Evaluating spatial processes and management strategies under changing anthropogenic influences on the ecosystem of the southern part of the North Sea

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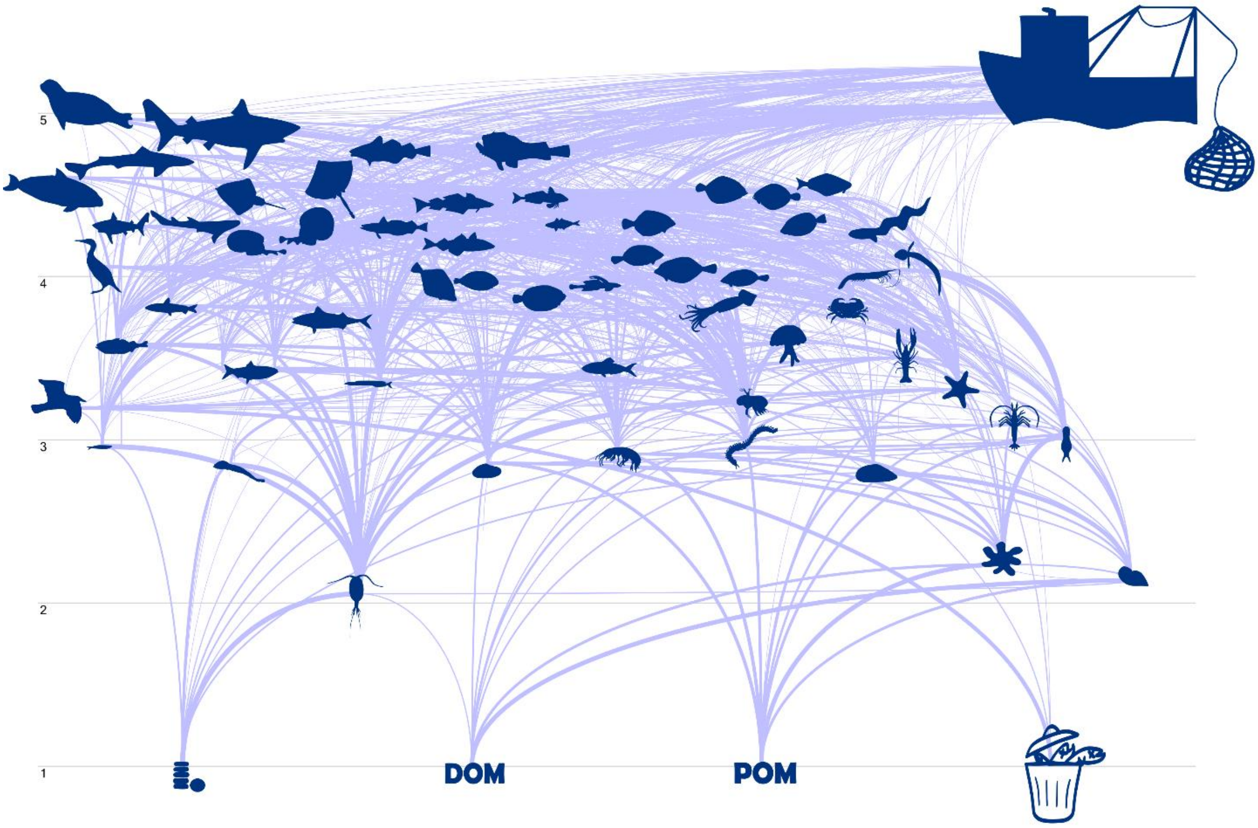

The ecosystem of the southern part of the North Sea

Preface

The work for this PhD study comprises two peer-reviewed publications as well as two publications under preparation. It was conducted at the Thünen Institute of Sea Fisheries from October 2016 to November 2021. It benefited from the CERES (Climate change and European Aquatic RESources) project, the PROBYFISH (Protecting bycaught species in mixed fisheries) project as well as the BioWeb project.

A focus of this cumulative thesis was placed on the evaluation of spatial management strategies in the southern part of the North Sea when exposed to varying anthropogenic pressures. For this, a set of modelling tools was employed, from single-species distribution models to a spatially resolved ecosystem model. The concept of the study was developed by myself together with my supervisors Prof. Dr. Möllmann and Dr. Alexander Kempf. In the following section, the contributions of each author of the publications is described.

Publication 1.

Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change

Núñez-Riboni, I., Taylor, M., Kempf, A., Püts, M. and Mathis, M.

The study was designed by Dr. Núñez-Riboni with the input of the other authors. I supported Dr. Núñez-Riboni with the construction of parts of the model and programming parts of the code. Furthermore, I examined the data for completeness and we discussed the results. The manuscript was primarily written by Dr. Núñez-Riboni with contributions of all authors. My main contribution was the bibliographical research and writing of the section about the biological effects of climate change on cod and its biology. This paper was published in ICES Journal of Marine Science, Volume 76, Issue 7, December 2019, Pages 2389–2403.

Publication 2.

Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea

Püts, M., Taylor, M., Núñez-Riboni, I., Steenbeek, J., Stäbler, M., Möllmann, M., Kempf, A.

The concept of this study was designed by myself with the support of Dr. Kempf and Dr. Taylor. All single species distribution models were created by myself with the advice from Dr. Kempf, Dr. Taylor and Dr. Núñez-Riboni. I created the spatial model Ecospace for the southern North Sea with support from J. Steenbeek by implementing the spatial-temporal framework. Advice on the underlying Ecopath and Ecosim model were given by Dr. Stäbler and Dr. Kempf. The skill assessment and results compilation was executed by myself with consultation of Dr. Kempf and Dr. Taylor. I wrote the manuscript and all authors contributed. This study was published in Ecological Modelling, Volume 431, 1 September 2020, 109189.

Publication 3.

Trade-off between fisheries, offshore wind farms and marine protected areas in the southern North Sea – winners, losers and effective spatial management

Püts, M., Taylor, M., Möllmann, M., Kempf, A.

This study was conceptualized by myself, advised by Dr. Kempf and Dr. Taylor. The implementation of trait based data and the extension of Ecospace with Marine Protected Areas and Offshore Wind Farms was executed by myself. I discussed the creation and implementation of affinities towards artificial hard substrate with Dr. Taylor and Dr. Kempf. Closure scenarios for trade-off analysis were constructed by myself with the advice of Prof. Dr. Möllmann as well as the other authors. Statistical results analysis was conducted by me. Additionally, I wrote the manuscript with the contribution of all authors. This manuscript is in preparation for publication.

Publication 4.

An ecosystem facing climate change: shifts in spatial patterns of ecosystem components in the southern part of the North Sea

Püts, M., Taylor, M., Kühn, B., Mathis, M., Möllmann, M., Kempf, A.

I created the concept of this study together with Dr. Kempf and Dr. Taylor, as well as the advice of Prof. Dr. Möllmann. The temperature data used for the projection of single species distribution models onto the two IPCC scenarios were contributed by Dr. Mathis and processed by B. Kühn. The Ecospace model was further developed from previous studies by myself. Subsequently, I analyzed the modelling results, considering the input of Dr. Kempf, Dr. Taylor and Prof. Dr. Möllmann. Furthermore, the manuscript was prepared by myself with the support and input of all authors. By the submission of this thesis, the manuscript is under preparation for publication.

Miriam Püts

Miriam Püts
(Doctoral candidate)

Prof. Dr. Möllmann
(First supervisor)

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Abbreviations

Abbreviation	*Definition*
AHOI	Adjusted Hydrography Optimal Interpolation
AIC	Akaike information criterion
AMO	Atlantic Multidecadal Oscillation
AMOC	Atlantic Meridional Overturning Circulation
AUC	Area under the response curve
BTS	Beam Trawl Survey
°C	degree Celsius
CFP	Common Fisheries Policy
CO_2	Carbon dioxide
CPUE	Catch per unit effort
CV	Cross-validation
DATRAS	Database of Trawl Surveys
EAFM	Ecosystem Approach to Fisheries Management
EBFM	Ecosystem-based fisheries management
EBM	Ecosystem-based management
EEZ	Exclusive Economic Zone
EMODnet	European Marine Observation and Data Network
Esri ASCII	Esri American Standard Code for Information Interchange map
EUNIS	European Nature Information System
EwE	Ecopath with Ecosim
FG	Functional group
GAM	Generalized additive model
GCM	Global climate model
GEBCO	General Bathymetric Chart of the Oceans
HFCM	Habitat Foraging Capacity Model
IBTS	International Bottom Trawl Survey
ICES	International Council for the Exploration of the Sea
INLA	Integrated nested laplace approximation
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature’s Red List of Threatened Species
LC	Length class
MEF	Model efficiency
MODIS	Moderate Resolution Imaging Spectroradiometer
MPA	Marine Protected Areas
MPI-ESM	Max Planck Institute Earth System Model
MPIOM	Max Planck Institute Ocean Model
MSFD	Marine Strategy Framework Directive
NAO	North Atlantic Oscillation
OBIS	Ocean Biodiversity Information System
OSPAR	Oslo-Paris convention
OWF	Offshore Wind Farm
PA	Presence/absence
PEAR	Pearson correlation
Q1	Quarter 1
Q3	Quarter 3

RCP	Representative Concentration Pathway
RMSE	Root mean squared error
SDG	Sustainable Development Goals
SDM	Species distribution model
SS	Sum of squares
SSFM	Single Species Fisheries Management
STECF	Scientific, Technical and Economic Committee for Fisheries
TL	Trophic level

Thesis Summary

The ecosystem in the southern part of the North Sea, like many other marine ecosystems around the world, is threatened by diverse anthropogenic and environmental pressures. It is being utilized heavily by the fishing industry and impacted by installations of renewable energy systems, shipping and aquaculture. Simultaneously, environmental drivers like climate change are adding stress to the ecosystem. All of these drivers can potentially change the structure of the ecosystem, especially by inducing shifts in species distributions. Spatial management of marine ecosystems aims to assess and address the individual and cumulative impacts of these pressures on the ecosystem, while evaluating trade-offs between conservation goals and economically important fishing procedures.

