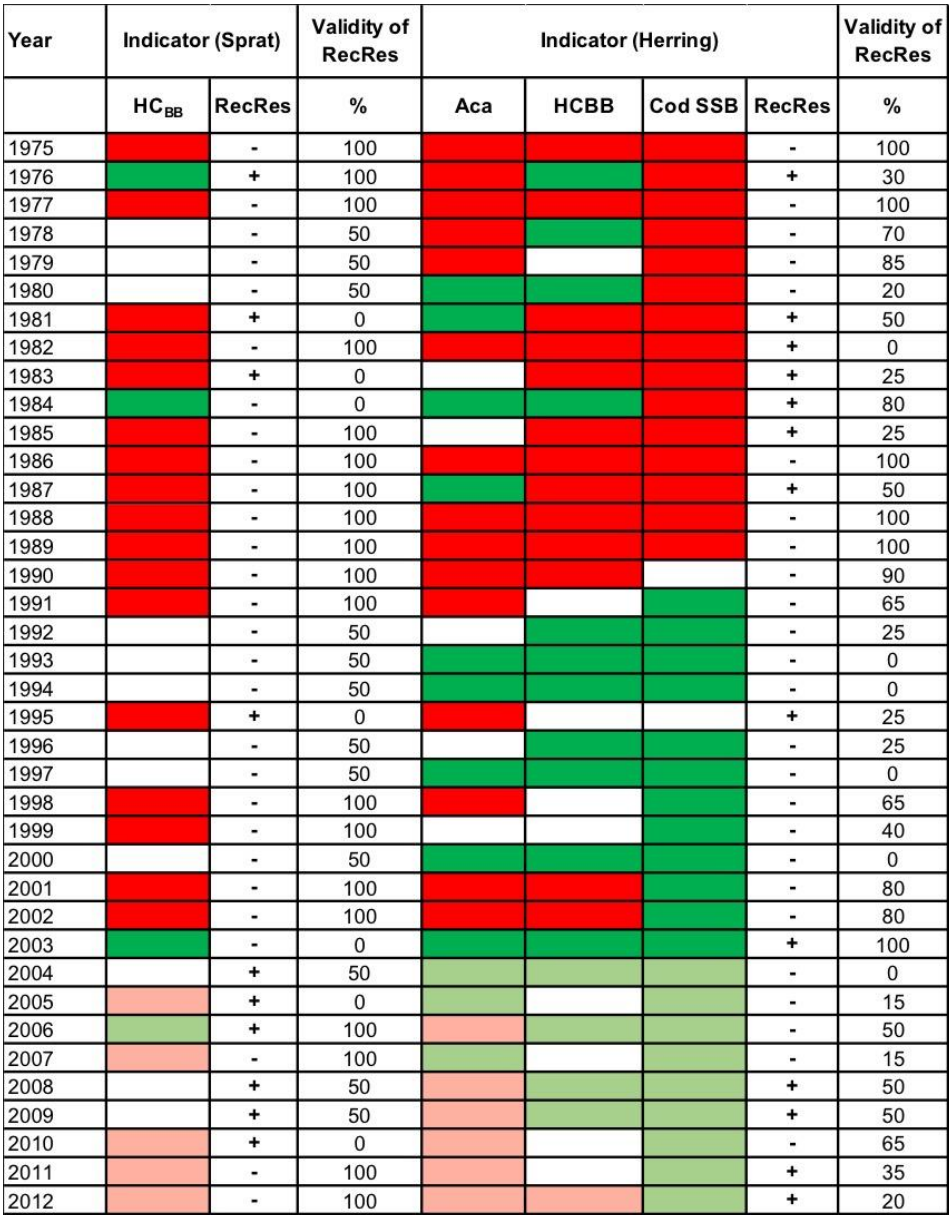


Figure 4: Potential ‚good‘ and ‚bad‘ recruitment environments for Baltic sprat based on threshold (54 m ± 3.0) derived from analysis over time and time period, respectively. Red = ‘bad’ = below threshold, green = ‘good’ = above threshold of depth [m] of 11 psu Isohaline in the Bornholm Basin which was the environmental indicator identified as relevant to Baltic sprat recuritment success for the time period 1975 – 2003. All Threshold values and standard deviations (SD) are in resprective unit of indicator.

Within the evaluation process of the indicator value and the RecRes, different rankings for the results were given (Table 3). For herring, the zooplankton (Acartia tonsa) prey abundance [mg m^3] in summer explained most of the variance and was therefore ranked highest (50%) of the three indicators found. The depth [m] of 11 psu isohaline in the Bornholm Basin was ranked as the second-best indicator for herring recruitment success and got 30 % validity. The last indicator that showed a significant correlation with herring recruitment was found to be Cod SSB [t] and got a 20% rank. For sprat recruitment, the most prominent indicator was found to be the depth [m] of the 11 psu isohaline in the Bornholm Basin. As we only detected one indicator, the comparison with the RecRes inevitably showed a 100% validity if RecRes and indicator results where congruent.

Table: 3: Color code of potential ‚good‘ and ‚bad‘ recruitment environments based on thresholds of Baltic sprat (Sprattus sprattus L.) and herring (Clupea harengus L.) derived from cross-validation analysis in the years 1975 to 2012, respectively. Red= ‘bad’ = below threshold, green= ‘good’ = above threshold, white = ± Standard Deviation (whitin SD range) of respective threshold. + / - symbols represent RecRes values of the particular year. Light red and green boxes (2004 - 2012) show potential recruitment envrionment after comparing results of test dataset to the observtions until 2012. Percentages display possible validity of result with respect to recruitment success. Ranking of indicators: sprat: HCBB = 100 %, herring: Acartia tonsa abundance = 50 %, HCBB = 30 % and Cod SSB = 20 %. If threshold value was found to be in the range of the SD, 0.5 % of original ranking was given for RecRes



Year	Indicator (Sprat)		Validity of RecRes	Indicator (Herring)				Validity of RecRes
	HC_{BB}	RecRes	%	Aca	HCBB	Cod SSB	RecRes	%
1975	🟥	-	100	🟥	🟥	🟥	-	100
1976	🟩	+	100	🟥	🟩	🟥	+	30
1977	🟥	-	100	🟥	🟥	🟥	-	100
1978		-	50	🟥	🟩	🟥	-	70
1979		-	50	🟥		🟥	-	85
1980		-	50	🟩	🟩	🟥	-	20
1981	🟥	+	0	🟩	🟥	🟥	+	50
1982	🟥	-	100	🟥	🟥	🟥	+	0
1983	🟥	+	0		🟥	🟥	+	25
1984	🟩	-	0	🟩	🟩	🟥	+	80
1985	🟥	-	100		🟥	🟥	+	25
1986	🟥	-	100	🟥	🟥	🟥	-	100
1987	🟥	-	100	🟩	🟥	🟥	+	50
1988	🟥	-	100	🟥	🟥	🟥	-	100
1989	🟥	-	100	🟥	🟥	🟥	-	100
1990	🟥	-	100	🟥	🟥		-	90
1991	🟥	-	100	🟥		🟩	-	65
1992		-	50		🟩	🟩	-	25
1993		-	50	🟩	🟩	🟩	-	0
1994		-	50	🟩	🟩	🟩	-	0
1995	🟥	+	0	🟥			+	25
1996		-	50		🟩	🟩	-	25
1997		-	50	🟩	🟩	🟩	-	0
1998	🟥	-	100	🟥		🟩	-	65
1999	🟥	-	100			🟩	-	40
2000		-	50	🟩	🟩	🟩	-	0
2001	🟥	-	100	🟥	🟥	🟩	-	80
2002	🟥	-	100	🟥	🟥	🟩	-	80
2003	🟩	-	0	🟩	🟩	🟩	+	100
2004		+	50	🟩	🟩	🟩	-	0
2005	🟥	+	0	🟩		🟩	-	15
2006	🟩	+	100	🟥	🟩	🟩	-	50
2007	🟥	-	100	🟩		🟩	-	15
2008		+	50	🟥	🟩	🟩	+	50
2009		+	50	🟥	🟩	🟩	+	50
2010	🟥	+	0	🟥		🟩	-	65
2011	🟥	-	100	🟥		🟩	+	35
2012	🟥	-	100	🟥	🟥	🟩	+	20

3.4 DISCUSSION

In a constantly changing world, that is mostly driven by anthropogenic decisions, realistic and established relationships between all the components of systems that are decided upon become increasingly necessary. In an ecosystem context, reliable correlations between a species of interest and its multiple pressures affecting species fitness, recruitment or mortality become an important tool if that species is of (economic) value to humans.

In fisheries, mechanisms underlying year-class strength of fish populations are hard to detect, as habitats and environmental drivers are almost borderless. To narrow all possible influences down to a few essential factors affecting different fish stocks and therefore make more well-grounded decisions, statistical models, biological knowledge, as well as time and passion need to be combined to fill the knowledge gap and to come closer to the goal of understanding the impossible.

The present analysis shows how diverse environmental factors can influence clupeid populations within an ecosystem. Neglecting individual stressors within a holistic approach to understand the interactions in a versatile entity would not do justice to either side of the coin and leads to a disconnection of individual components.

This work serves as an evaluation study of the method introduced by MacPherson et al., present study, Chapter II) on EB cod. Here, available data was used to understand possible environmental drivers connected to recruitment success of sprat (*Sprattus sprattus* L.) and herring (*Clupea harengus* L.) in the Central Baltic Basin between 1975 and 2009. For both species, we used the biomass of one-year-olds and shifted it back to the year of birth, as variability in eggs and first-feeding larvae are crucial to estimate and reliable predictions are challenging to interpret (Baumann et al., 2006). A challenge that lies within assessments from spawning stock sizes are the uncertainty included in input data, as surveys of stock size etc. is not very precise (e.g. Needle, 2002). Using this data in different model scenarios, can under- or overestimate stock sizes and hence conclusions drawn from that (Gårdmark et al., 2011) may by highly faulty.

The derived environmental indicators estimated in this study are a result of SSB – recruitment relationships that can contain autocorrelation and noise from the assessment model in the first place. In order to keep the correlations as 'clean' as possible, we accounted for possible error-structure in the data by applying autocorrelation methods and cross-validation techniques. By fitting single indicators to the time series rather than an approach combining multiple environmental indicators to one as done by Gårdmark et al. (2011), we avoid possible overlay of indicator signals that affect the correlation. This is why we assume, that the derived mechanisms from the recruitment correlations have a realistic foundation.

For sprat, abiotic factors within the Bornholm Basin (depth [m] of 11 psu isohaline layer and temperature within 'reproductive volume' (see Plikishs et al., 1993)) explained most of the variance and/or showed a signal in more than one time period tested. This finding indicates that, along with the strength of cod recruitment and the presence of zooplankton in summer, abiotic strains are a dominant factor influencing recruitment success. Other studies (Voss et al., 2012) also point to the fact that the depth of the saline layer plays an important role as sprat primarily prey on cladocerans in summer which are typically located above or within the halocline (Hoziosky et al., 1989). Interestingly, the only zooplankton species that showed a relationship with sprat recruitment in our study was the abundance of *Bosmina* sp. in summer - a plentiful cladoceran in Baltic waters that prefers warmer, less saline waters in spring (Sidrevics, 1984, Möllmann et al., 2000).

The temperature and salinity in the Bornholm Basin were mentioned by Nissing et al. in 2003 as important abiotic factors affecting egg survival, as these two factors are relevant to fruitful hatching success. The matter becomes a bit tricky, as egg distribution changes within the developmental cycle from the deep isohaline layer to the surface layer characterized by less saline water masses (Paramanne et al., 1994). The present study agrees with the fact that the depth of the halocline in the Gotland and Bornholm Basin seems to be of importance for sprat recruitment. The identified temperature indicators showed a strong analogy with two of the three tested time periods (P2, P3), but was not used for further analysis as the standard deviation showed a ± of 1.89 °C and put all years in an interstage, leaving them incommensurable to the RecRes (Table 2). Nevertheless, temperature plays an important role for the successful development of sprat, as the development of eggs and larvae are temperature dependent in specific water layers (Petereit et al., 2008).

Ideal temperatures for prosperous offspring was found to be above 4°C by Rechlin (1967) and Grauman & Yula (1989) and supports the data used in this study, as the derived threshold for the temperature relevant for successful sprat recruitment in the Bornholm Basin was 5.5°C in the years 1984 to 2003.

For herring, the most prominent indicator affecting recruitment was the biomass of the calanoid copepod *Acartia tonsa*, which showed a significant correlation in all time periods tested (1975 – 2003). *Acartia* sp. is the main food source for herring larvae in the Central Baltic (Cardinale et al., 2009) and its recruitment success depends largely on small inflows transporting warm and saline rich waters into the Baltic (Mohrholz et al., 2006). Hence, even though temperature did not show any significant relationship with herring recruitment success in the present study, one has to keep in mind that drivers for a prosperous offspring may lie in lower trophic levels and are not directly observed in derived results but play an important role when discussing possible recruitment indicators for respective species.

Along with the availability of specific prey species, the depth [m] of the 11 psu isohaline and the cod SSB showed correlations with recruitment success of herring. Again, the depth of the saline layer can be seen as an essential indicator for food availability, as most zooplankton species depend on the abiotic conditions above or within this layer (Möllmann et al., 2000). This indicator could also be interpreted as a secondary mechanism, as this saline water layer affects the cod biomass directly, as stated in Chapter I of this study. The spawning biomass of cod showed significant coherence with herring recruitment, even when cod SSB was low, as cod represents the main predator of clupeids in all life stages. For the analysis of successful recruitment of clupeids in the Baltic, it becomes apparent that, in comparison with the results of cod, abiotic as well as biotic factors play an important role that need to be considered if an overarching (management) approach is to be implemented.

The evaluation of the RecRes as suitable response variables for environmental mechanisms impacting recruitment success showed that the key indicator (depth of 11 psu isohaline within Bornholm Basin) defined for sprat agreed to RecRes in 23 years of 28 years and only failed in 2 of the 9 years tested in the prediction period. Results can serve as a robust guide for environmental drivers affecting sprat recruitment success, as egg development and prey availability highly depend on this water layer.

For herring, the evaluation of the RecRes as beneficial response variables cannot be easily ascertained, as years show varying results. Here is a concrete example of the complexity of environmental pressures affecting one species. Even though years of no match were not more prevalent than in the sprat example, the percentages of agreement ranged from 25 to 100 % with no clear visible pattern. In the prediction period, years of total mismatch with the RecRes and the key indicators were sparse, but again, the frequency of the match ranged from 15 to 65 %, indication, so that the correlated indicators highly interact and even overlap their signals in some years, making recruitment predictions difficult. Here, we suggest the identification of more and different environmental indicators and data from different subdivisions, as herring spawn in areas that were not part of this study (e.g., coastal areas of subdivisions tested, as well as Gulf of Riga, Archipelago Sea, Bothnia Sea, etc., see Cardinale et al., 2009), and adults undergo extensive feeding migrations (Parmanne et al., 1994) in summer and autumn, making it even harder to asses a realistic estimation of the annual spawning stock strength. Because of migration and different spawning grounds, the herring stocks in the Baltic have been classified as different stocks, which adds another challenge to a waterbody with no boundaries. Also, assessments have often overestimated spawning stock biomass and underestimated fishing mortality in the Central Baltic (Möllmann et al., 2011), dragging even more uncertainties along the data series. Obviously, herring results can only be used as a trend for discussing recruitment variability rather than using assumptions without any support from other sources. The evaluation of the method described in Chapter II cannot be applied to the herring assessment data without great caution and fundamental expert knowledge. However, the sprat indicators seem to be a more robust set of environmental factors influencing recruitment that can be derived from our method introduced in Chapter II for EB cod.

The results of the present study show, how difficult precise conclusions on particular relationships are, if abiotic and biotic drivers are never determined. Especially the herring example illustrates, how much future work needs to be done and how to assess spawning stock size differently in order to identify clear mechanisms underlying recruitment success. For herring we can conclude that the method used can be applied and reveals indicators that are biologically understandable but are not strong enough to be implemented in a decision making (management) context yet.

For sprat, the method worked quite well and revealed a set of environmental indicators influencing sprat recruitment. One key indicator (depth of 11 psu isohaline within Bornholm Basin) and its respective threshold could be crystalized that can now be used to counter the environmental changes within a system mostly caused by humans. There is still work that needs to be done but this study proves, that simple methods can illustrate complex correlations and help us understand the past and observe the future.

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Chapter IV

Paternal effects on early life history traits in Northwestern Atlantic cod, *Gadus morhua L*.

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Paternal effects on early life history traits in Northwest Atlantic cod, *Gadus morhua*

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Summary

It is important to understand parental effects on early life history of fish as manifested, for example, in individual fitness of offspring. Immediately after fertilization, parental contributions (both genetic and non-genetic) to embryos will affect larval ontogeny, physiology, morphology and survival. In marine fish, rates of natural mortality are highest during early life and are negatively correlated with rates of growth and body size. In these early life stages (eggs, larvae, young juveniles) subtle differences in mortality can cause large differences in recruitment and year-class success. Therefore, it is particularly critical to understand factors that contribute to variability in mortality during early life. This study focuses on evaluating the potential influence of paternity on rates of mortality and development in eggs and larvae of Northwest Atlantic cod, *Gadus morhua*. To accomplish this 12 males and two females were crossed using a full-factorial breeding design. Paternity had a strong influence on fertilization success, hatching success, cumulative embryonic mortality, larval standard length, eye diameter, yolk-sac area, and cumulative larval mortality. Female 1 showed an overall 'weaker' performance of offspring than Female 2, indicating that deviances can stem from differences in female quality. Nevertheless, paternal contributions to embryonic and larval development were still evident despite differences in female quality, showing that sire effects on offspring are undeniable and can serve as important sources of variation during early life stages in fishes. Overall, these findings have implications for furthering the understanding of recruitment variability and can be used to optimize reproductive output for the aquaculture industry. In addition, the data suggests that the choice of mate during spawning can play a large role in offspring fitness.

Introduction

Fish populations, both farmed and wild, depend upon good quality gametes for the production of viable offspring (Brooks et al., 1997). Maternal contributions to progeny are the product of both nuclear-genetic and extra-nuclear, non-genetic material in the form of yolk (Rideout et al., 2004). Female age, size, condition, and spawning experience (among others) are maternal factors that can have a great influence on egg quality (e.g. size, yolk content, yolk quality in terms of lipids and specific fatty acids) (Blaxter, 1988; Chambers and Leggett, 1996; Rideout et al., 2005). In several species of fish, egg quality has been shown to affect growth and survival of offspring during embryonic and larval stages of development (Elliott and Baroudy, 1995; Cunningham and Russell, 2000).

On the contrary, paternal contributions to the progeny are solely the product of nuclear-genetic material (sperm) and only a limited number of studies have demonstrated that paternal genetic effects contribute to variation in morphology and performance during early life history (ELH) of fishes (see Høie et al., 1999; Vollestad and Lillehammer, 2000; Rideout et al., 2004). This is mainly due to the fact that researchers often pool milt from multiple males and thus those studies are not equipped to detect potential paternal differences that may arise during ELH (Bekkevold et al., 2002; Rideout et al., 2004). However, when designed to test for these paternal effects, many experiments have shown that paternity can in fact account for a significant portion of variation in phenotypic expression and survival during ELH, as noted in the Atlantic herring, *Clupea harengus* (Høie et al., 1999), brown trout, *Salmo trutta* (Vollestad and Lillehammer, 2000), and haddock, *Melanogrammus aeglefinus* (Rideout et al., 2004). Furthermore, previous studies on winter flounder, *Pseudopleuronectes americanus*, reported paternal effects on fertilization success, as well as on survival and development of embryos and larvae (Butts and Litvak, 2007a,b). A series of experiments on haddock embryos suggested that paternity influenced hatching success and the length of larvae at hatch (Rideout et al., 2004; Probst et al., 2006). However, studies performed on Atlantic cod (*Gadus morhua*) in the Baltic Sea and Atlantic herring have reported no effect of paternity on ELH traits, or if so only via maternal-paternal interactions (Chambers and Leggett, 1992; Trippel et al., 2005; Bang et al., 2006).

In this study, we used Northwest Atlantic cod as our experimental organism. Cod is a demersal fish that is comprised of many populations that differ in their spawning grounds, migration patterns, and genetic composition (Ruzzante et al., 1996). The species has not only been an important species in the history of fisheries (Innis, 1954; Kurlansky, 1997) but is also a key trophodynamic player for marine communities in the North Atlantic and adjacent seas (Scott and Scott, 1988; Köster and Möllmann, 2000; Bundy and Fanning, 2005). Severe declines in stocks of cod due to heavy exploitation (overfishing) in the 1980s and 1990s led to the development of large-scale aquaculture protocols of this species (Delghandi et al., 2004; Rosenlund and Skretting, 2006). Previous research on paternal effects in early life stages of Northwest Atlantic cod have been restricted to total embryonic mortality from fertilization to hatch (Trippel and Neilson, 1992; Trippel and Morgan, 1994). No research to

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date has been conducted on Northwest Atlantic cod to examine if paternity influences temporal patterns of mortality during embryogenesis as well as offspring characteristics during the first few weeks post-hatch.

Thus, the objectives of this study were to evaluate the potential influence of paternity on rates of mortality and development in eggs and larvae of Northwest Atlantic cod. Understanding the paternal factors underlying embryonic and larval morphology and survival can help improve our knowledge on recruitment variability (e.g. adjusting the stock component of a stock-recruitment relationship for gamete quality; Nash et al., 2008) and can also be used to optimize reproductive output for the aquaculture industry by identifying desirable phenotypic and genotypic traits (Pickering, 1993).

Materials and methods

Broodstock collection and husbandry

Northwest Atlantic cod were collected by long-line trawl near Cape Sable Island, Nova Scotia, Canada (43°N, 65°W; NAFO subdivision 4X) in October 2006. Each fish was implanted with a passive integrated transponder (PIT) tag. During the spawning season (January to April) fish were maintained in a flow-through seawater system between 3 and 5°C. Fish were fed to satiation a diet composed of frozen northern shortfin squid, *Illex illecebrosus*, and Atlantic mackerel, *Scomber scombrus*, as well as an artificial 10 mm pellet diet (EWOS Canada, Surrey, BC, Canada).

In order to minimize the stress experienced by broodstock during handling, fish were anesthetized with 60 ppm MS-222 (AquaLife TMS; Syndel International, Vancouver, BC, Canada) prior to stripping of gametes. Body weight and total length were recorded before each gamete collection event, and Fulton's condition factor ($K = [W/L^3] \times 100$) was calculated. Slight pressure was applied to the abdomen of each fish and milt samples were collected into 250 ml dry beakers. Extra care was taken to avoid contamination of milt by seawater, urine, or faeces. Immediately after collection samples were held at 5–6°C. For females exhibiting signs of ovulation (i.e. enlargement of the abdomen), eggs were stripped (as outlined for milt) and collected into 1-L dry plastic beakers and held at 5–6°C before being distributed to separate beakers for fertilization (see below). Gametes from 12 Males and Female 1 were collected on 15 February 2010, and gametes from the same 12 Males and Female 2 were collected on 26 February 2010 (Table 1).

Experimental design

All experiments were conducted in a temperature-controlled room at 5–6°C. Eggs (20 ml) from each female were added into each of 12 beakers (1-L) and gently mixed with 0.2 ml milt from one of the 12 males. A total of 5 ml UV-treated seawater (31–32 ppt) was then added and the contents were mixed after 2 min. After 10 min, eggs were rinsed through a 1 mm mesh with an ample quantity of UV-treated seawater. After rinsing, eggs were transferred into clean 2.5-L beakers to incubate. In total, this procedure produced 12 half-sibling families per female (1 half sibling family per beaker).