In order to scientifically support management decisions and inform stakeholders on the effects of spatial ecosystem management, a set of statistical tools can be applied. This statistical toolbox is filled with various approaches from species distribution models to complex end-to-end food web models that account for anthropogenic pressures and environmental influences. Combining different modelling approaches can foster the strength of each method, which will likely be necessary to evaluate the effect of spatial management measures on the ecosystem in its entirety. This PhD thesis aimed to demonstrate the advantages and disadvantages of two approaches: species distribution models and a spatially resolved ecosystem model. Furthermore, it assessed the benefits of utilizing the strength of both modelling techniques when investigating various spatial management issues. These issues encompass (i) the spatial distribution of fishing in the southern part of the North Sea, (ii) the exclusion of such fisheries due to conservation areas as well as renewable energy installations and (iv) the possible consequences of climate change for the ecosystem and its management.

Publication 1 focused on a single species of high commercial importance in the North Sea, Atlantic cod (*Gadus morhua*), and its suitable thermal habitat. In the last few decades, a geographical displacement of cod has taken place. Applying a single-species distribution model, results of this study support the theory, that one major driver behind this displacement is temperature and the suitability of the thermal habitat of cod. While the thermal suitability increased north of 56° N, it decreased south of this boundary between 1967 and 2015. The Intergovernmental Panel on Climate Change (IPCC) applies a set of scenarios with possible increases in greenhouse gas and therefore temperature predictions, so called Representative Concentration Pathway (RCP) scenarios.

Predictions with the strongest increase in emissions and temperature, the RCP8.5 scenario, were applied to the model the future thermal habitat suitability of cod. The results revealed that the central and northern North Sea would remain thermally suitable for cod. Furthermore, south of Skagerrak and the edge of the Norwegian trench will be key zones of thermal habitat suitability for cod in the future. Locally high resolution of spatial scales of temperature predictions enabled these predictions.

Using knowledge about habitat preferences gained from single species distribution models to increase the precision of a spatially resolved ecosystem model, **Publication 2** aimed to identify possible guidelines on how to define habitat preferences when combining these two modelling approaches. For this, an Ecospace model was created to simulate a spatial representation of the ecosystem in the southern part of the North Sea. Single species distribution models can be utilized to inform Ecospace about habitat preferences, which allows for a realistic spatial distribution of functional groups in the ecosystem model. In this study, two types of habitat preferences expressed by presence/absence or abundance of a functional group were tested in combination with the ecosystem model. While habitat preferences defined through the abundance of a species showed precise hot spots, results of this study revealed that this precise definition was too restrictive when combining it with a process-oriented food web model. Accounting for shifts in species distribution can be achieved by updating these habitat preferences during the execution of the model. Overall, this study showed that accounting for these shifts every five years significantly increased the statistical fit of the model to observed data. Unfortunately, Ecospace does not have an implemented routine yet to perform a proper skill assessment of the model. Therefore, **Publication 2** also focused on possible evaluation tools. Temporal, spatial and spatio-temporal indices were evaluated. The evaluation revealed the necessity of all three types of indices in order to assess the fit of a model in its entity when considering the skill assessment of a spatio-temporal ecosystem model.

The parameterized Ecospace model was further applied to evaluate different types of pressures on the ecosystem and assess the impact of possible management scenarios (**Publication 3** and **Publication 4)**. The focus in **Publication 3** was placed on the impact of spatial closures to fisheries due to the implementation of existing and planned offshore wind farms and marine protected areas. Ecological indicators were used to describe the ecosystem and evaluate the effect of closures in the study area.

Several closure states were tested, including two additional hypothetical closures based on the location of high Kempton’s Q and high biomass of endangered species according to the International Union for Conservation of Nature’s Red List of Threatened Species. Using a baseline run without any fishing restrictions as a comparison, all scenarios revealed an overall small but negative impact on the ecosystem and catch. Focusing on biomass-related indicators, it became apparent that the increase inside the closed areas could not outweigh the loss of biomass outside the closed areas. One possible explanation is the re-distribution of fishing effort among the remaining open areas, which caused an increase of fishing pressure. Therefore, three closure scenarios were further tested with a reduction in fishing effort. The outcomes showed that a reduction in fishing effort in addition to the area closures may be necessary as an added management measurement to achieve an overall positive impact on the ecosystem in the entire study area.

In **Publication 4**, **s**patially explicit temperature predictions were implemented in Ecospace to address climate change as important environmental issue and to describe potential effects on the ecosystem. These temperature predictions represent carbon emission scenarios RCP4.5 and RCP8.5 as used by the IPCC. Functional response curves for almost all functional groups in the model were linked to these spatial temperature trends. Species distribution shifts and changes in trophic interactions driven by climate change were evaluated at both species and ecosystem levels using the ecosystem indicators outlined in **Publication 3**. Both RCP projections induced shifts in the distribution of various functional groups, yet to a different extent. Mid-century, the disparity between both RCP projections and therefore the changes in the ecosystem were minor. However, at the end of the century the deviations to a baseline scenario with constant temperatures were three times higher for RCP8.5 than for RCP4.5. Overall, only two indicators were positively impacted by climate change while all other indicators decreased with warming, especially in the shallow, most southern regions of the study area. Here, temperature increase was strongest and exceeded thermal optima for many functional groups. Focusing on selected commercial fish species, a reduction in biomass under climate change was most notably for the biomass of the gadoid species Atlantic cod (*Gadus morhua*), as they decreased in the entire study area. Contrary, the biomass of the flatfish European sole (*Solea solea*) increased with the changing temperature conditions.

Zusammenfassung

Wie viele Ökosysteme weltweit wird das Ökosystem im südlichen Teil der Nordsee bedroht durch verschiedene anthropogene und umweltbedingte Einflüsse. Es wird stark durch die kommerzielle Fischerei, Installationen zur Förderung von erneuerbaren Energien, die Schifffahrt und die Nutzung durch Aquakulturanlagen beeinflusst. Zeitgleich erhöhen verschiedene Umwelteinflüsse, wie zum Beispiel der Klimawandel, den Stress auf das Ökosystem. Alle diese Faktoren haben das Potential, die Struktur des Ökosystems zu beeinflussen, besonders wenn sie zu Veränderungen in der Artenverteilung führen. Räumliches Management mariner Ökosysteme hat das Ziel, diese Stressoren unter Berücksichtigung der Trade-offs zwischen Zielen des Naturschutzes und ökonomisch wichtigen Fischereiprozessen sowohl einzeln als auch gemeinsam zu bewerten und zu thematisieren.

Eine Reihe statistischer Methoden kann eingesetzt werden, um Managemententscheidungen wissenschaftlich zu unterstützen und Stakeholder über die Auswirkungen des räumlichen Ökosystemmanagements zu informieren. Dieser statistische „Werkzeugkasten“ ist gefüllt mit verschiedenen Methoden, von Artverbreitungsmodelle bis hin zu komplexen End-zu-End Ökosystemmodellen, welche anthropogene Belastungen und Umwelteinflüsse berücksichtigen. Um den ganzheitlichen Effekt räumlicher Managementmaßnahmen auf das Ökosystem zu bewerten, ist die Kombination verschiedener Modellierungsansätze notwendig. Ein Ziel dieser Promotionsarbeit war es, Vor- und Nachteile zweier methodischer Ansätze aufzuzeigen: der Artverbreitungsmodelle und ein räumlich aufgelöstes Ökosystemmodell. Darüber hinaus wurden die Vorteile der ergänzenden Nutzung beider Modelltechniken aufgezeigt und genutzt, um verschiedene räumliche Managementfragen zu evaluieren. Diese Fragen umfassen (i) die räumliche Verbreitung der Fischerei im südlichen Teil der Nordsee, (ii) den Ausschluss der Fischerei, sowohl aus Umweltschutzzonen als auch aus Bereichen mit Anlangen zur Förderung erneuerbarer Energien, (iii) und mögliche Konsequenzen für das Ökosystem und das Management durch den Klimawandel.

Veröffentlichung 1 konzentriert sich auf eine der kommerziell wichtigsten Arten in der Nordsee, den Kabeljau (*Gadus morhua*), und sein geeignetes Habitat in Zusammenhang mit Temperatur. In den letzten Jahrzehnten hat eine Verschiebung des Kabeljau Bestandes stattgefunden.

Die Ergebnisse, welche mit Hilfe eines Artenverteilungsmodelles erhoben wurden, unterstützen die Theorie, dass die Temperatur und die Eignung des damit in Zusammenhang stehenden

Habitats der Hauptgrund für diese Verschiebung sind. Zwischen 1967 und 2015 hat die Eignung des Habitats nördlich von 56°N zugenommen, während sie südlich dieser Grenze gesunken ist. Das Intergovernmental Panel on Climate Change (IPCC) wendet eine Reihe von Szenarien an, die einen möglichen Anstieg in Treibhausgasen und die daraus resultierenden Temperaturen beschreiben, so genannte „Representative Concentration Pathway“ (RCP). Um die zukünftige Eignung des Habitats für Kabeljau in Bezug auf Temperatur zu modellieren, wurde das RCP8.5 Szenario genutzt, welches den stärksten Anstieg in Emissionen und Temperaturen beschreibt. Die Ergebnisse zeigten, dass die Temperaturen in der zentrale und nördliche Nordsee weiterhin gut geeignet sind für Kabeljau. Weiterhin wurden der südliche Skagerrak und der Rand der Norwegischen Rinne als Schlüsselzone identifiziert. Diese genauen Vorhersagen wurden vor allem durch die örtliche hohe räumliche Auflösung der Temperatur-Vorhersagen ermöglicht.