A sterile 1 ml plastic pipette (tip cut off to prevent damage to embryos) was used to transfer ~300 embryos into 250 ml beakers; (six replicate beakers for each male-female combination = total of 72 beakers per female). Each beaker was filled with 220 ml of UV-treated seawater. Beakers were arranged randomly and kept at a constant temperature (~6.0°C) to avoid any microclimate differences that might have influenced developmental characteristics of embryos and larvae. An 11 h light (~100 lux) and 13 h dark light regime was used. A 70% water exchange was conducted each day by carefully siphoning out water. Embryos were transferred to a new beaker at an age of 6 days post-fertilization (dpf).

Data collection

Sperm concentration. Spermatocrit (defined as the ratio of packed sperm cells to the total volume of milt × 100) was used to estimate sperm concentration (Rakitin et al., 1999). The mean of the three measurements per male was used for statistical analyses.

Egg size. Fifty eggs were randomly sampled from each female. Digital images were captured for groups of eggs using a microscope (Leica MZ95, 40× magnification)

Table 1
Total length (L) and body weight (W) of Atlantic cod, *Gadus morhua*, broodstock using 12 males to generate half-sibling families

Broodstock	Length (cm)	Weight (g)	Condition factor	Spermatocrit (%) Experiment 1	Spermatocrit (%) Expeiment 2
Male 1	47.6	1676	1.55	39	39
Male 2	65.1	3474	1.26	33	39
Male 3	54.6	2598	1.60	59	52
Male 4	48.5	1682	1.47	60	61
Male 5	58.6	2016	1.00	46	43
Male 6	67.9	4179	1.34	47	47
Male 7	48.1	1231	1.11	49	36
Male 8	62.5	3164	1.30	60	61
Male 9	52.4	1525	1.06	36	30
Male 10	55.4	2127	1.25	36	35
Male 11	57.1	1832	0.98	42	41
Male 12	55.8	2690	1.55	48	50
Female 1	57.9	3015	1.55	–	–
Female 2	40.2	1415	2.18	–	–

Condition factor calculated with $W/(L^3) \times 100$.
Mean spermatocrit (%) given for each experiment.

equipped with a digital camera (Q Imaging MicroPublisher 3.3RTV) and QCapture Pro software. The diameter of each egg was measured using Image Pro software.

Fertilization success. At ~16 h post-fertilization, digital images of all eggs/embryos from each male-female combination were recorded using the same method as previously mentioned. Fertilization success was calculated as the percent fertilized eggs. Fertilized eggs were identified by the presence of cell cleavage (>4 cell stage), and those not showing cleavage were considered unfertilized (Kjørsvik and Lønning, 1983). Nonviable eggs (oversized opaque and discoloured) were excluded from the analysis.

Cumulative embryonic mortality. Dead eggs/embryos were removed daily and counted. Dead embryos were easily identified: they were white, opaque and lying on the bottom. Live eggs occasionally sank to the bottom of each beaker, particularly close to time of hatching. Care was taken not to remove these viable embryos. Cumulative mortality (%) until the time of first hatching was calculated for each half-sibling combination.

Hatching success. Beakers were examined every 24 h for hatched larvae. Once hatching began, the number of larvae in each beaker was counted daily and all larvae were removed using a plastic pipette. Hatching success was expressed as the total number of viable larvae divided by the total number of fertilized eggs. Hatched larvae were transferred into 100-ml beakers and maintained under the same environmental regimes as above. All larvae that hatched from Female 1 were used for further experimentation, while 20 larvae per male-female combination were used for Female 2.

Larval morphology. At the time of peak hatch (age 0 days post-hatch, dph), larval standard length (SL; ±0.1 mm), maximum eye diameter (ED; ±0.1 mm), and total yolk-sac area (YA; ±0.1 mm) were assessed for ~20 larvae per half-sibling family. These measurements were performed on digital images obtained using equipment described above.

Cumulative larval mortality. Hatched larvae were not fed and were examined and counted daily until death by starvation. Dead larvae were removed from the beakers using a sterile 1 ml plastic pipette. Cumulative mortality rates were calculated for each male-female combination.

Statistical analyses

All statistical analyses were performed using SAS software (v.9.1; SAS Institute Inc., Cary, NC, USA; SAS Institute Inc., 2003). Residuals were tested for normality (Shapiro-Wilk test) and homogeneity of variance (plot of residuals vs predicted values). Data were transformed when necessary to meet the assumptions of normality and homoscedasticity. Egg and larval morphological characteristics (ED, SL, YA) were $\log_{10}$ transformed to meet the model assumptions, while percentage data (i.e. fertilization success, cumulative embryonic mortality, and hatching success) were arcsine square-root transformed. Alpha was set at 0.05 for main effects and interactions. Treatment means were contrasted using the least squares means method (LSMEANS/CL adjust = TUKEY). The Kenward-Roger and Satterthwaite procedures were used to approximate the denominator degrees of freedom for unbalanced and balanced data, respectively (Spilke et al., 2005). All data are presented as mean ± standard error (SE). A t-test was used to compare egg diameters between the two females.

ANOVA models (see below) were run separately on each female because our primary interests were to examine the potential influence of paternity on rates of mortality and development in eggs and larvae. Fertilization success, hatching success and larval morphological traits were analyzed using one-way ANOVA models. Cumulative embryonic and larval mortality were analyzed using repeated measures ANOVAS containing the sampling day, and male main effects, and the sampling day × male interaction. When interactions were detected, reduced one-way ANOVA models were run on sampling day to determine the effect of paternity. The reduced models involved only pre-planned comparisons and did not include repeated use of the same data, thus α-level corrections for *a posteriori* comparisons were not necessary.

Results

Body weight, total length, K, and spermatocrit for the broodstock are shown in Table 1.

Egg size

The mean diameter of eggs from Female 1 (1.58 ± 0.10 mm) was significantly greater than that (1.42 ± 0.13 mm) for Female 2 ($T_{99} = 10.75$, $P < 0.05$).

Fertilization success

Fertilization success for the males crossed with Female 1 ranged from 82.72 to 90.83%, while the males crossed with Female 2 ranged from 70.55 to 100.0% (Fig. 1a). The paternal effect was non-significant for Female 1, but showed a significant influence on Female 2 (Fig. 1a; Table 2).

Hatching success

The time required for embryos to hatch was very uniform among all half-sibling groups, for both females, with the first hatched larvae occurring at 17 dpf and the final hatch at 23 dpf. Peak hatch occurred at 22 and 21 dph for Females 1 and 2, respectively (Fig. 1b). Mean hatching success of embryos for Female 1 was low (ranged from 0 to 4.20%), but was higher and more variable for Female 2 (ranged from 10.24 to 63.04%; Fig. 1b). Significant paternal effects were evident in both females (Fig. 1b; Table 2).

Cumulative embryonic mortality

Cumulative embryonic mortality for the different males ranged from 97.5 to 100% for Female 1 and from 33.5 to 94.3% for Female 2 (Fig. 2). More than 90% of the mortality occurred during the first 6 dpf for the embryos of both females; greatest mortality occurred at ages 4 and 5 dpf (Fig. 2). The repeated measures ANOVA models revealed that there were significant first-order sampling day × male interactions for Female 1 ($F_{231,1190} = 7.77$, $P < 0.0001$), and Female 2 ($F_{220,1189} = 3.52$, $P < 0.0001$; Fig. 2). Therefore the models were revised into separate one-way ANOVA models at each sampling day for each female. The paternal effect was

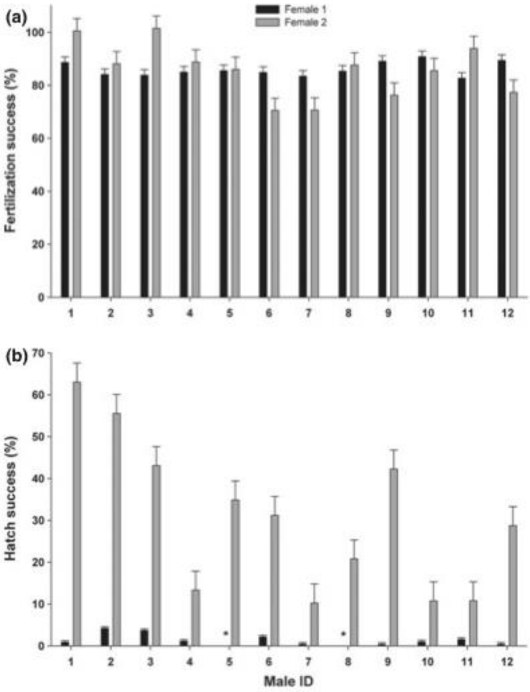

Fig. 1. Mean fertilization and hatching success of Atlantic cod (*Gadus morhua*). Males (n = 12) and females (n = 2) crossed using a full-factorial breeding design. ANOVA models run separately for Female 1 (black bars) and Female 2 (grey bars), as primary interests were to examine potential influence of paternity on (a) fertilization, (b) hatching success. Error bars = least square means standard error. Asterisk = no hatched larvae

significant aon all sampling days, except for Female 1 at 22 dpf (Fig. 2; Table 2).

Larval morphology

Mean larval SL at hatch for the different males ranged from 2.356 to 3.860 mm for Female 1 and 4.143 to 4.906 mm for Female 2 (Fig. 3a). Mean ED for larvae from the different males ranged from 0.272 to 0.318 mm for Female 1 and 0.288 to 0.369 mm for Female 2 (Fig. 3b). Mean YA ranged from 0.600 to 1.065 mm^2 for larvae from Female 1 and 0.197 to 0.628 mm^2 for larvae from Female 2 (Fig. 3c). The paternal effect was significant in both females for each morphological trait (Table 2).

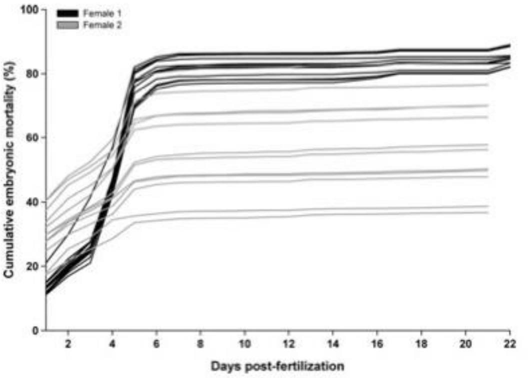

Fig. 2. Cumulative embryonic mortality (%) of Atlantic cod (*Gadus morhua*), 1–22 days post-fertilisation. Mean values displayed for Female 1 (black) and Female 2 (grey)

Cumulative larval mortality

Due to low numbers of hatched larvae, data from Female 1 were excluded from statistical analyses. For Female 2 the repeated measures ANOVA model revealed a significant first-order sampling day × male interaction ($F_{198,1018} = 1.44$, P = 0.001). Therefore the model was revised into separate one-way ANOVA models at each sampling day. A non-significant paternal effect was detected from 1 to 7 dph (Table 2), while a significant effect was detected from day 8 to 19 dph (Fig. 4; Table 2).

Discussion

The present study revealed strong paternal effects on early life history of Northwest Atlantic cod, *Gadus morhua*. Paternal influences were obvious in every trait that was investigated during this experiment, despite large differences in offspring between the two females. Female 1 showed an overall weaker offspring performance than Female 2, indicating that deviances can stem from differences in female quality.

Table 2
Summary of statistics (d.f.N = numerator degrees of freedom, d.f.D = denominator degrees of freedom, *F* = *f*-value, P = P-value) used to examine paternal effects on early life history traits of Northwest Atlantic cod, *Gadus morhua*

	Female 1				Female 2			
Dependent variable	d.f.N	d.f.D	F	P	d.f.N	d.f.D	*F*	P
Fertilization success	11	60	1.58	0.128	11	60	4.90	<0.0001
Hatching success	11	59	12.00	<0.0001	11	60	15.80	<0.0001
Cumulative embryonic mortality	11	60	≥ 1.94	≤ 0.052	11	60	≥ 2.27	≤ 0.022
Larval standard length	9	86	3.46	0.001	11	211	3.08	<0.001
Larval eye diameter	9	86	4.02	<0.001	11	211	2.35	0.01
Larval yolk area	9	86	1.41	0.198	11	211	9.77	<0.001
Cumulative larval mortality (1–7 dph)	–	–	–	–	11	60	≤ 1.33	≥ 0.230
Cumulative larval mortality (8–19 dph)	–	–	–	–	11	60	≥ 2.00	≤ 0.044

Separate analyses run for each Female.
dph, days post hatch.

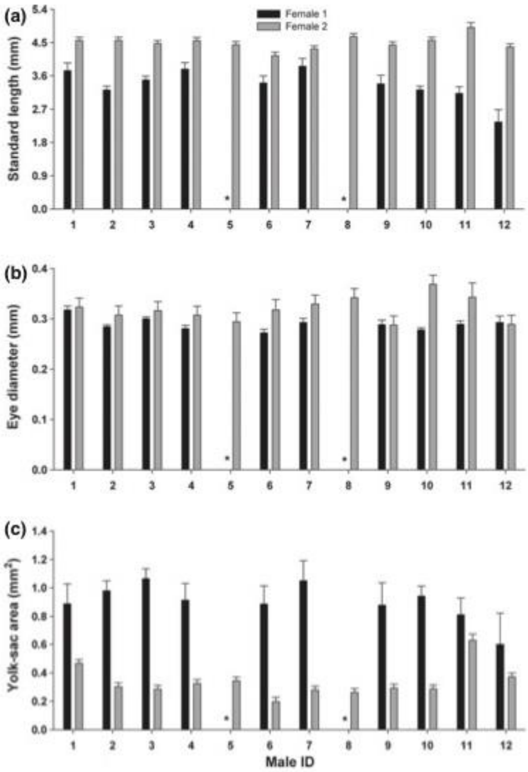

Fig. 3. Larval standard length (a), eye diameter (b), and yolk-sac area (c) of Atlantic cod (*Gadus morhua*), age 0 days post-hatch. Males (n = 12) and females (n = 2) crossed using a full-factorial breeding design. ANOVA models run separately for Female 1 (black bars) and Female 2 (grey bars) because the primary interests were to examine the potential influence of paternity on larval morphology. Error bars = least square means standard error; Asterisk = no hatched larvae

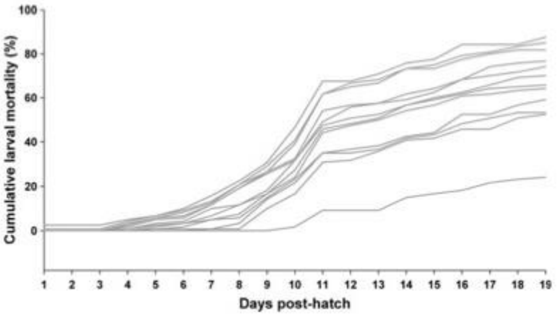

Fig. 4. Cumulative larval mortality (%) of Atlantic cod (*Gadus morhua*), 1–19 days post-hatch. Mean values shown for Female 2 (grey). Due to low numbers of hatched larvae, data from Female 1 were excluded from statistical analyses

Nevertheless, paternal contributions to larval development were still evident despite differences in female quality, showing that male effects on offspring are undeniable and can serve as important sources of information regarding breeding and rearing conditions.

Fertilization success of eggs was high in the present study in both females (71.9–90.5%). These results agree with previous findings which reported mean fertilization success in Atlantic cod between 60 and 90%, and in Baltic cod between 96.2 and 98.9% (Trippel and Morgan, 1994; Trippel et al., 2005). Paternal influences were evident for fertilization success in Female 2, which shows that paternity has an influence on the development of offspring during early life stages (Butts et al., 2009).

In our study, hatching success was variable among crosses, which has been observed in previous studies on Atlantic cod (Trippel and Morgan, 1994), Icelandic cod (Marteinsdottir and Steinarsson, 1998) and haddock (Moksness and Selvik, 1987; Probst et al., 2006). In some crosses, no larvae survived until hatch, further evidence that egg quality from Female 1 was poor. Furthermore, paternal influences were obvious in both females, which underlines the findings on Northwest Atlantic cod and Atlantic haddock where hatching success was significantly influenced by paternity (Trippel and Morgan, 1994; Probst et al., 2006).

Similar to other studies on cod (Geffen et al., 2006) and Atlantic menhaden (*Brevoortia tyrannus*) (Ferraro, 1980), high embryonic mortality rates occurred in both females during the first half of embryogenesis. This period, just after gastrulation, has been described as a vulnerable phase that often coincides with high embryonic mortality (Geffen et al., 2006). Both females revealed significant paternal influences throughout these stages, indicating that the paternal effect is not to be underestimated during early larval development.

In the present study, the eye diameter showed paternal influences as well as yolk-sac area and standard length for both females, which was also reported in haddock by Rideout et al. (2004), who found larval morphometrics to be strongly influenced by the sire. Being larger at an earlier age is an advantageous trait since larval size is positively related to swimming ability, and increased swimming ability results in greater prey encounter rates and capture events (Drost, 1987; Gallego, 1994). Larger larvae may also have a better chance to detect and escape from predators (Blaxter, 1986) and with their larger eyes have better prey detection (Blaxter, 1986; Job and Bellwood, 1996).

Cumulative larval mortality began to increase in both females at 5–7 days post-hatch, which is the time when most of the yolk available for a larva was exhausted and exogenous feeding began (Hunt von Herbing et al., 1996). Only larvae from Female 2 could be statistically analysed due to a disproportionate number of hatched larvae of Female 1. In Female 2 however, paternal influences were evident starting at day 8 post-hatch, indicating after the maternal non-genetic contribution (yolk) is exhausted, that paternal effects become evident. This finding underlines that paternal effects persist past embryogenesis. Other studies have also demonstrated paternal effects on larval and juvenile survival/traits in marine fish (Butts and Litvak, 2007a,b) Because there were equal numbers of larvae in each beaker, density-dependent mortality rates as mentioned in Sclafani et al. (2000), can be excluded.

Differential losses in our study due to the sire strongly support the significance of female choice in matings in the wild. Male characteristics of importance in female selection are commonly body size, condition and behavioural displays as well as aggression toward other males associated with courtship behaviour (Hutchings et al., 1999; Rowe and Hutchings 2004; Trippel and Neil, 2004; Pitcher et al., 2009). Our findings are based on artificial fertilization/matings. An interesting experiment would be to assess whether a dominant male, one that is frequently chosen for mating by females in a communal spawning tank (e.g. Hutchings et al., 1999; Trippel et al., 2009), leads to more viable offspring than if the females had mated with other available males. This could be performed by conducting artificial matings/crosses among fish in a spawning tank and compare the fitness of these offspring to genotyped offspring collected from 'natural' matings in the spawning tank. This type of research would shed new light on supporting or not supporting female choice and the advantages of male courtship and perceived sire fitness.

In conclusion, this research will contribute to the development of Atlantic cod aquaculture, broaden the knowledge-base concerning paternal effects on early life history stages of marine fish, and further our understanding on recruitment variability (e.g. adjusting the stock component of a stock-recruitment relationship for gamete quality). Results of this work also suggest that the mixing of sperm from different males should be avoided, as it could possibly serve to mask maternal and paternal variation.

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Chapter V

GENERAL DISCUSSION

5. GENERAL DISCUSSION

Baltic fish stocks undergo annual fluctuations in fishing intensity, depending on demand and total allowable catch (TAC) quotas. But apart from the inevitable effects that the consumption of fish is causing, environmental and climatic pressures also control the year-class strength (recruitment) and therefore the stock as a whole. An important task for ecosystem-based managers to assure sustainable fisheries in the future, is the identification of suitable environmental indicators that have great impact on the recruitment success of specific species (e.g. Rice & Rochet 2005). If these indicators can be used as an easy to measure pressure on the stock, annual evaluations of the risk and adaptations to changes need to be implemented. Evaluating indicators and potential risk in frequent time fractions is an essential step in a management context, as fishing pressure has to be adapted according to the (changing) environmental impacts. In their Integrated Ecosystem Assessment (IEA) framework, Levin et al. (2009) highlight the importance of risk analysis after identifying management goals and defining ecosystem indicators.

The results of the presented chapters are a novel approach to find suitable environmental indicators (and their respective thresholds, Chapters II, III) that can be used for the approximation of recruitment success of Baltic fish stocks, namely cod, sprat and herring (Chapters II, III), and Atlantic cod (Chapter IV). The findings are based on observations drawn from annual research surveys, a simple hands-on statistical approach, as well as extensive lab work. Indicators derived from different approaches underline scientific understanding that have been found in previous studies regarding environmental and genetic impacts on recruitment. Findings prove that approaches to filling knowledge gaps are plentiful and that outcomes from different methods can be linked to illuminate environmental correlations from different angles. Derived indicators are found to be significant in relation with the used RecRes per time period in Chapters II and III and show possible relationships of ecological connections between a fish species and its environmental factors. Even though the indicators found are restricted to an area (Eastern Baltic), the applied method can be used as a first approach to find the most prominent factors influencing fish stocks in other territories. The findings of Chapter IV indicate that despite changing environmental conditions, the intrinsic factors, such as fitness of the males and females, yolk content of the eggs, as well as mortality of sperm, could also play an important role of the annual offspring success.

As the name indicates, indicators show possible relationships between one or a group of species and its / their response to environmental factors. This correlation can then be used in environmental reporting, research and management actions (Spellerberg, 2005). In general, indicators are identified by observing and analysing the ecosystem of interest and its components and attributes in correlation with the aim generalized from the scoping process (e.g. Levin et al., 2014). Environmental factors that are directly linked to the aim (e.g. species) should be easy to measure, reproduce, comprehend and monitor, as slight variations could change the overall relationship significantly. If ecosystem attributes are not directly measurable, indicators can serve as proxies for them (Fulton et al., 2005). As knowledge and resources are usually not fully utilized, indicators should consist of ecosystem attributes that are considered to be representative of the system (Jennings, 2005). Ecological indicators (e.g., size distributions, aggregate community, energy flows) are proposed by Large et al. (2013), Link et al. (2010) and Blanchard et al. (2010) as a tool to classify ecosystem states and functions in order to understand pressure-response relationships within a system. Nevertheless, a result can only be as good as the input data itself, meaning that any mechanisms and predictions based on correlative relationships to natural variability should be handled with caution, as uncertainty due to measuring error, lack of data and false (stock size) assessments can be magnified through the analysis (Needle, 2002; Gårdmark et al., 2011).

All recruitment indicators related to environment or genetics from this study have been found before in previous studies (see above) and are therefore well understood, support physiological knowledge that has been verified, and are more or less easy to measure, particularly the abiotic factors. All of the above attributes of the recruitment indicators derived fall well into the framework conceived by Rice & Rochet (2005), as their recommendation includes, indicators that are well-studied, cost effective, easy to measure and supported by historical time series. In this context, our set of recruitment indicators for Baltic clupeid stocks can serve as an additional and strong support for decision making approaches in management contexts.