Um die Präzision eines räumlich aufgelösten Ökosystemmodells zu verfeinern, wurde in **Veröffentlichung 2** Wissen genutzt, welches über Habitat-Präferenzen aus Artverbreitungsmodellen gewonnen wurde, und Leitlinien erarbeitet, wie diese beiden Modellieransätze miteinander genutzt werden können. Hierfür wurde ein Ecospace-Modell erstellt, um das Ökosystem des südlichen Teils der Nordsee im Raum darzustellen. Verbreitungsmodelle einzelner Arten wurden genutzt, um das Ecospace Modell zu parametrisieren, um so eine realistische räumliche Verbreitung der funktionellen Gruppen im Ökosystemmodell zu erreichen. In dieser Studie wurden Habitat-Präferenzen basierend auf Anwesenheit/Abwesenheit und Abundanz einer funktionellen Gruppe in Kombination mit dem Ökosystemmodell getestet. Auch wenn Habitat-Präferenzen basierend auf Abundanz klare Hot-Spots aufgezeigt haben, haben die Ergebnisse dieser Studie gezeigt, dass in Kombination mit einem prozessorientierten Modell diese präzise Definition von Habitat-Präferenzen zu restriktiv ist. Durch das Aktualisieren dieser Habitat Präferenzen während der Ausführung des Modells kann eine Verschiebung der Verbreitung der funktionellen Gruppen erfasst werden. Insgesamt hat die Studie gezeigt, dass eine Aktualisierung der Verbreitungen jeweils alle fünf Jahre signifikant die Modellanpassung an beobachteten Daten erhöht. Leider gibt es in Ecospace noch keine eingebaute Routine, um ein geeignetes skill assessment durchzuführen. Daher stehen auch mögliche Evaluierungsparameter im Fokus von **Veröffentlichung 2**. Zeitliche, räumliche und zeitlich-räumliche Indices wurden evaluiert.

Diese Evaluierung zeigte auf, dass es nötig ist, alle drei Arten von Indices anzuwenden um die Modellanpassung eines räumlich-zeitlich aufgelösten Ökosystemmodells in seiner Ganzheit zu erfassen.

Das parametrisierte Ecospace Modell wurde angewendet, um die Auswirkungen verschiedener Arten von Stressoren auf das Ökosystem zu evaluieren und den Einfluss möglicher Managementmaßnahmen zu bewerten (**Veröffentlichung 3** und **Veröffentlichung 4**). Im Fokus von **Veröffentlichung 3** steht der Einfluss räumlicher Schließungen für die Fischerei auf Grund der Implementierung von existierenden und geplanten Offshore-Windparks und mariner Schutzzonen. Hierfür wurden ökologische Indikatoren genutzt, um das Ökosystem zu beschreiben und den Effekt dieser Schließungen um Studiengebiet zu untersuchen. Mehrere Schließungen wurden getestet, inklusive zweier zusätzlicher, hypothetischer Schließungen basierend auf der räumlichen Verbreitung hoher Kempton’s Q Werte und Biomasse gefährdeter Arten, basierend auf der Roten Liste der Weltnaturschutz-Organisation (International Union for Conservation of Nature). Ein Durchlauf ohne jegliche Einschränkungen der Fischerei wurde mit allen Szenarien verglichen und alle Szenarien wiesen einen insgesamt kleinen, aber negativen Einfluss auf das Ökosystem und den Fang auf. Wenn man die Biomasse-Indikatoren betrachtete, wurde deutlich, dass der Anstieg innerhalb der geschlossenen Gebiete nicht die Verluste außerhalb dieser Gebiete ausgleichen konnte. Eine mögliche Erklärung ist die Umverteilung des Fischereiaufwandes auf die verbliebenen Gebiete, wodurch es zu einem Anstieg des Fischereidrucks kam. Die Ergebnisse zeigten, dass eine zusätzliche Reduktion des Fischereiaufwandes als weitere Managementmaßnahme nötig sein könnte, um einen insgesamt positiven Einfluss auf das Ökosystem im gesamten Studiengebiet zu erreichen.

Für **Veröffentlichung 4** wurden räumlich explizite Temperaturvorhersagen in Ecospace eingebaut, um den Klimawandel als wichtigen Umwelteinfluss zu adressieren und mögliche Einflüsse auf das Ökosystem zu beschreiben. Diese Temperaturvorhersagen repräsentieren die Kohlenstoff-Emissions-Szenarien RCP4.5 und RCP8.5, wie sie vom IPCC genutzt werden. Funktionelle Beziehungen zu Temperatur wurden für fast alle funktionellen Gruppen im Modell eingebaut. Die durch den Klimawandel hervorgerufenen Veränderung der Verbreitung der Arten und die Veränderungen in den trophischen Interaktionen wurden auf einem Arten- und Ökosystemlevel mit Hilfe der in **Veröffentlichung 3** beschriebenen Indikatoren bewertet.

Beide RCP-Projektionen führten zu Veränderungen in der Verbreitung mehrerer funktioneller Gruppen, wenn auch zu einem unterschiedlichen Ausmaß. In der Mitte des Jahrtausends, waren die Unterscheide zwischen den zwei Projektionen und daher auch der Unterschied zwischen den Veränderungen im Ökosystem gering. Am Ende des Jahrtausends jedoch waren die Unterschiede zwischen dem Basis-Szenario ohne Temperaturveränderungen und RCP8.5 dreimal so hoch wie für RCP4.5. Insgesamt hatten die ansteigenden Temperaturen nur auf zwei

Indikatoren einen positiven Einfluss, während alle anderen gesunken sind, besonders in dem flachen, südlichsten Teil des Studiengebietes. Hier stiegen die Temperaturen am meisten an und überstiegen das Temperatur-Optimum für viele funktionelle Gruppen. In Bezug auf ausgewählte kommerziell gefischte Fischarten war ein Rückgang in Biomasse im gesamten Studiengebiet für den Atlantischen Kabeljau (*Gadus morhua*) am deutlichsten. Im Gegenteil dazu hat die Biomasse der Seezunge mit den veränderten Temperaturen deutlich zugenommen.

1. *General Introduction*

Ecosystems (or ecological systems) are defined as the entity of living organisms in a given area and their surrounding environment (Tansley, 1935; Odum, 1953). Based on early definitions, the ecosystem concept has been further developed to encapsulate the flow of through the system, which is equal the sum of production and respiration (Lindeman, 1942; Odum, 1968). Interspecific predator-prey relationships are embedded in the ecosystem concept and are described by food webs (Emmerson, 2012). In the 1920s, Elton (1927) defined the food web as the entity of food chains in a system. This notion was refined by Lindeman (1942) by describing the tropho-dynamics in the system.

Various studies have focused on different aspects of marine ecosystems and food web structure since, among the most frequent topics are functionality (e.g. Thrush et al., 2017; Griffith et al., 2018; Rogers et al., 2020; Merillet et al., 2021) as well as environmental factors and human stressors (e.g. Gissi et al., 2021; Kortsch et al., 2019; Todd et al., 2019), structural studies (e.g. Dunne et al., 2004; Quesne and Jennings, 2012; Jonsson et al., 2015) and climate change (e.g. Bentley et al., 2017; Serpetti et al., 2017; Bryndum-Buchholz et al., 2019; Kim et al., 2019; Lotze et al., 2019; Coll et al., 2020). Despite these scientific efforts and the early acknowledgement of food webs and definitions of ecosystems, multiple challenges are still eminent when studying ecosystems and their complex processes (Borja, 2014; Borja et al., 2020). Strengthening the understanding of ecosystem processes and functionality is particular crucial now as our oceans face the increasing cumulative effects of pressures such as resource exploitation and climate change. The implementation of this knowledge into spatial ecosystem-based management (EBM) can support the sustainable harvest of marine resources, maintain ecosystem services, and support the conservation of vulnerable species (Long et al., 2015; Dolan et al., 2016; Link and Browman, 2017; Tam et al., 2019).

1.1 *Ecosystem-based management in a spatial context*

Over the last decades, various policies and directives were introduced, that aim to sustain single species, entire ecosystems and oceanic features by regulating human activities (Katsanevakis et al., 2011). Most of these regulations address the importance of an ecosystem-based approach to management and the protection of vulnerable ecosystem components and features (Cormier et al., 2017; Rudd et al., 2018).

As one of the most prominent, multi-national agreements focusing on environmental protection in the marine realm, the Marine Strategy Framework Directive (MSFD), was adopted to reach the goal of 'good environmental status' (GES) until 2020 by mandating an ecosystem-based approach to management (Directive 2008/56/EC, 2008). In order to determine the GES, a list of eleven descriptors was agreed upon, many focusing on ecosystems, food webs or biological diversity (Directive 2008/56/EC, 2008). Moreover, the United Nations (UN) defined 17 Sustainable Development Goals (SDGs) in a resolution adopted by the General Assembly on 25 September 2015. Of these goals, target 2 of SDG 14 (Life Below Water) sets out to maintain and restore healthy marine ecosystems, demanding sustainable management and protection to ensure their productivity (UN, 2015). Most recently, the Green Deal was proposed by the European Commission, which includes the Biodiversity Strategy 2030, a proposition to further strengthen the protection of biodiversity and the restoration of damaged ecosystems (COM/2020/380).

Human activities and the allocation of marine space on a global scale is regulated by the United Nations Convention on the Law of the Sea (UNCLOS; UN, 1982). Within Europe, two legislations were implemented by the European Union to regulate human activities in the ocean, ensure sustainable exploitation, and progress EBM. Firstly, the regulation on fishing activities in Europe, the Common Fisheries Policy (CFP) calls for an ecosystem-based approach to fisheries management to minimize the impacts of fishing on the environment (Regulation 1380/2013/EU). Secondly, the Maritime Spatial Planning (MSP) directive aims to 'organize human activities in marine areas to achieve ecological, economic and social objectives' (Directive 2014/89/EU, Article 3 (2)). Each Member State is obliged to implement MSP to enable the co-existence or co-use of marine areas, supporting the development of different economic sectors while accounting for environmental features by using an ecosystem-based approach (Directive 2014/89/EU).

Management and assessment of marine resources with a focus on fisheries can be broadly allocated into four categories: Single Species Fisheries Management (SSFM), Ecosystem Approach to Fisheries Management (EAFM), Ecosystem-based Fisheries Management (EBFM) and Ecosystem-based Management (EBM; Figure 1; Dolan et al., 2016). The most traditional approach, which has been widely applied, is SSFM. It focusses on the stock assessment of a single species and its associated fisheries.

The next two levels incorporate ecosystem considerations, the focus placed on a single species in an ecosystem context (EAFM) or on the entire community (EAFM). The most complex level is EBM, which is an integrative approach, that considers all sectors of ocean-usage (Link and Browman, 2014). Unfortunately, despite EBM being a widely discussed and demanded concept, a common and precise definition is still lacking (Long et al., 2015). In general, this concept acknowledges the complexities of the entire ecosystem, including anthropogenic impacts and its management (Link and Browman, 2017). It considers trade-offs between different sectors and evaluates cumulative effects of various pressures on the ecosystem generated by the different sectors included in the assessment (Smith et al., 2017). Despite the high demand for this type of management, implementation into real life management is slow (Link and Browman, 2017).