5.1 Abiotic Recruitment indicators

5.1.1 Isohaline Layer and Reproductive Volume

In Chapters II and III, the most prominent abiotic indicator that was found to correlate with the used response variable (RecRes) was the depth of the 11 psu isohaline either in the central Baltic (Chapter II, cod) or in the Bornholm Basin (Chapter III, herring and sprat). As the Baltic is a semi-enclosed system, saline and oxygenated water only enters through Kattegat on an irregular basis, leaving the Baltic inhabitants in a harsh environment where adjustment to environmental conditions is needed. The stratification of the water column generates different conditions for different species and/or life stages, as the salinity defines more or less ideal scenarios for egg survival along with other abiotic factors such as oxygen and temperature and biotic factors, e.g., abundance of prey and eggs, fitness of spawning stocks etc. (Berner et al., 1989; Lablaika et al., 1989; Kosior & Netzel, 1989; Grauman & Yula, 1989). The upper layer of the brackish Baltic contains ~ 7 – 8 psu and is separated from the more saline layer (10 – 18 psu) by a permanent isohaline ± 11 psu (Nissling et al., 2002). Depending on where in the Baltic, the isohaline is located at a depth between 50 and 240 m (Nissling et al., 2003; Plikshs et al., 1993), forcing the isohaline-dependent species to migrate vertically. In particular, the Bornholm Basin represents an important spawning ground for Baltic cod and sprat stocks (MacKenzie et al., 2000). As cod eggs require salinities slightly higher than 11 psu and adequate oxygen supply (above 2 ml/l), the isohaline and the layer below are the limiting factor for successful recruitment (Mohrholz et al., 2006). Due to increases in river discharge since the early 1980s and the lack of inflow events from the North Sea, the isohaline layer has sunk deeper, leading to a very low cod egg survival rate because the depth of the Baltic basins involve low oxygen contents that left the eggs to die (Plikshs et al., 1993). This shows how important the depth of the 11 psu isohaline is for i) cod egg survival and therefore recruitment success found in Chapter II, and ii) for sprat and herring recruitment success as sprat eggs also depend on the depth of the 11 psu isohaline layer for successful development in spring (Nissling et al., 2003) and herring depend on the essential zooplankton food sources within the 11 psu isohaline layer as juveniles and adults (Cardinale et al., 2003). Additionally, cod eggs and larvae are a nutrient rich food source for sprat and herring larvae and adults as the clupeids overlap temporally and vertically with the cod spawning season (Köster & Möllmann, 2000; Köster & Schnack, 1994; Sparholt, 1994; Aro, 1989). For herring, the isohaline layer could also represent a secondary pressure affecting recruitment since cod, as the main predator of herring in the Baltic, is highly affected by this factor, as favorable saline conditions for cod (Fig. 4a, Chapter II) connote negative years for Baltic herring recruitment (Fig. 3c, Chapter III). Looking at the findings from Chapters II and III it becomes clear, that species have a different level of resilience towards certain environmental conditions, since the threshold for the depth to the 11 psu differs significantly between cod (110 ± 1.27, Fig. 4a, Chapter II) and the clupeids (54 ± 3.00 / 58 ± 2.00, Fig. 3a & 4, Chapter III). For one, the correlation differs spatially, as the found indicator for cod was in the central Baltic and for the clupeids in the Bornholm Basin. Secondly, the depth of the different areas allows for different depth and therefore threshold values. The saline layer also correlated in other regions with clupeid' RecRes (herring = Central Baltic, sprat = Gotland Basin; Table 1 & 2, Chapter III) but were not used for further analysis as the standard deviations showed a lot of variability, indicating a high degree of uncertainty in the data. Nevertheless, with different time periods and/or other data, the thresholds of these findings could also be used within a set of prominent indicators for recruitment success of clupeids in the Baltic.

No matter the location and threshold value, one fact becomes apparent: in the 80's the isohaline layer was unfavorable for all three examined species, marking a clear natural answer to an ecosystem that fell out of balance due to lacking inflow events and heavy fishing pressure that forced the system into a new (stable) state (Möllmann et al., 2009, Österblom et al., 2010).

In Chapter I, the size of the reproductive volume (RV) of the central Baltic and the Gotland Basin showed a significant correlation with the annual recruitment success of EB cod. This is not surprising, as the RV is an environmental occurrence especially defined for cod by Plikshs at al. in 1993. Their study accumulated the knowledge on cod physiology and early life history traits and reduced the substantial condition for successful cod spawning and egg development to water masses called 'reproductive volume'. Here, the water contains ± 11 psu and 2ml/l oxygen and represents the ideal condition for cod reproduction as the eggs can float in an oxygen rich water layer. As the Baltic only occasionally gets fresh water through Kattegat from the North Sea, the amount of oxygenated water is limited in time and volume. If inflow events are sparse, the size of the RV obviously declines as the oxygenated water fades. Correlated with the salinity content mentioned above, recruitment success is low. Figure 4b (Chapter II) shows well how single years mirror the major inflow events of the Baltic, e.g., 1993 after a sixteen year stagnation period in the central Baltic, where only small inflows exchanged water marginally (Huber et al., 1994).

In Chapter IV, the hydrographical conditions were man made and therefore ideal for egg development. In Atlantic cod, the ideal condition for sperm activation are 20 - 30 psu (Litvak & Trippel, 1998), whereas in the Baltic cod it was found to be > 11 psu by Nissling & Westin (1997).

Here it becomes obvious, how differences in space generate different adaptations to the environment. These distinctions have to be known and considered when conducting any kind of ecosystem models in order to do justice to the species analyzed.

5. 2 Biotic Recruitment indicators

5.2.1 Cod Recruitment and Spawning Stock Biomass (SSB)

Cod and clupeids overlap temporally in the Baltic, because the extended spawning season of cod from March to August (Bagge et al., 1994) coincides with the feeding period of herring that return from the coastal spawning grounds into deeper water layers (Aro, 1989). Also, sprat use the same hydrographical conditions for spawning as cod. This overlap evokes a predator-prey relationship that is profitable for both families at different times: cod eggs and nearly hatched larvae serve as prey for sprat and herring (Köster & Schnack, 1994), whereas sprat and herring larvae provide food for older larvae and juveniles of cod and other forage fish species (Ross et al, 2013). Our findings conclude that a cod SSB [t] corresponds with herring recruitment success and show a threshold of 196 tons (± 16.00, Table 1, Chapter III) to be significant for herring recruitment success. For sprat, the indicator was cod recruitment (Threshold = 283 [10^3 Ind] ± 184.85, Table 2, Chapter III) that has significant influence on successful sprat recruitment. Both indicators show the food web dynamics of a relatively simple interplay of three species and need to be considered when looking at recruitment dynamics holistically.

5.2.2. Zooplankton Abundance

Sprat and herring are the main predators of calanoid copepods in the Baltic. Möllmann et al. (2004) found the species *Pseudocalanus, T. longicornis* and *Acartia sp*. to be the most dominant zooplankta in the clupeid's diet. With the data used, only *Acartia* and *Bosmina* sp. were found to correlate with the response variable of herring and sprat. In the present study, only summer measures of zooplankton abundance were used for the analysis, allowing for some bias and uncertainty as it would be more precise if other seasons would also be included in the analysis and would possibly then show correlations with clupeid's recruitment variability. Sprat, for example, adjust their feeding according to the availability in spring and summer from a *Pseudocalanus sp.* dominated diet in spring to a *T. longicornis* and *Acartia sp*. dominated diet in summer (Möllmann et al., 2004). Our results suggest that the *Acartia* abundance in summer is of importance for the herring recruitment success. The biotic indicator representing possible diets for the sprat stock was found to be the cladoceran *Bosmina*. *Pseudocalanus* did not show any correlation with the response variables in any time period.

In general, it is harder to measure abiotic pressures precisely in the field, as they are influenced by multiple (e.g., abiotic and biotic) forces and hence data is much more prone to uncertainty than abiotic factors alone.

5.2.3 Parental contributions to recruitment success of Atlantic cod

The indicators for successful recruitment in Atlantic cod in Chapter IV were found to be mostly of maternal origin, as the egg quality dictated embryonic mortality, hatching success, larval mortality as well as morphological traits. Since the maternal contribution to the fertilized egg is much greater than the paternal contribution (i.e., sperm contain virtually no extra-nuclear material), it is commonly assumed that the impact of maternal effects largely outweighs paternal effects (Thorpe & Morgan, 1978; Chambers & Leggett, 1996). The second female, however, revealed some paternal influences on the embryos since the egg size and quality remained the same within the cross. The results of this study indicate that even though paternal influences might be overshadowed by maternal factors, paternity does affect early life history traits to some extent. The comparison (T-tests, Kruskal-Wallis test) of each cross shows, that differences do exist and are clearly driven by differences among males in their genetic contribution to the developing embryo. Egg quality and size as a factor affecting embryonic growth is an obvious explanation for differences in standard length at the day of hatch. Larvae of the second trial were up to 75% larger than the offspring of the first trial, indicating that these larvae probably have a higher chance of entering the juvenile stages alive and therefore contribute to a successful recruitment. This has been stated by Chambers & Leggett (1987) and Amara & Lagardère (1995) who found that high embryonic and early larval mortality rates depend on growth, which means that faster growing larvae usually achieve the juvenile stage more rapidly and are therefore exposed to planktonic predators for a shorter time period, which again benefits the recruitment success and has been described by Cushing & Harris (1973), Anderson (1988) and Cushing (1990) as the match - mismatch and the growth – predation hypothesis. In addition, fast growing individuals are larger and, hence, potentially less vulnerable to predators as well as more mobile and therefore have a better chance to escape than slow-growing fish at the same age (bigger - is – better hypothesis, e.g., Houde, 1987; Bally & Houde, 1989). The offspring of the second female in this study would probably have a higher recruitment success due to a larger hatch size and faster growth over the first 19 days post hatch compared to the offspring of the first female that revealed a poor hatching and larval survival success.

In this chapter, mechanisms underlying recruitment are gained from two extensive lab experiments under ‘natural’ conditions, that are not influenced by other pressures found in a real-life scenario. In this way, we can understand biotic / parental contributions to recruitment success, but results are also uncertain as natural systems are obviously more complex than a beaker. Nevertheless, the study shows, that genetic parental condition is a driving factor for successful offspring that has to be considered in a decision-making process along with environmental mechanisms found to be relevant in Chapters II and III. Kraak et al., (2010) pointed out the fact that most stock assessments use SSB as a proxy for recruitment measurements, instead of actual egg production per stock, assuming a constant egg production per unit of stock size. This assumption can truly lead to false assessment values, if offspring quality and quantity depends on parental fitness and age (Wright & Trippel 2009) in addition to environmental pressures (Lambert, 2008; Marshall, 2009).

Understanding genetic recruitment dynamics becomes even more important when the overall fitness of fish stocks decline, as recently observed in the eastern and western Baltic cod stocks (ICES, 2013). Here, not only the stocks underwent a drastic change in the mean weight structure of adult cod, the stocks have also been witnessed to shift spatially (Eero et al., 2014), which automatically changes the environmental pressures that the species are dealing with. If parental fitness is to be assumed to affect number and quality of eggs significantly, which was a major result of Chapter IV, then inevitably these findings have to be considered in the set of environmental recruitment indicators derived in Chapter II as key processes underlying the future of Baltic cod stocks. Shifts within a system, whether in weight structure, prey availability or predation pressure serve as a valuable reminder for the scientific community that assumptions are only made on short temporal windows and can change within short time periods. This awareness demands continuous monitoring of derived correlations and an unbiased view on environmental interactions.

5.3 Parental condition and recruitment success

5.3.1 Condition Factor

The applied Fulton's condition factor (K) assumes isometric growth of an individual, i.e,. growth with unchanged body proportions. It is a measure that relates the actual weight of a body to an 'expected weight' which is calculated as a function of its length L. Even though isometric growth cannot be assumed in a lot of cases, many fish do show length – weight relationships with regression coefficients similar to 3. Using the exponent 3 can be considered simply as a method of transforming linear dimensions of length to the cubic dimensions equitable in the discussion of weight. The occurring problem with correlation between condition factors and length means that only populations with similar length distributions should be compared. Ricker (1975) supported the use of the Fulton's condition factor for this purpose. Looking at the condition factor of the broodstock calculated previous to the experiment, it becomes clear that high values describing the condition of an adult male do not match the actual observations. Males with 'low' condition (CF = 1) sired embryos that had relatively high survival rates whereas males with 'high' condition (CF = 2.61) sired eggs with lower hatching success (Table 1, Chapter IV). No clear suggestion about the condition factor and its effect on high or low numbers of offspring can be made here since no correlation between the sire's condition and its offspring was evident. This simply means that the fitness of progeny cannot be foreseen by looking at the father's condition factor. Nevertheless, the condition factor of female 2 was much higher than that of female 1 and produced embryos that had a higher fitness in terms of high percentage of hatch of relatively large larvae. It can be stated that drawing attention to the condition factor can be expedient in this case when only looking at the dams.

The findings of Chapter IV suggest that along with environmental factors, intrinsic attributes of both males and females also play an important role when looking at recruitment success. Even though this chapter is based on an experimental set up, its findings draw attention to new and essential aspects of a holistic approach to understanding recruitment dynamics in fish that need to be considered when attempting an overarching understanding of reality.

5.4 Response variable and threshold derivation

As recruitment success is defined as the residual variation of the SSB and recruitment interrelation, the recruitment residuals (RecRes) can be used as a good proxy to analyse relationships between recruitment success and environmental pressures. By using the RecRes, the parental effect is accounted for and the residual variation is assumed to originate from biotic and abiotic factors impacting early life history traits of the species of interest (Pauly, 1984). In Chapters II and III, the use of the RecRes in different time periods per species revealed valuable knowledge on how recruitment indicators can be derived in a simple approach and thresholds for each defined indicator can be obtained. These thresholds can then be used to identify possible positive and negative years for the stock's life cycle and can be easily implemented in management contexts. Depending on the time period used, the identified thresholds differed slightly. The 5-fold cross-validation process helped define the best possible value per indicator and species. Standard deviation of the threshold was used to define an intermediate state to give another angle to recruitment environment. The state or quality of the recruitment environment is then indicated by the direction of deviation of the observed indicator from its threshold value. Hence, positive deviations from the threshold indicate "good" and negative deviations indicate "bad" recruitment environment for EB cod.

In step 6 (Diagram 1), where the RecRes were compared to the threshold results of the longest time period tested per species, the RecRes revealed divergent results in some years (Table 2, Chapter II; Table 3, Chapter III). Here it becomes evident that the RecRes cannot explain all the variability in recruitment success, but the approach can be used to detect possible trends that can be used for further analysis. However, the example of the depth of 11 psu isohaline shows, that the stronger an indicator represents the trends, the better the RecRes can be used for the analysis of recruitment success as only three years showed < 50 % consensus with cod recruitment in Table 2, Chapter II. This, on the other hand, indicates that the method is a good canon to be used for forecast approaches, as it represents a robust technique to gain first ideas of how recruitment could change in future years.

Before concluding the main findings of the present study, an outlook on future work as well as some new ideas (Infinity Risk Assessment Loop, Fig. 5) on how to deal with derived indicators to furthermore bring (marine) management to sustainable standards are presented and discussed below.

5.5 Outlook for future work

Changes of condition within any system are natural processes and lead to new states that bring another side of the ambience to light. A shift in a given regime does not necessarily mean a hindrance to its members since it can become a favorable and stable new state that holds virtues on every corner; though in many cases a big change typically generates disadvantage for parts of the system. Studying shifts within a regime is always accompanied by questions regarding the possible advantages and disadvantages of its users as well as the stressors responsible for the change. Stressors can be of a natural (e.g., climatic) or human-induced (e.g., executed policy) kind and are therefore predictable to varying degrees. A likely continuing sad example, the global emigration of nations escaping catastrophes such as hurricanes and war that make life unbearable, shows the difference of stressors and illuminates how diverse the topic is. Looking at the examples above, it becomes clear that changes within a system can occur abruptly (meteorological disturbance) or over a time span of unknown length (ongoing war) and over large spatial scales. Furthermore, most regime shifts are not only triggered by one set event but a combination of determinants that can be internal as well as external to the system (e.g. Ellner & Turchin, 1995). Once the type of the shift and its stressors have been pinpointed, the question arises, if an early warning would have led to precaution that could have averted the consequences of the (inevitable) disaster.

In order to expedite ecosystem-based management to an even more practical approach to understanding and supporting natural systems and changes therein, a holistic management cycle suggested by Levin et al. (2010) needs to be implemented. The present study focuses on simple regression methods on a single-species basis, as we wanted to investigate the difficulties that lie within the least time-consuming method as a pioneer for the scientific community that works within the Baltic ecosystem. The following section portrays the importance of risk assessment within the management loop that should be conducted in any way. Derived recruitment indicators found in this study can easily be applied in a risk assessment approach, as they fall into criteria compiled by Hobday et al. (2011), as described below.

5.5.1 Risk analysis

Many different approaches to and definitions of risk assessment (Burgman, 2005; Pitcher & Preikshot, 2001) are in use and need to be distinguished as it is not always necessary and useful to perform a complete risk assessment that includes all recommended stages of a risk management cycle or framework, as it is rather complex and time consuming and therefore inefficient in some contexts.

Risk assessment analysis in marine management harbors a variety of goals and definitions that need to be clearly communicated and decided upon with the stakeholders and group of interest. The range of approaches could include economic and/or social aspects, it can aim for defining objects in fishery management that are not achieved (Hobday et al., 2011). Depending on data availability, qualitative risk assessment is employable, especially if data and knowledge of ecological interactions are sparse (Fletcher, 2005; Astles et al., 2006; Walker, 2005; Campbell & Gallagher, 2007). If adequate data is available, the use of quantitative and semi-quantitative approaches is advised (Stobutzki et al., 2002; Zhou & Griffiths, 2008).

No matter the question behind the risk assessment, the procedure should include most of the following attributes in order to obtain a reliable approach to the identified risk (Hobday et al., 2011):

a) Extensive (consider all possible stressors)
b) Applicable to many subjects (apply to not only one species/fisheries)
c) Reproducible (Data and methods should be comprehensible)
d) Easy to understand (for stakeholders, fishermen, scientists, …)
e) Effective in cost and time (set realistic limits of resources)
f) Scientifically plausible (justify approach and results)
g) Implementable in a management context (identify suitable management actions)
h) Evaluate actions (always consider uncertainty in analysis)

Looking at all the mentioned above criteria it becomes clear, that some trade-offs have to be made in order to put a risk assessment analysis into practice. #

5.5.2 Expert opinion

The Level 1 analysis within a risk assessment is based on expert opinion, which is defined as the knowledge that is developed through technical practices, training or experience of a qualified person (Booker & McNamara, 2004). In ecology and management contexts, expert opinions are used where empirical data are unavailable or scarce or the timeframe to a decision is limited (Sutherland, 2006; Kuhnert et al., 2010). In contrast to an extensive quantitative risk assessment based only on analysis and data, the input of expert knowledge provides a wide range of possibilities, relationships and links between drivers and processes that can give valuable information on how the system works and where to start solving a problem, estimating a parameter or analyzing the data (Sutherland et al., 2008; Martin et al., 2005). Using expert knowledge to give direction to a certain set of indicators, analysis or management action not only gives an overview of the knowledge / opinion in place, and therefore a helpful tool on the road to understanding a changing system, but could be used, in the case of the derived indicators from this study, for example, in a questionnaire to verify which indicator is considered most important for Baltic species in order to invest time and money more efficiently.

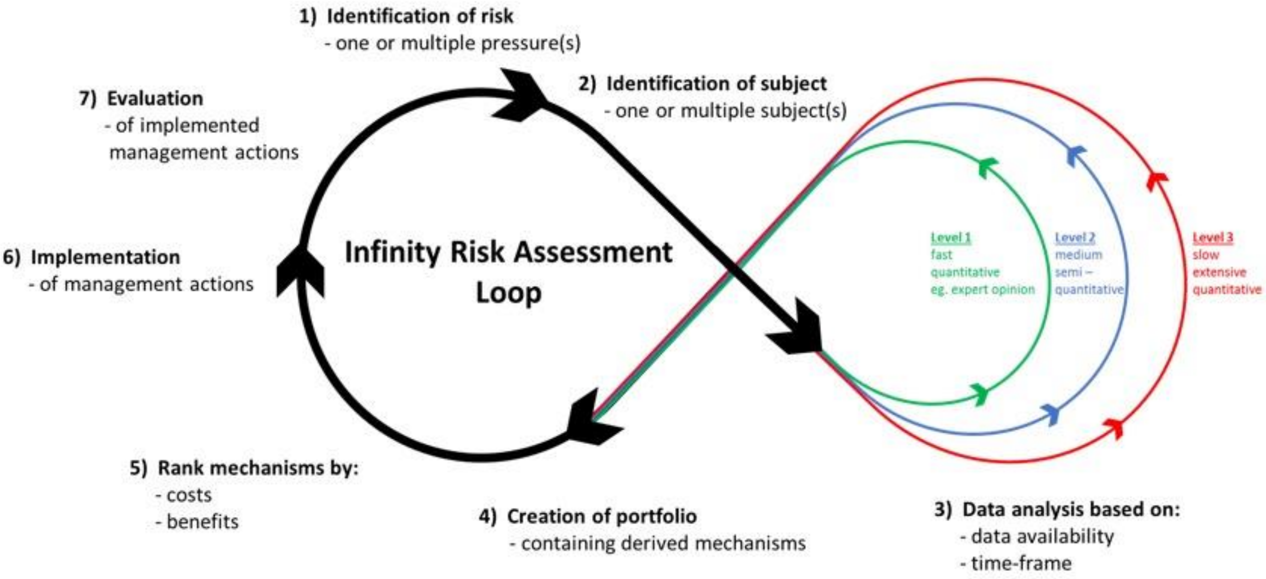

Figure 1: Infinity Risk Assessment Loop. Describing 7 steps of how to deal with (environmental) pressures and their respective risk before implementing findings into management actions. Step 1: Identification of risk, Step 2: Identification of Subject, Step 3: Data analysis on different levels ranging from fast (Level 1) to time consuming (Level 3). Step 4: Creation of portfolio containing derived mechanisms, Step 5: Rank mechanisms, Step 6: Implementation of management actions, Step 7: Evaluate / Monitor implemented actions.

5.5.3 7 Step Risk Analysis – Infinity Risk Assessment Loop

After identifying a set of suitable candidate indicators relevant for the subject of interest (e.g. Levin et al., 2014), the potential risk resulting from human or natural pressures on these indicators needs to be evaluated in the first step. There can be single or multiple pressures / stressors on a subject. Also, the type of pressures can be very diverse and are well summarized in e.g. Halpern et al. (2009). If we use the depth of the 11 psu isohaline in the Baltic as an example, one (climatic) risk on this indicator could be the lack of inflow events from the North Sea into the Baltic, as these events bring fresh saline and oxygenated waters into the boundaries of the Baltic (HELCOM 1996). Step 2: after identifying the type and amount of pressures, the same procedure has to be done for the identification of the possible subject(s): which species / habitat / area? Is it one / many? Is it a target / by-catch / threatened / endangered / protected species? In any case, the base information for further analysis is gathered and defined, in which class (1-3) of the base information is it sorted: class 1: single pressure on single subject; class 2: single pressure on multiple subjects; class 3: multiple pressures on multiple subjects (for more information see Holsman et al., 2016). Using our main indicator, we can conclude from our findings that the isohaline layer of 11 psu is relevant in various areas / basins of the Baltic (Gotland Basin = cod & sprat, Bornholm Basin = herring & sprat), in three species at the least (cod, herring, sprat), that are partly declining in stock size and can therefore be considered as threatened. Once the classes are determined, the analysis based on the time and data situation can be carried out (step 3). Questions asked here are: how much time do we have? What kind of data do we have / need for the desired outcome? How extensive do we want the analysis / result to be? The decision results in different levels (1-3) of analysis, in which level 1 represents a method for fast screenings of the situation and gap analysis in a management context, if information is quickly needed. The analysis is qualitative and often includes expert opinion or the like. A semi-quantitative approach is the level 2 method, where a mix of expert opinion and data analysis state interventions and special links within the subjects / system. Last but not least, a level 3 analysis is the choice whether sufficient data and time is available in order to execute an extensive, quantitative analysis that can estimate cumulative effects of the subject and system as well as reference points and thresholds of the management context. We performed a level 3 analysis using (simple) regression models in all three chapters of this study to define biotic and abiotic indicators relevant to recruitment.