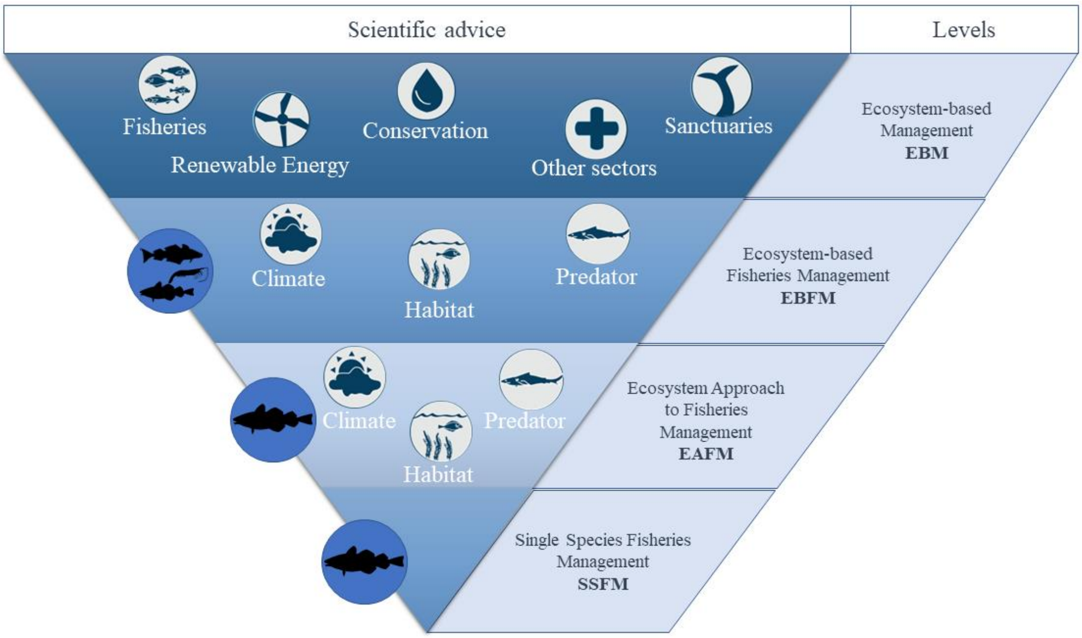

Figure 1: *Levels of marine resource management (modified from Dolan et al., 2016)*

Ecosystem-based marine spatial management (EB-MSM) is a combined framework of an ecosystem-based approach to management and marine spatial planning (Domínguez-Tejo et al., 2016). It addresses the competition of marine space by various sectors, such as fisheries, offshore wind farms or the oil and gas industry, and aims to align them with conservation objectives. A key component in EB-MSM policies are Marine Protected Areas (MPAs) as a conservation tool in the framework of managing activities in the marine realm (Katsanevakis et al., 2011).

MPAs are protection tools demanded by many regulations, for example in the MSFD or the Biodiversity Strategy 2030 (Directive 2008/56/EC, 2008; COM/2020/380). Within European waters, these MPAs are either in the so-called Natura 2000 network, a coordinated network of conservation areas among member states, or nationally designated areas (Fraschetti et al., 2018; Mazaris et al., 2018) All management frameworks require scientific input as decision foundation, which are often derived from various modelling approaches.

1.2 *Modelling tools to support spatial management*

1.2.1 Species distribution models (SDMs)

It is crucial to understand the drivers of single species distributions prior to understanding the entire ecosystem and its spatial structure. In spatial management, the distribution of key species in an ecosystem needs specific attention, as a shift in their distribution can alter predator-prey relationships and therefore ecosystem dynamics (Wallingford et al., 2020). Therefore, species distribution models, sometime also called ecological niche models or habitat models, are an important tool to evaluate general distribution patterns as well as shifts in these distributions and their relationship to environmental parameters (Elith and Leathwick, 2009).

The foundation of species distribution modelling is the assumption, that the distribution of a species represents its ecological niche (Elith and Leathwick, 2009). Modelling approaches aim to evaluate the relationship between specific environmental parameters with the presence or abundance of a species in an identical geographical region. Using these relationships, response functions can be derived for all parameters and applied, to predict habitat preferences and consequently spatial distribution of a species. Species distribution modelling is thus often used to simulate the impacts of environmental change (i.e. changes in temperature or changes in nutrients) and management strategies (i.e. excluding human usage for conservational purposes, the introduction of artificial structures) on the spatial distribution of species (e.g. Reiss et al., 2014; Snickars et al., 2014; Mannocci et al., 2017; Schickele et al., 2020). For the marine realm, several species distribution modelling techniques are often applied. Most common approaches include a variety of generalized linear/additive models (e.g. Guisan et al., 2002; Kempf et al., 2013; Otto et al., 2018; Fu et al., 2019), random forest (e.g. Kijewski et al., 2019; Luan et al, 2020), multivariate adaptive regression splines (e.g. Reiss et al., 2011; Rose et al., 2016), or Bayesian Belief Network approaches (e.g. Coll et al., 2019; Pennino et al., 2020). These modelling methods allow the evaluation of a response variable to a set of predictor variables.

The selection of predictors that are relevant to the distribution of the species as well as the decision of the modelling method can influence the robustness and realism of a prediction (Elith & Leathwick, 2009). Simultaneously, a wide range of evaluation measures (e.g. Akaike-Information-Criterion or Bayesian-Information-Criterion), allows the selection of the right model (Akaike, 1973; Schwarz, 1978). Applying a cross-validation allows to evaluate the predictive capabilities of a model, therefore the fitness of a model (Piccard and Cook, 1984).

Various topics have been addressed with species distribution modelling ranging across all trophic levels of the ecosystem (e.g. Reiss et al., 2010; Broennimann et al., 2012). Climate change is one of the most common and widely considered anthropogenic effects in species distribution models across all trophic levels (Weinert et al., 2016; Pinsky et al., 2021; Lima et al., 2022), especially the relationship between latitudinal shifts in species distributions and climate change has been studied around the world (Pinsky et al., 2020). The relocation of commercial resources, but also the distribution of vulnerable species or introduction of non-native predators are frequently modelled (D’Amen and Azzurro, 2020; Le Marchand et al., 2020; Lowen et al., 2016; Parravicini et al., 2015). Additionally, potential spatial management strategies are often evaluated, such as the impact of fishing effort re-distribution due to changes in the political environment (e.g. Brexit) or due to conservational measurements, such as no-take zones for fisheries (Fredston-Hermann et al., 2018; Probst et al., 2021).

Finally, species distribution models have been used in combination with ecosystem models to inform the complex structure of process-oriented models of specific distribution patterns and habitat affinities. Response functions derived from the relationship between presence/abundance of a species can be applied to inform ecosystem models about environmental drivers (Grüss et al., 2016) or the resulting distribution maps can be directly incorporated (Coll et al., 2019).

1.2.2 Ecosystem modelling - Ecopath with Ecosim and Ecospace

Integrating ecosystem properties into management requires a comprehensive understanding of physical, chemical and biological processes (Heymans et al., 2018). Therefore, multiple model frameworks or ensemble models might be needed. Ocean modelling frameworks, for example the Regional Ocean Modelling System (ROMS; Moore et al., 2011) provide insights into regional physical-oceanographic properties, while bio-geo-chemical models like the European Regional Seas Ecosystem Model (ERSEM) focus on carbon and nutrient cycles (Baretta et al., 1995). End-to-end food web models like StrathE2E or Atlantis allow the inclusion of physical drivers and the analysis of fishing impacts (Heath, 2012; Bossier et al., 2018). Atlantis also allows the exploration of spatial dynamics, including socio-economic factors (Audzijonyte et al., 2019).

One of the most applied modelling frameworks used to construct mass balanced food web representations, including environmental pressures and anthropogenic impacts, is Ecopath with Ecosim and its spatial component Ecospace (EwE; Christensen and Walters, 2004). EwE was created by Jeff Polovina (1984) and has been continuously enhanced ever since (Christensen and Pauly, 1992). The model suit is comprised of three interlinked components: Ecopath, Ecosim and Ecospace. Prior to evaluating spatial and temporal complexities of the ecosystem, an Ecopath model has to be created (Christensen et al., 2008). Ecopath is a static, mass-balanced snapshot that entails parameters describing the general structure of the food web, all consumptions and the exploitation due to fishing fleets (Christensen and Pauly, 1992; Figure 2). Species are represented within biomass pools, creating functional groups. These functional groups can be composed of a single species but also a group of taxonomic species with similar habitat and dietary needs. Pools may be further split into ontogenetic linked groups called ‘multi-stanzas’. Necessary inputs for each functional group (i) to simulate ecosystem effects are biomass (B_i), production and consumption per biomass (P/B_i and Q/B_i), ecotrophic efficiency (EE_i) and a diet matrix for each prey (j; DC_{ij}). Ecotrophic efficiency is the proportion of the production that is used in the system. Furthermore, catch information (Y_i) and potential other exports have to be included.

Two master equations are applied to reproduce flows within the system (Figure 5), production (1) and consumption (2):

$$P_i = Y_i + B_i \times M2_i + E_i + BA_i + P_i \times (1 - EE_i) \qquad (1)$$

and

$$Q_i = P_i + R_i + UN_i \qquad (2)$$

including total predation rate ($M2_i$), net migration rate (E_i), potential biomass accumulation (BA_i), respiration (R_i) and unassimilated food (UN_i; Christensen et al., 2008).

Ecosim enables the portrayal of temporal dynamics of the ecosystem induced by environmental as well as fishing impacts (Christensen and Pauly, 2004; Walters et al., 2000, 1997). It introduces the concept of the foraging arena theory, which distinguishes between a vulnerable and invulnerable state of prey towards its predator (Ahrens et al., 2012). They therefore directly affect the consumption rates Q_i of a predator (Christensen et al., 2008). Model simulations are often fitted to biomass, catch, effort or fishing mortality reference and forcing time series to best reflect changes over time (Scott et al., 2016).