After conducting an analysis of choice, a portfolio needs to be created (step 4) which summarizes all possible mechanisms derived as a result of step 3. Before using these mechanisms as management actions in step 6, a careful rank of usefulness and calculation of costs and benefits of actions needs to be conducted (step 5), as not every obvious management action is affordable in the long run or of any use for the original question asked. The evaluation of the identified and implemented management actions in step 7 closes the cycle as it not only reappraises the past, in this step the link to the new as-is state is given and new pressures and situations are relevant (Fig. 1). Our example indicator is cost-efficient and relatively easy to measure and therefore serves as a good example to be used as a key pressure for Baltic species for assessing possible recruitment variability and derived from that year class strengths of spawning stock biomass. This indicator could be used to adjust fishing pressure annually according to the respective threshold of 11 psu saline layer depth.

5.6 Conclusions

The results of the present study show how trends in recruitment success can be detected simply. These trends can then be used in other contexts, such as ecosystem-based-fisheries-management plans, assessments of stock relationships or in the calculation process of the total allowable catch (TAC) quota. In the Baltic, the most vulnerable indicator being associated with recruitment success of cod, sprat and herring turned out to be the depth of the 11 psu isolhaline layer, as it defines the hydrographical setting for successful egg development of cod and sprat eggs and lush feeding grounds for larvae and juveniles of all three species investigated (see Chapters II and III). Using RecRes as the response variable to recruitment turned out to be a robust measure for the detection of recruitment variability in Chapters II and III. However, despite the environmental factors that affect successful offspring, physiological traits, such as egg and larval size, as well as the fitness and condition of the SSB, all play an important role in prosperous recruitment per year, as the results of Chapter IV reveal. Following this thought, it becomes clear that not only the quantity but also the quality of the spawners has to be considered when taking any kind of action towards a holistic ecosystem-based management plan, as the indicators for recruitment are divers. Deriving a set of indicators that approximately explain recruitment variability of a stock requires frequent measuring and monitoring of all pressures that are believed to drive recruitment. But besides extensive data collection resulting in environmental long-time trends, a pool of various methods for deriving indicators has to be (and has been) established for multiple method approaches. Not to mention an unprejudiced view of sometimes inexplicable observations by scientists to derive results and possible explanations that are driven by the environment rather than by human interests. As the results from this study shows, extrinsic and intrinsic pressures are driving mechanisms of recruitment variability, that can be used to enforce management actions (e.g. setting TACs), if biotic data, such as weight- / length- at age, and abiotic environmental pressures are monitored and evaluated conscientiously and if statistical methods are constantly questioned and developed further. This study discusses the need of multiple methods to find suitable correlations between recruitment and environment as well as the difficulties that lie within concluding mechanisms from tightly linked correlations, such as recruitment and spawning stock biomass. However, results of Chapters II and III show that the residuals of the spawning stock biomass and recruitment relationship (RecRes) coupled with biologically well-founded knowledge of life cycle and feeding behaviors, can serve as a solid proxy for trends in recruitment.

Nevertheless, if recruitment is below a certain level, e.g., EB cod at approx. 150.000 individuals (Chapter II), or if egg / female quality is too poor (Chapter IV), it doesn't really matter what the environmental factors are, as recruitment will remain low for a few years (Fig. 1, Chapter II) and can only recover slowly from its critical state. For ecosystem-based-(fisheries)-management, this brings another task to the surface, as it is of great importance to not allow the stock to fall beneath the critical threshold that is unique to each species and its relative indicator.

The presented work is a step towards understanding an always changing system as a whole. Most ecosystem modelling and analysis cannot incorporate all aspects of relationships, impacts and dependencies by which a system is defined. Aside from the infinite biological and physical interactions within a dynamic system, the viewpoint of the observer is a critical aspect of the outcome and intention of the research conducted, as "reality" is always defined by the observer (Lau, 2005). Nevertheless, in order to understand a system scientifically and subjectively, further work needs to be done in regard to identifying key indicators per species so the observations made can be translated into a well-understood, holistic approach towards a sustainable management action.

5.7 References

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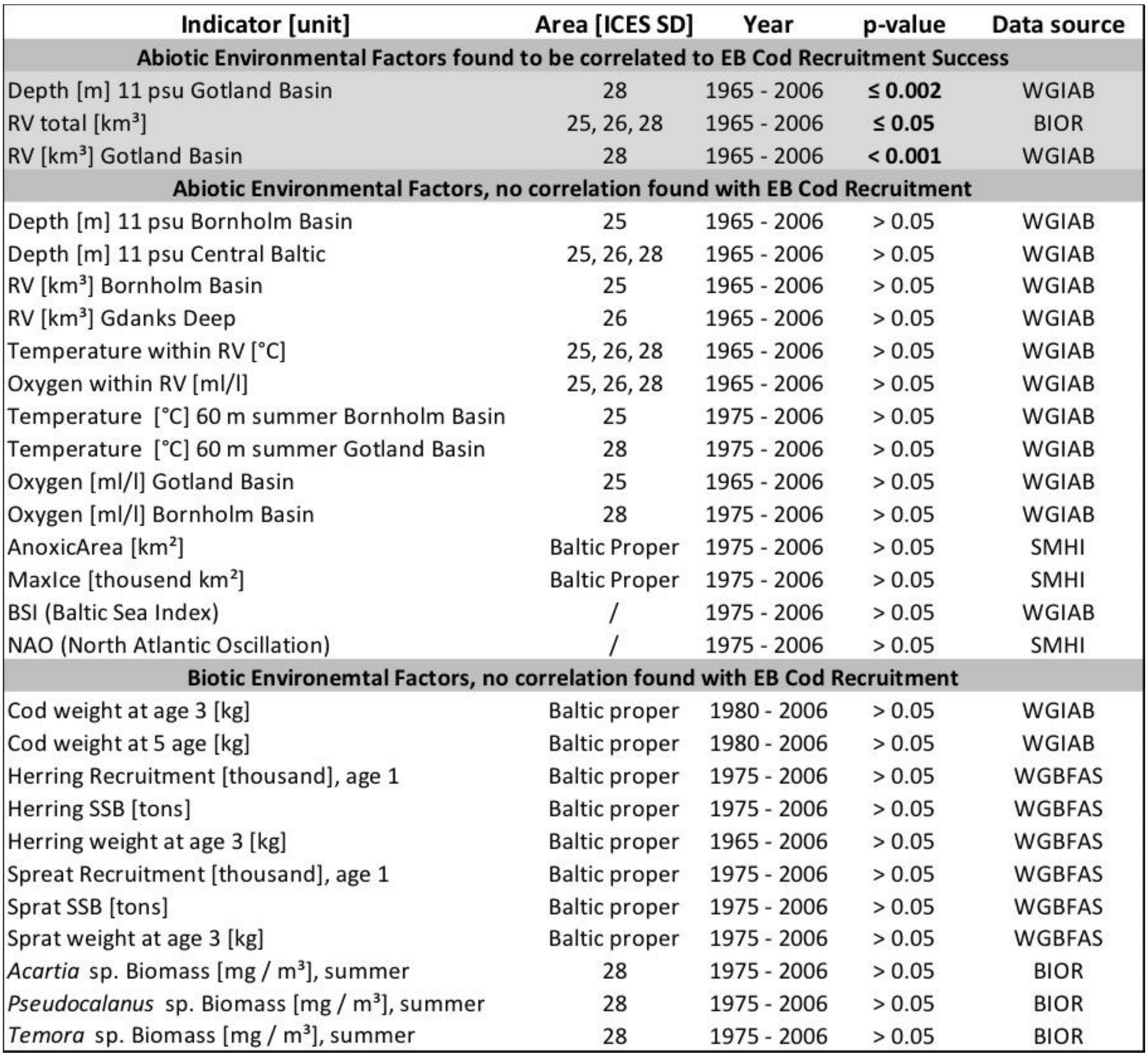
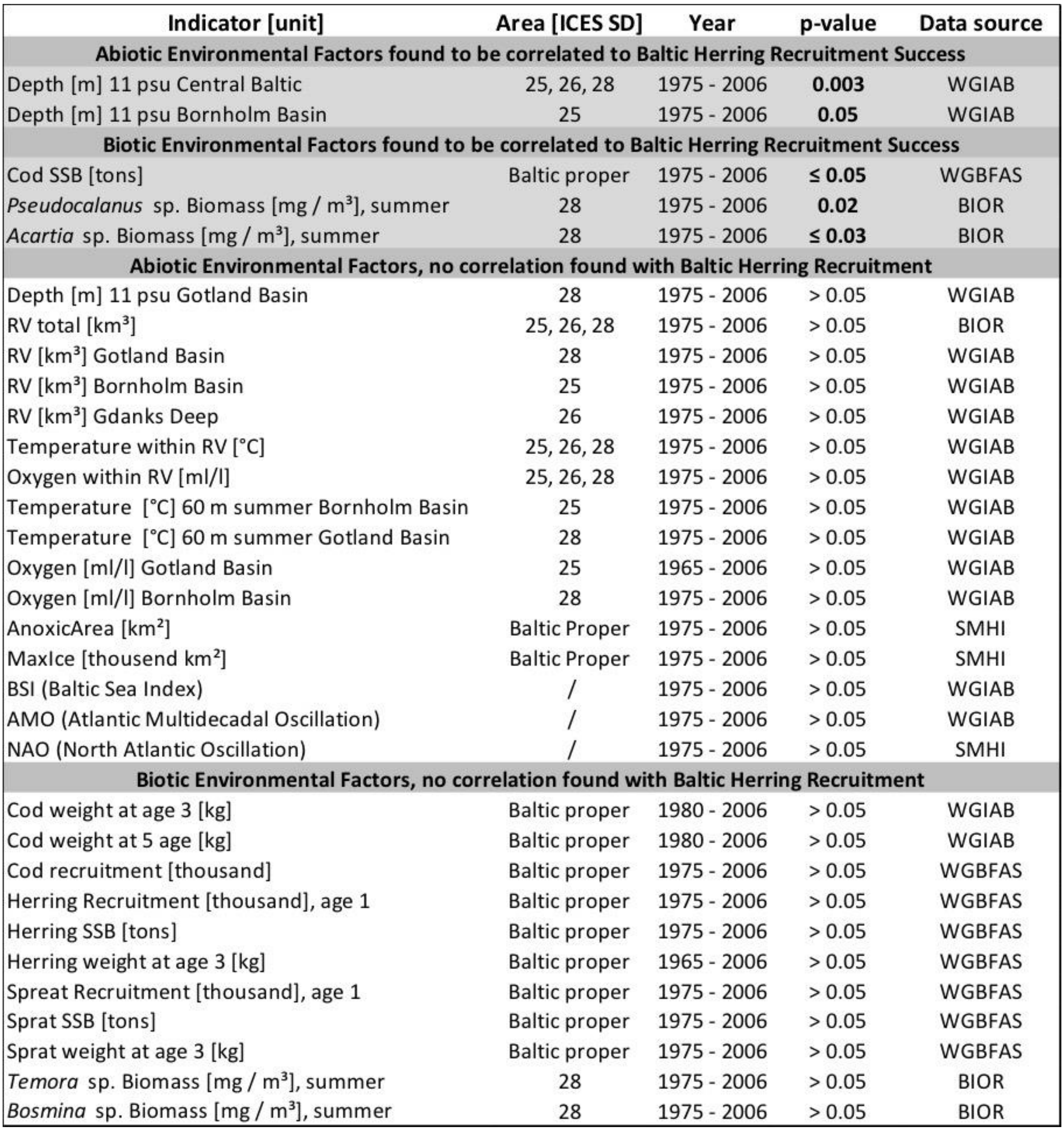
6. Appendix

Table A1: Full set of environmental variables tested as indicators for EB cod (*Gadus morhua L.*) recruitment success, per area (ICES subdivisions) and year in Chapter II. P-values indicate correlation with recruitment success. P-values marked as > 0.05 indicate no correlation between respective indicator and cod recruitment success. List of abbreviations for data source see below.



Indicator [unit]	Area [ICES SD]	Year	p-value	Data source
Abiotic Environmental Factors found to be correlated to EB Cod Recruitment Success				
Depth [m] 11 psu Gotland Basin	28	1965 - 2006	**≤ 0.002**	WGIAB
RV total [km³]	25, 26, 28	1965 - 2006	**≤ 0.05**	BIOR
RV [km³] Gotland Basin	28	1965 - 2006	**< 0.001**	WGIAB
Abiotic Environmental Factors, no correlation found with EB Cod Recruitment				
Depth [m] 11 psu Bornholm Basin	25	1965 - 2006	> 0.05	WGIAB
Depth [m] 11 psu Central Baltic	25, 26, 28	1965 - 2006	> 0.05	WGIAB
RV [km³] Bornholm Basin	25	1965 - 2006	> 0.05	WGIAB
RV [km³] Gdanks Deep	26	1965 - 2006	> 0.05	WGIAB
Temperature within RV [°C]	25, 26, 28	1965 - 2006	> 0.05	WGIAB
Oxygen within RV [ml/l]	25, 26, 28	1965 - 2006	> 0.05	WGIAB
Temperature [°C] 60 m summer Bornholm Basin	25	1975 - 2006	> 0.05	WGIAB
Temperature [°C] 60 m summer Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Gotland Basin	25	1965 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Bornholm Basin	28	1975 - 2006	> 0.05	WGIAB
AnoxicArea [km²]	Baltic Proper	1975 - 2006	> 0.05	SMHI
MaxIce [thousend km²]	Baltic Proper	1975 - 2006	> 0.05	SMHI
BSI (Baltic Sea Index)	/	1975 - 2006	> 0.05	WGIAB
NAO (North Atlantic Oscillation)	/	1975 - 2006	> 0.05	SMHI
Biotic Environemtal Factors, no correlation found with EB Cod Recruitment				
Cod weight at age 3 [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Cod weight at 5 age [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Herring Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring weight at age 3 [kg]	Baltic proper	1965 - 2006	> 0.05	WGBFAS
Spreat Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat weight at age 3 [kg]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Acartia sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.05	BIOR
Pseudocalanus sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.05	BIOR
Temora sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.05	BIOR

Table A2: Full set of environmental variables tested as indicators for Baltic herring (*Clupea harengus L.*) recruitment success, per area (ICES subdivisions) and year in Chapter III. P-values indicate correlation with recruitment success. P-values marked as > 0.05 indicate no correlation between respective indicator and herring recruitment success. List of abbreviations for data source see below.



Indicator [unit]	Area [ICES SD]	Year	p-value	Data source
Abiotic Environmental Factors found to be correlated to Baltic Herring Recruitment Success				
Depth [m] 11 psu Central Baltic	25, 26, 28	1975 - 2006	**0.003**	WGIAB
Depth [m] 11 psu Bornholm Basin	25	1975 - 2006	**0.05**	WGIAB
Biotic Environmental Factors found to be correlated to Baltic Herring Recruitment Success				
Cod SSB [tons]	Baltic proper	1975 - 2006	**≤ 0.05**	WGBFAS
Pseudocalanus sp. Biomass [mg / m^3], summer	28	1975 - 2006	**0.02**	BIOR
Acartia sp. Biomass [mg / m^3], summer	28	1975 - 2006	**≤ 0.03**	BIOR
Abiotic Environmental Factors, no correlation found with Baltic Herring Recruitment				
Depth [m] 11 psu Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
RV total [km^3]	25, 26, 28	1975 - 2006	> 0.05	BIOR
RV [km^3] Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
RV [km^3] Bornholm Basin	25	1975 - 2006	> 0.05	WGIAB
RV [km^3] Gdanks Deep	26	1975 - 2006	> 0.05	WGIAB
Temperature within RV [°C]	25, 26, 28	1975 - 2006	> 0.05	WGIAB
Oxygen within RV [ml/l]	25, 26, 28	1975 - 2006	> 0.05	WGIAB
Temperature [°C] 60 m summer Bornholm Basin	25	1975 - 2006	> 0.05	WGIAB
Temperature [°C] 60 m summer Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Gotland Basin	25	1965 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Bornholm Basin	28	1975 - 2006	> 0.05	WGIAB
AnoxicArea [km^2]	Baltic Proper	1975 - 2006	> 0.05	SMHI
MaxIce [thousend km^2]	Baltic Proper	1975 - 2006	> 0.05	SMHI
BSI (Baltic Sea Index)	/	1975 - 2006	> 0.05	WGIAB
AMO (Atlantic Multidecadal Oscillation)	/	1975 - 2006	> 0.05	WGIAB
NAO (North Atlantic Oscillation)	/	1975 - 2006	> 0.05	SMHI
Biotic Environmental Factors, no correlation found with Baltic Herring Recruitment				
Cod weight at age 3 [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Cod weight at 5 age [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Cod recruitment [thousand]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring weight at age 3 [kg]	Baltic proper	1965 - 2006	> 0.05	WGBFAS
Spreat Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat weight at age 3 [kg]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Temora sp. Biomass [mg / m^3], summer	28	1975 - 2006	> 0.05	BIOR
Bosmina sp. Biomass [mg / m^3], summer	28	1975 - 2006	> 0.05	BIOR

Table A3: Full set of environmental variables tested as indicators for Baltic sprat (*Sprattus sprattus* L.) recruitment success, per area (ICES subdivisions) and year in Chapter III. P-values indicate correlation with recruitment success. P-values marked as > 0.05 indicate no correlation between respective indicator and sprat recruitment success. List of abbreviations for data source see below.

Indicator [unit]	Area [ICES SD]	Year	p-value	Data source
Abiotic Environmental Factors found to be correlated to Baltic Sprat Recruitment Success				
Depth [m] 11 psu Gotland Basin	28	1975 - 2006	**0.04**	WGIAB
Depth [m] 11 psu Bornholm Basin	25	1975 - 2006	**0.001**	WGIAB
Temperature [°C] 60 m summer Bornholm Basin	25	1975 - 2006	**≤ 0.01**	WGIAB
Biotic Environmental Factors found to be correlated to Baltic Sprat Recruitment Success				
Cod recruitment [thousand]	Baltic proper	1975 - 2006	**0.02**	WGBFAS
Bosmina sp. Biomass [mg / m³], summer	28	1975 - 2006	**0.01**	BIOR
Abiotic Environmental Factors, no correlation found with Baltic Sprat Recruitment				
Depth [m] 11 psu Central Baltic	25, 26, 28	1975 - 2006	> 0.05	WGIAB
RV total [km³]	25, 26, 28	1975 - 2006	> 0.05	BIOR
RV [km³] Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
RV [km³] Bornholm Basin	25	1975 - 2006	> 0.05	WGIAB
RV [km³] Gdanks Deep	26	1975 - 2006	> 0.05	WGIAB
Temperature within RV [°C]	25, 26, 28	1975 - 2006	> 0.05	WGIAB
Oxygen within RV [ml/l]	25, 26, 28	1975 - 2006	> 0.05	WGIAB
Temperature [°C] 60 m summer Gotland Basin	28	1975 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Gotland Basin	25	1965 - 2006	> 0.05	WGIAB
Oxygen [ml/l] Bornholm Basin	28	1975 - 2006	> 0.05	WGIAB
AnoxicArea [km²]	Baltic Proper	1975 - 2006	> 0.05	SMHI
MaxIce [thousend km²]	Baltic Proper	1975 - 2006	> 0.05	SMHI
BSI (Baltic Sea Index)	/	1975 - 2006	> 0.05	WGIAB
AMO (Atlantic Multidecadal Oscillation)	/	1975 - 2006	> 0.05	WGIAB
NAO (North Atlantic Oscillation)	/	1975 - 2006	> 0.05	SMHI
Biotic Environmental Factors, no correlation found with Baltic Sprat Recruitment				
Cod weight at age 3 [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Cod weight at 5 age [kg]	Baltic proper	1980 - 2006	> 0.05	WGIAB
Cod SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Herring weight at age 3 [kg]	Baltic proper	1965 - 2006	> 0.05	WGBFAS
Spreat Recruitment [thousand], age 1	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat SSB [tons]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Sprat weight at age 3 [kg]	Baltic proper	1975 - 2006	> 0.05	WGBFAS
Acartia sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.05	BIOR
Temora sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.05	BIOR
Pseudocalanus sp. Biomass [mg / m³], summer	28	1975 - 2006	> 0.06	BIOR

Abbreviations for Data Sources:

BIOR	Institute of Food Safety, Animal Health and Environment
SMHI	Swedish Meteorological and Hydrological Institute
WGBFAS	Working Group on Baltic Fisheries Assessment (ICES)
WGIAB	Working Group on Integrated Assessments of the Baltic Sea (ICES)

We would like to thank all institutions for providing data for us.

Outline of Publications

The following overview outlines the three manuscripts included in the thesis, as well as the contributions from co-authors. The studies resulting in Chapter II and II was funded by MYFISH (Maximising yield of fisheries while balancing ecosystem, economic and social Concerns Call (part) identifier: FP7-KBBE-2011-5) , the study resulting in Chapter IV was funded by the EU-COST Activity FRESH (Fish Reproduction and Fisheries) and the DAAD (Deutsche Akademischer Austauschdienst). The research was supported in part by Genome Canada, Genome Atlantic, and the Atlantic Canada Opportunities Agency through the Atlantic Cod Genomics and Broodstock Development Project.

Manuscript 1 (Chapter II)

Anticipating “good” or “bad” prospects for offspring of commercially important fish populations – objectively identifying indicators and thresholds for Eastern Baltic cod recruitment environment - M-M. MacPherson, Christian Möllmann, Rabea Diekmann, Saskia Otto, Anna Gårdmark: all authors designed the statistical modell, data was provided by ICES, M-M. MacPherson conducted the data analysis with support of S. Otto, A. Gårdmark and R. Diekmann. M-M. MacPherson wrote the text under close supervision of C. Möllmann and A. Gårdmark, who critically reviewed the manuscript and provided valuable comments.

Manuscript 2 (Chapter III)

Identifying recruitment indicators and thresholds for Baltic herring (Clupea harengus L.) and sprat (Sprattus sprattus L.) by using a single-species approach developed for their top predator: Eastern Baltic Cod (Gadus morhua L.) - M-M. MacPherson, Christian Möllmann, Saskia Otto, Anna Gårdmark: M-M. MacPherson designed and conducted the data analysis on the base of Chapter I, data was provided by ICES. M-M. MacPherson wrote the text under close supervision of C. Möllmann and A. Gårdmark, who critically reviewed the manuscript and provided valuable comments.

Manuscript 3 (Chapter IV)

Parental contributions to early life history traits of Northwest Atlantic cod, Gadus morhua – Journal of Applied Ichthyology 29 (2013), 623–629, Muriel-Marie Kroll, Myron A. Peck, Ian A.E. Butts, Edward A. Trippel: M-M. MacPherson and E. A. Trippel designed the sampling protocol and the experimental set-up. M-M. MacPherson conducted the experiment under supervision of E. A. Trippel. M-M. MacPherson conducted the data analysis under close supervision of I. E. A. Butts. M-M. MacPherson wrote the text under supervision of M. A. Peck, who critically reviewed the manuscript and provided valuable comments.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift **„Ecosystem Assessment: Developing Environmental and Intrinsic Recruitment Indicators for Cod (*Gadus morhua L.*), Herring (*Clupea harengus L.*) and Sprat (*Sprattus sprattus L.*) in the Baltic and beyond"** selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den 17. März 2020

Muriel-Marie MacPherson

MacPherson
LANGUAGE INSTITUTE

Certification of Written English Quality

I hereby confirm that the thesis by Muriel-Marie MacPherson entitled "Ecosystem Assessment: Developing Environmental and Intrinsic Recruitment Indicators for Cod (*Gadus morhua* L.), Herring (*Clupea harengus* L.) and Sprat (*Sprattus sprattus* L.) in the Baltic and beyond" has been prepared according to excellent written English language standards.

Sincerely,

____
Keith MacPherson
Founder
MacPherson Language Institute