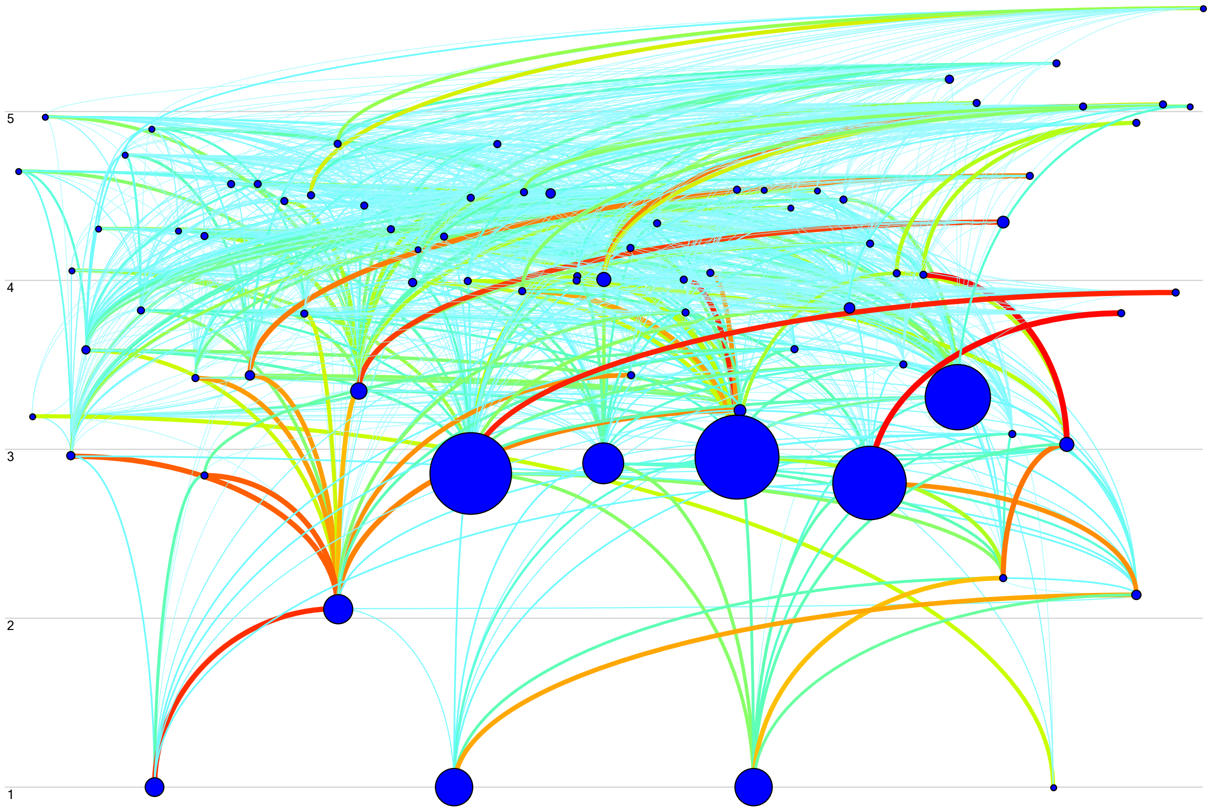

Figure 2: *Ecopath flow diagram of the ecosystem in the southern part of the North Sea. Functional groups and fleets are represented by nodes. The relative size of functional group nodes denotes their biomass while the size of fleet nodes denotes the size of their catch. Lines represent the flow of energy and are scaled to reflect the relative energy flow. The y-axis denotes group trophic level.*

Finally, Ecospace enables the evaluation of environmental pressures and various impacts of economic activities on the ecosystem in a spatial context (Walters et al., 1999). Temporal dynamics introduced in Ecosim are transformed onto a two-dimensional grid. Based on habitat structures, food availability, predator pressure, the allocation of fishing opportunities and the distribution of primary production, biomass of all functional groups is allocated across the modelled area (Christensen et al., 2008). This allows the evaluation of a wide range of impacts that can potentially restructure the spatial compositions of the ecosystem as well as the associated fisheries. Spatial management strategies to account for these impacts on the ecosystem can be tested by evaluating the impact on individual functional groups or standardized ecological indicators (Coll and Steenbeek, 2017).

Examples include the evaluation of shifts in distribution of species due to climate change (Cashion et al., 2020; Bourdaud et al., 2021; de Mutsert et al., 2021), the impact of man-made structures serving as artificial reefs (Serpetti et al., 2021) or the impact of MPAs (Le Quesne and Codling, 2009; Metcalfe et al., 2015; Abdou et al., 2016; Pitcher, 2016).

In order to support the implementation of the ecosystem-based approach into spatial management, common boundaries have to be defined which allow the modelling and assessment of local ecosystems. In Europe, assessments and advices are subdivided into thirteen so-called ecoregions defined by the International Council for the Exploration of the Sea (ICES; ICES, 2004). One of these ecoregions is the Greater North Sea. This semi-enclosed shelf sea entails four subareas: the northern North Sea, the southern North Sea, the Skagerrak and Kattegat region and the English Channel (Figure 3).

Figure 3: *Ecoregions in European waters (ICES, 2020a)*

1.3 *The ecosystem of the southern part of the North Sea*

This thesis focusses on the structure and spatial management of the ecosystem in the southern part of the North Sea, which encompasses areas 4b and 4c as defined by ICES. It is limited in the south by the Dover Strait up to the northern end of Scotland (Figure 4). France, Belgium, the Netherlands, Germany, Denmark and the UK enclose this ocean basin, which results in strong land-based and anthropogenic influences (Emeis et al., 2015).

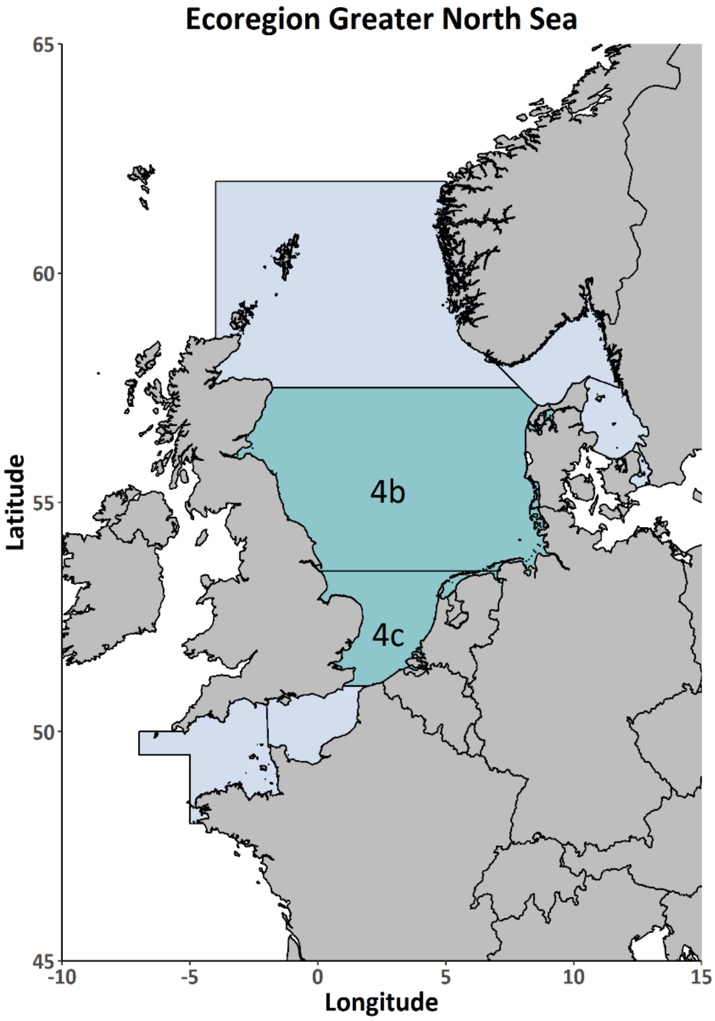

Figure 4: *Greater North Sea ecoregion (blue shaded areas), southern part of the North Sea (4b and 4c) highlighted in turquoise*

The North Sea subarea is characterized by distinct features. While the northern part is characterized by currents emerging from the Atlantic and a depth between 100 m and 800 m (Norwegian trench), the maximum depth of the shallow southern North Sea is below 100 m (Sündermann and Pohlmann, 2011; Van Ledden et al., 2014). During winter, the lowest temperatures in the North Sea occur in the German Bight and increase beyond 100 m depth, displaying a clear South-North gradient (Heessen et al., 2015).

This gradient changes during the summer, in which the temperatures of the northern North Sea beyond 100 m depth are comparable to the winter temperatures, while there is a steep latitudinal gradient along the coastal areas (Heessen et al., 2015). The North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) are two of the most important environmental drivers of atmospheric changes in the North Sea, influencing the ocean dynamics (Quante and Colijn, 2016).

The seabed of the southern part of the North Sea primarily consists of sand and mud habitats, with sparse hard substrate sediments (Bockelmann et al., 2018). Species composition and community structure in the North Sea is closely related to distinct habitat structures and depth contours (Neumann et al., 2012). Within the southern part of the North Sea, the 50 m depth contour represents the most distinct boundary for benthic and fish communities. North of this depth contour, communities are dominated by sessile epibenthic species, while communities towards the south are dominated by free-living epibenthic species (Callaway et al., 2002). Large-scale patterns in the community structure of demersal fish, epifauna and infauna reveal several characteristic communities in the North Sea. In the southern North Sea, these communities can be further divided into assemblages near the English channel and coastal communities (Reiss et al., 2010).

Primary production is one of the most important components in the food web of the North Sea, defined by strong bottom-up effects between primary production and higher trophic levels (Capuzzo et al., 2018; Stäbler et al., 2019). Primary production is driven by riverine inflows and changes in temperatures, with higher densities along the coast-lines than in stratified water masses (Moll, 1998), yet an overall decrease across the North Sea in recent decades (Capuzzo et al., 2018). In the shallow, coastal regions of the southern North Sea, the density of primary production is highly influenced by tidal mixing. Further offshore at the frontal zone between stratified and mixed water masses, tides enable nutrient replenishment following the spring bloom (Zhao et al., 2019).

Zooplankton in the North Sea ranges from ciliates to large gelatinous medusa. The communities in the southern North Sea are dominated by coastal and neritic species, such as various copepod species and fish larvae (Krause et al., 2003). Two key species in the zooplankton community are the boreal *Calanus finmarchicus* and the neritic, more lusitanian species *Calanus helgolandicus*, both varying in spatial distributions, temperature affinity and life cycle, being an important food source for planktivorous fish (Planque and Fromentin, 1996;

Beaugrand et al., 2003). Gelatinous zooplankton is dominated by Scyphozoa in the southern North Sea, some of the most abundant species are *Aurelia aurita* (common jellyfish), *Cyanea lamarckii* (blue jellyfish) and *Cyanea capillata* (lion's mane jellyfish; Lynam et al., 2004). Squid biomass has increased across the entire North Sea from 1980 to 2014, with the most abundant species being *Alloteuthis subulata* (European common squid) and *Loligo forbesii* (veined squid; Oesterwind et al., 2010; van der Kooij et al., 2016).

Bioturbation and thus nutrient and oxygen fluxes are driven by the benthic community in the North Sea (Neumann et al., 2021). Furthermore, they are an important food source for higher trophic levels such as fish and crustaceans (Reiss et al., 2011; Silberberger et al., 2018). They can be distinguished into infauna and epifauna, depending on their main habitat position (Basford et al., 1990). Key species in the epifaunal community in the southern North Sea include *Asterias rubens* (common starfish), *Carcinus maenas* (shore crab) and *Mytilus edulis* (blue mussel). Infaunal species include *Abra alba* (white abra) and annelids such as *Nephtys cirrosa* (white catworm; Reiss et al., 2010).

The fish community in the North Sea is represented by pelagic and demersal fish species (Daan et al., 1990). Pelagic forage fish include *Clupea harengus* (Atlantic herring), *Sprattus sprattus* (sprat) and *Ammodytidae* (sandeels), which are important prey species for seabirds and larger, piscivorous fish (Engelhard et al., 2014). Demersal fish in the North Sea are represented by round- and flatfish. The gadoid species *Gadus morhua* (Atlantic cod) and *Merlangius merlangus* (whiting) are among the most important roundfish species for both, ecosystem functionality and commercial fisheries and have been for decades (Pope and Macer, 1996). Flat fish species in the North Sea encompass a variety of species including *Solea sole* (common sole), *Pleuronectes platessa* (European plaice) and *Limanda limanda* (dab), most which are targeted species for demersal fisheries (Rijnsdorp et al., 1992; Engelhard et al., 2011).

There is a broad variety of top predators inhabiting the southern part of the North Sea. Many shark and ray species constitute the elasmobranch community in the southern part of the North Sea, which has experienced strong compositional changes during the last century (Sguotti et al., 2016). The community shifted from large species (such as the thornback ray *Raja clavata*) that were of interest to commercial fisheries to less valuable and smaller species (like the starry ray *Amblyraja radiata*). Recently those trends seem to be reversing for some of the species (Sguotti et al., 2016). One of the most prominent top predators of the class mammalia mammals is the harbor porpoise *Phocoena phocoena*.

It is the most common small cetacean species in the North Sea, especially in the English Channel and the southern regions (Hammond et al., 2002). Nevertheless, in some regions, such as the north-eastern part of the German Exclusive Economic Zone (EEZ), the abundance of harbor porpoises decreased and the causes are not well understood (Nachtsheim et al., 2021). Finally, seabirds including guillemots, gulls and gannet are an important predatory component of the North Sea ecosystem, as they prey on different forage fish species, such as sandeels (Anderson et al., 2014; Hamer et al., 2007; Kubetzki and Garthe, 2003).

1.4 *Cumulative impacts on the ecosystem in the southern part of the North Sea*

The ecosystem in the southern part of the North Sea is subject to diverse environmental pressures, which are mostly enhanced or induced by human activities (Emeis et al., 2015). Cumulative effects by multiple economic sectors and environmental pressures complicate the analysis of their impact on the ecosystem, especially when investigating the causes of species distribution shifts (Stelzenmüller et al., 2018). Structural and functional changes of the ecosystem are likely to have significant ramifications for the systems ecology and associated economy; hence this thesis focusses on the analysis of impacts precipitated by one environmental pressure (climate change) and two economic sectors (fishing and renewable energy).

1.4.1 Impacts of climate change

Climate change and its impact on the environment is one of the greatest present and future challenges facing the world (Gattuso et al., 2018). In their latest report, the Intergovernmental Panel on Climate Change (IPCC) has revised earlier predictions and stated that without reducing greenhouse gas emissions immediately, warming will exceed 1.5°C and maybe even 2°C. This would have catastrophic consequences such as an increase in heatwaves, heavier rainfalls with possible flooding, increased precipitation and reduction of ice cover (IPCC, 2021). For the oceans, continuously high levels of greenhouse gas emissions will continue to increase sea temperatures, decrease pH levels and lead to a decrease in oxygen (IPCC, 2021). Ocean currents, which enable the exchange of water masses, nutrient transport and affect the world’s climate, are shown to have already weakened in the past, which is thought to be due to increasing temperatures. This effect is predicted to increase in the future (Douarin et al., 2015; EASAC, 2021).

The extent of future changes depends on the amount of greenhouse gases introduced by humans' actions, which may adapt over time (IPCC, 2021). Therefore, multiple possible outcomes need to be considered in scientific advice and political discussions. Among these predictions are Representative Concentration Pathways (RCPs) scenarios. These describe possible greenhouse gas emissions and the accompanying temperature scenarios which are used in the IPCC assessments (Moss et al., 2010; IPCC, 2014). Two of the most commonly applied scenarios are RCP4.5 (intermediate emissions) and RCP8.5 (high emissions, 'worst case'). For the southern part of the North Sea, both RCP scenarios project an increase in temperature, with a similar increasing trend until 2050. Post 2050, RCP 4.5 and RCP 8.5 predictions diverge, with maximum annual mean sea surface temperature (SST) predictions of 12.2°C under RCP4.5 and 13°C under RCP8.5 (Figure 5, regionally coupled ocean-atmosphere climate system model MPIOM/REMO; Mikolajewicz et al., 2005; Sein et al., 2015). SST is expected to increase strongly under future predictions, particularly in the shallower, well mixed regions when compared to the northern North Sea with stratified water masses (Holt et al., 2012).

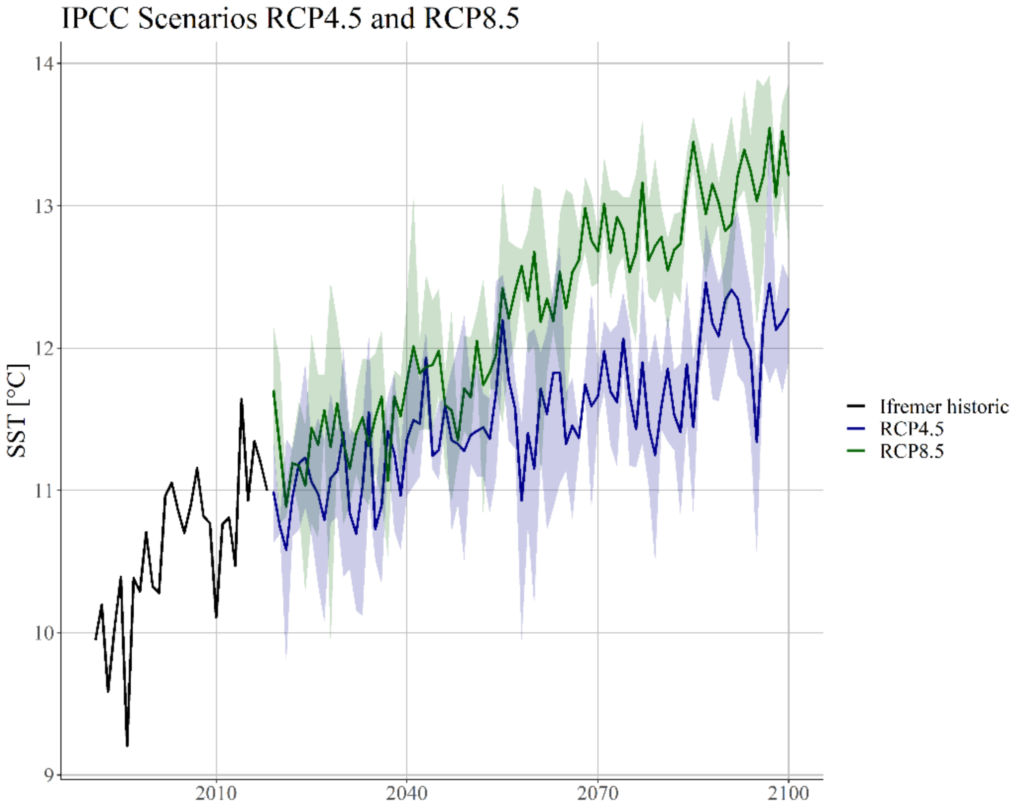

Figure 5: Historical SST measurements and projected SST range for RCP4.5 and RCP8.5. Data: 1. Ifremer historic; highly resolved re-analysis product (ODYSSEA NW+IBI Sea Surface Temperature analysis; product unit SST-IFREMER-BREST-FR, downloaded 06.07.2021). 2. RCP ensemble runs; regionally coupled ocean-atmosphere climate system model MPIOM/REMO (Mikolajewicz et al., 2005; Sein et al., 2015).

Consequences of these increasing temperatures are already visible on a species as well as an ecosystem level (Bryndum-Buchholz et al., 2019; Pinsky et al., 2020; Tittensor et al., 2021). On a species level, increasing temperatures can cause physiological reactions, i.e. decreased growth, changes of size at maturity or reproduction rates (Butzin and Pörtner, 2016; Pörtner and Peck, 2010). Mobile species like fish tend to avoid habitats with unfavorable temperatures, which leads to changes in migration patterns or distributional shifts (Pinsky et al., 2020). A deepening of demersal fish assemblages in European waters was detected, which reflects a northward shift as latitudinal response to warming temperatures, primarily for temperature specialists (Dulvy et al., 2008; Baudron et al., 2020). Distributions of Lusitanian species might shift further north, or populations already existing in the North Sea might increase in abundance due to an increase in productivity enabled by an expansion of their thermal habitats (Beaugrand et al., 2002; Petitgas et al., 2012).

In the past, increasing temperatures as well as climate events such as cold-boreal conditions or warmer temperatures than usual have impacted the ecology of the North Sea (Edwards et al., 2002), inducing changes in competition dynamics and causing spatio-temporal mismatches between predator and prey (Cushing, 1990).

Mismatches in phytoplankton blooms and the migration patterns of pelagic communities have occurred in the past as response to changes in temperatures (Edwards and Richardson, 2004). These climate induced changes in ecosystem structure and function can lead to a shift in ecosystem state known as a regime shift (Beisner et al., 2003). Two regime shifts were detected in the North Sea, one in the late 1970s and one in the 1980s, with the latter being triggered by changes in water temperature (Edwards et al., 2002). Taxonomic and functional changes in macrofaunal communities in the south-eastern North Sea took place in 2000 and 2010, driven primarily by SST and the North Atlantic Oscillation Index (NAOI; Meyer et al., 2019).

1.4.2 Fishing activities and their consequences

A variety of fisheries with different fishing gear operate in the southern part of the North Sea, harvesting resources but also reshaping the ecosystem and the environment (ICES, 2020b). The main countries economically profiting from fishing in the southern part of the North Sea are the United Kingdom, Denmark, Belgium, the Netherlands and Germany (STECF, 2020). Despite declining landings and fishing effort over the last decades, around 6600 vessels are still active in the Greater North Sea ecoregion (ICES, 2020b). Pelagic fisheries mainly target herring and mackerel while otter trawls target a variety of demersal fish, including cod and whiting. Both operate throughout the entire southern North Sea (ICES, 2020b). The most important bottom-contact fisheries aiming at flatfish in the southern North Sea is the beam-trawl fisheries, which primarily target sole and plaice but also turbot and brill (Rätz and Mitrakis, 2012; ICES, 2021a). Other fishing gears used in the southern part of the North Sea include static fishing gears such as gillnets (targeting flatfish and demersal fish) and pots (targeting edible crabs and lobster), and the dredge fisheries targeting scallops (ICES, 2020b). Regulated by the CFP, fishing effort for most commercially exploited stocks in European waters is controlled by quotas and total allowable catch (TAC; Regulation 1380/2013/EU). Quotas are assigned on the principle of relative stability, a concept introduced early in the CFP. It postulates the quota distribution between fishing nations based on traditional catch shares (Hoefnagel et al., 2015).

TACs are set annually and are based on the assessments from ICES and the Scientific, Technical and Economic Committee for Fisheries (STECF; Regulation 1380/2013/EU). Until now, these assessments have mostly been single-species assessments. Yet, for some fisheries these assessments are the foundation for a management under mixed-fisheries considerations, one example in the southern North Sea is the management of demersal fish stocks (ICES, 2021b).

Fishing introduces various additional pressures on the ecosystem aside from the exploitation of commercially important species. One of the largest issues is the impact of fishing gear on the ocean floor. Especially in the southeastern part of the North Sea, mobile bottom-contacting gear causes great physical disturbance during fishing in nearshore areas (ICES, 2020b). The disturbance of the seafloor due to trawling is diverse; it ranges from habitat modification, loss of predators and therefore shifts in the trophic structure to deviations in the diversity of species and processes in the ecosystem (Thrush and Dayton, 2002). A second subject that needs to be addressed is the impact of by-catch, since not only targeted species get caught by the different fishing fleets. By-catch by non-selective fishing gear poses a threat to all species in the ocean, especially highly vulnerable and endangered species (Kennelly and Broadhurst, 2021; Vinther and Larsen, 2004). Elasmobranchs (sharks and rays) often end up as by-catch (Stevens et al., 2000). The impact of fishing on marine birds on the other hand is more diverse, with direct and indirect effects. Direct by ending up as by-catch in the fishing nets and indirect by impacting important food sources by exploitation (Furness and Tasker, 2000). Furthermore, scavenger birds have evolved to be highly dependent on discards produced by the fisheries and a reduction in discard rates as a result of management decisions may even pose a threat to the seabird community (Votier et al., 2004).

1.4.3 Offshore renewable energy installations

In order to move from fossil fuels to renewable energies the installation of alternative forms of energy production need to be promoted (Directive 2018/2001/EU). With the modern way of life, the amount of energy required expedites the planning and construction of renewable energy installations, both onshore and offshore. The biggest sector within the renewable energy sector is offshore wind, with the majority of the installed capacity located in the North Sea (WindEurope, 2019). However, the implementation of offshore wind farms (OWFs) requires large oceanic spaces, hence demanding spatial management to evaluate possible locations as well as solutions for co-existence or co-use of these areas (Stelzenmüller et al., 2021).

Because most fishing is restricted within the individual offshore wind farms (Lukic et al., 2018), it could potentially serve as a conservation measure for the ecosystem (Hammar et al., 2016). From an ecological point of view, these OWFs have contrasting impacts on the ecosystem, depending on the species in focus (Raoux et al., 2017). The biggest potential impact, which is similar to other installations like oil and gas platforms but also ship or plane wrecks, is the introduction of hard substrate into the otherwise muddy or sandy southern North Sea.

Man-made structures serve as artificial reefs, providing shelter and increasing local biodiversity (Leewis, 2000; Lengkeek, 2013). Furthermore, they display a high connectivity serving as a bridge between different species communities (UNDINE, 2018). Artificial structures attract different predator species, as they increase the nursery and feeding opportunities (Reubens et al., 2014; Stenberg et al., 2015; Hooper et al., 2017; Raoux et al., 2017). Cod, plaice and thornback ray show a seasonal increase in abundance around artificial structures (Wright et al., 2018). Particularly OWFs allow a strong increase in benthic biomass (Dannheim et al., 2020). Firstly, the surrounding scour protection introduces additional hard substrate, with increased hiding opportunities (Krone et al., 2013). Secondly, the expansion into the water column leads to a higher secondary production, due to increased availability of phytoplankton and increased abundance in filter feeders, especially the permanently attached *Mytilus edulis* (Slavik et al., 2019). Unfortunately, OWFs also have negative impacts on the ecosystem. The expansion of artificial structure into the water column can potentially alter water currents and therefore impact the structure of the sediment in the near vicinity. This in turn can have a strong influence on the benthic community (Klunder et al., 2020). The construction and decommission phases of the OWFs completely change the structure of the existing community (Fowler et al., 2020, 2018; Lemasson et al., 2021). The pilling noise during the construction phase is thought to be especially harmful to marine mammals (Thomsen et al., 2006). Safety measures like the installations of bubble curtains try to mitigate such effects (Nehls et al., 2007). Finally, seabirds show a high vulnerability towards OWFs due to collision potential (Garthe et al., 2017; Garthe and Hüppop, 2004).

In order to align these needs for oceanic space with conservational goals, extensive scientific knowledge is required at both a single-species and ecosystem level. For this purpose, various modelling techniques can be applied to evaluate the individual and cumulative impacts of the different economic sectors, potential trade-offs between ecological and economical goals, as well the impact environmental pressures have on the ecosystem.

1.5 *Main objectives of this thesis*

The pressure on the southern part of the North Sea and its ecosystem is high and an extensive understanding of mechanisms to support spatial management is essential. This thesis aims to support this understanding by utilizing different modelling approaches, as single and ensemble modelling approach, to reduce the gap between single-species and ecosystem approaches in spatial modelling as well as spatial management.

First, the focus is placed on the habitat preferences in terms of thermal habitat suitability for a single species, the Atlantic cod (*Gadus morhua*). As one of the most important commercial fish species in the southern part of the North Sea, cod is central to many management efforts. Collapses in abundance as well as distributional shifts have shaped the structure of the stock. Therefore, **Publication 1** focusses on the identification of preferred thermal ranges for cod in different life stages in the North Sea, the distribution of past and present suitable thermal habitats and a small-scale prediction of suitable thermal habitats in the light of climate change.

The knowledge of how to combine species distribution model outputs with a process-oriented food web model is scarce. Hence, **Publication 2** describes the construction of the spatio-temporal ecosystem model Ecospace for the southern part of the North Sea and evaluates the best approach to include single species distribution information in the model on a spatial and temporal scale. Furthermore, it presents guidelines on a novel skill assessment approach accounting for the temporal, spatial and spatial-temporal fit of an Ecospace model.

Publication 3 and **4** evaluate the impact of different stressors on the ecosystem and possible implications for spatial management based on changes in ecological indicators. Trade-offs between conservational management (MPAs), OWFs and fisheries are evaluated in **Publication 3**. Furthermore, the impact of hypothetical closures to fisheries for conservational purposes in alternative locations are assessed and the necessity of applying additional management measures to counteract trophic interactions and reallocation of fishing effort is tested. **Publication 4** once again addresses climate change and the impacts of warming, yet this time at an ecosystem level.

The main questions addressed in this thesis are:

1. How can different modelling approaches be combined to best support spatial management? What are the advantages and disadvantages of each individual approach? (Publication 1 and 2)
2. What tools need to be applied in a skill assessment of a spatial explicit ecosystem model? What uncertainties need to be considered and how can they be validated in both modelling approaches? (Publication 1 and 2)
3. What are the main spatial patterns of various ecosystem indicators in the southern part of the North Sea? How do they change when impacted by shifts in fishing effort due to spatial closures? What are possible consequences of climate change? Which conclusions can be drawn for spatial ecosystem-based management? (Publication 3 and 4)
4. How does climate change potentially impact the important commercial fish species Atlantic cod? What can we learn about the suitable thermal habitat? Are there any differences and commonalities between the predictions of a single species or ecosystem context? (Publication 1 and 4)

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2. Publication 1

Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change

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Abstract

Previous studies have identified changes in habitat temperature as a major factor leading to the geographical displacement of North Sea cod in the last decades. However, the degree to which thermal suitability is presently changing in different regions of the North Sea is still unclear, or if temperature alone (or together with fishery) is responsible for this displacement. In this study, the spatial distribution of different life stages of cod was modelled from 1967 to 2015. The model is fit point-to-point, spatially resolved at scales of 20 km. The results show that suitability has decreased south of 56°N (more than 12% in the Southern Bight) and increased north of it (with maximum of roughly 10% in southern Skagerrak). Future changes to suitability were estimated throughout the century using temperature projections from a regional climate model under the IPCC scenario RCP8.5. The results show that southern Skagerrak, the central and northern North Sea and the edge of the Norwegian trench will remain thermally suitable for North Sea cod throughout the century. This detailed geographical representation of thermally-suitable key zones for North Sea cod under climate change is revealed for the first time through the improved resolution of this analysis.

2.1 *Introduction*

Atlantic cod (*Gadus morhua*) is one of the most important and studied commercial fish species of the North Sea (Cohen et al., 1990). Hedger et al. (2004), Engelhard et al. (2014) and Nicolas et al. (2014) have shown that over the last decades, the geographical distribution of North Sea cod has changed from the shallow south-western to deeper, north-eastern parts of the North Sea. However, none of these previous studies have quantified the impact of temperature changes on the distribution of the suitable habitat for North Sea cod, spatially resolved at both long-term temporal and high resolution spatial scales. Additionally, it remains uncertain if the past temperature trends in the North Sea imply an increase or a decrease of thermal suitability of cod in the North Sea in general (Blanchard et al., 2005) and if they alone are responsible for cod's displacement or if fishery pressure also plays a role (Engelhard et al., 2014).

In the present study, a species distribution model was developed for different life stages of cod based on Generalized Additive Models (GAMs) fitted to data of the North Sea International Bottom Trawl Surveys IBTS spanning almost five decades (1967-2015). Modelling changes to fish habitat is not only important to understand the mechanisms influencing geographical distribution, but also allows for projecting future changes under scenarios of climate change. Such projections are important to assess the risk of local extinction of species (Thomas et al., 2004; Cheung et al., 2009), predicting ecological and economical variations in the fisheries and, thus, for long-term planning on mitigating climate change impact. Future projections of fish habitat under climate change either focus on regional (Queirós et al., 2016) or global scale changes (Cheung et al., 2009), although global climate model (GCM) projections are typically used as a source of future conditions in both cases. Global studies generally show that suitable habitats for many species are shifting towards the poles under climate change. However, GCMs are unable to resolve shelf sea dynamics appropriately, including the small-scale changes in temperature occurring on regional scales. Therefore, they lack some of the detail necessary for assessing impacts on marine ecosystems and it remains uncertain how exactly fish habitats are likely to be redistributed in the North Sea as a result of future climate change.

Cheung et al. (2009) explicitly addressed the issue of scale, and stated that future models should use a “finer resolution” in physical and biological data. Moreover, while studies treating various species are good for a general understanding of the ecosystem (e.g. Queirós et al., 2016), results from studies focusing on specific individual species are also needed. The benefits from such studies are similarly to those of regional over global models, i.e., a higher degree of detail.

In this study, changes of geographical distribution of North Sea cod under climate change were projected from 2020 to 2100 by using temperature changes according to the scenario RCP8.5 (Cubasch et al., 2013) of the Intergovernmental Panel on Climate Change (IPCC). The model used to simulate this temperature projection was a high-resolution, regionally-coupled ocean-atmosphere climate system model. The use of a regional, instead of a global, climate model should allow for unprecedented detail for projecting the future distribution of cod in the North Sea under climate change.

2.2 *Materials and Methods*

In this study, the spatial distribution of different life stages of cod is modelled with generalized additive models (GAMs; Hastie and Tibshirani, 1986). The fundamentals about data and analysis are given in this section. For simplicity, details about the choices relating data, model equations and degrees of freedom are given in Appendix S1 of the Supplementary Material.

2.2.1 Fish abundance data

Fish abundance data used in this study were catch per unit effort (CPUE) per fish length class per haul for cod (*Gadus morhua*) from the 1st quarter (Q1; January, February, March) North Sea International Bottom Trawl Surveys (IBTS) from 1967 to 2015. Data from Q1 were chosen over the third quarter (Q3) because the time series are longer. The data were obtained from the Database of Trawl Surveys (DATRAS, 2017) of the International Council for the Exploration of the Sea (ICES).

CPUEs for each haul were added in three length classes: 0 to 24.9 cm, 25 to 39.9 cm and 40 to 140 cm. These length classes, denoted here as $LC_{0\text{-}25}$, $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$, are deemed to represent different life stages with potentially different habitat requirements.

While cod below 25 cm mainly represents recruits of age 0 and 1, fish between 25 and 40 cm start to mature (mainly age 2) and 40 cm is around the length at which 50% of individuals are mature in recent years (Marty et al., 2014). A zero CPUE was used if no fish of a certain length class were caught in a haul.Annual abundance by age of the entire North Sea cod stock, as derived from the ICES stock assessment (ICES, 2017), was used as an explanatory variable to account for the effect of overall population size on spatial patterns (i.e. density-dependent effect).

2.2.2 Environmental data

Past changes (1967-2015) of bottom temperature were taken from the Adjusted Hydrography Optimal Interpolation (AHOI; Núñez-Riboni and Akimova, 2015). This physical-statistical model is based on *in situ* observations and stability of the water column. AHOI's domain in the North Sea spans from 48 to 62°N and from 6°W to 12°E, with a spatial resolution of 0.2°×0.2°.

A projection of the ocean future state (2020-2100) under climate change was obtained from the dynamical downscaling of the global model MPI-ESM (Max Planck Institute Earth System Model) performed with a high-resolution version of the regionally coupled ocean-atmosphere climate system model MPIOM/REMO (Mikolajewicz et al., 2005; Sein et al., 2015). The model's horizontal resolution in the North Sea ranges from about 5 km at the southern coast to about 12 km at the northern boundary. A climate scenario conforming to the Intergovernmental Panel on Climate Change (IPCC), the Representative Concentration Pathway 8.5 W m^{-2} (RCP8.5; Cubasch et al., 2013) was chosen. This scenario is considered an upper limit of increasing atmospheric greenhouse gas with carbon dioxide (CO_2) concentrations in the year 2100 of about four times the preindustrial level.

By comparing model output with AHOI data for the period 1960-2005, an offset between hydrographic observations and model results was calculated for each grid cell. This offset was added to the output of RCP8.5 climate scenario to obtain a realistic future prognostic of the hydrography changes.

2.2.3 Annual CPUE maps

Matching of CPUE to temperature is hindered by differences in spatial and temporal scales between IBTS and AHOI data. AHOI are smooth maps over the complete North Sea at the monthly time scale while IBTS data are point location observations, which differ from each other even when taken inside short periods of time (few hours) and small distances (few kilometres). Both temperature and fish distribution are subject to high-frequency and short-range variations which are not resolved by the available data and are, thus, aliased to the resolvable scales (Clancy, 1983).

Additionally, both geophysical (tides, internal waves, eddies, atmospheric low and high pressure regimes) and fishery noises (schooling and avoidance of the net) are physically unrelated and thus matching both “raw” datasets yields a large noise-to-signal ratio, making the habitat modelling difficult.

To translate the IBTS data to the time and space scales of the AHOI data, year-quarter CPUE maps similar to the AHOI maps were created on a 0.5°×0.5°grid. This scale was chosen as characteristic sampling scale of the IBTS because it is roughly the average distance between the IBTS observations. Cod abundance was mapped for each year from 1967 to 2015 on our 0.5°×0.5°grid by using the GAM:

$$g(\hat{y}) = s_M(lon, lat), \qquad (1)$$

where the dependent variable $\hat{y}$ is cod CPUE, $g(\cdot)$ is a link function and s_M is a smooth function called “scatterplot smoother”. The approach of Wood (2017) (his Section 5.5.1) is followed here and s_M was chosen as a two-dimensional thin plate spline depending on longitude and latitude (Equation 5.7 of Wood, 2017 with $d=2$ and $m=2$). The model parameters are found by fitting the model to the CPUE observations through iteratively re-weighted least squares. Values of the basis dimension k for s_M were chosen ranging from roughly 20 to 100 depending on the number of data available each year (details in Appendix S1).

To deal with the many zero CPUE values, a hurdle approach (Maunder and Punt, 2004) was used, expressing the model as the product of two models:

$\hat{y} = \hat{y}_P \cdot \hat{y}_{CPUE}$, (2)

where $\hat{y}_P$ (the sub-index “P” is for “presence”) is a model describing the probability of catching (CPUE > 0) or not catching (CPUE = 0) fish, taking continuous values between 0 and 1. $\hat{y}_{\mathrm{CPUE}}$ represents CPUE for the regions where fish are present (i.e., for CPUE > 0).

Both $\hat{y}_P$ and $\hat{y}_{CPUE}$ are defined with Equation 1, but each one with a different probability distribution and link function: For $\hat{y}_P$ a binomial distribution with canonical link *logit* (Maunder and Punt, 2004) was chosen, while for $\hat{y}_{CPUE}$, a gamma distribution with logarithmic link.

These maps are direct representations of the observed CPUE and thus will be called herewith “observations”.

Because AHOI has a resolution higher than 0.5°, it must be downsampled (IEEE, 1979) to avoid aliasing. Therefore, AHOI temperature was low-passed with a Gaussian filter with correlation scale of 0.5° in all directions and the resulting field was interpolated on the 0.5°×0.5°grid of the CPUE maps.

2.2.4 Matching past CPUE and hydrography changes

Because they are mapped on the same grid, matching CPUE and temperature is simply performed grid-point to grid-point. However, in regions with no fish data (for instance, the Norwegian trench) CPUE obtained from Equations 1 and 2 is only poorly estimated (it can be extrapolated by s_M rather than interpolated from near-by fishery hauls). Such poor CPUE estimates should be excluded from the fit of the habitat model.

To define a region where the annual GAMs estimates are robust for each year, a geographical region containing all haul positions, but excluding regions scarce in data, was calculated with a Delaunay triangulation (Swan and Sandilands, 1995). Matching CPUE and hydrography was performed only on grid points lying inside Delaunay triangles with all three sizes smaller than 1 geographical degree (see Figure 1).

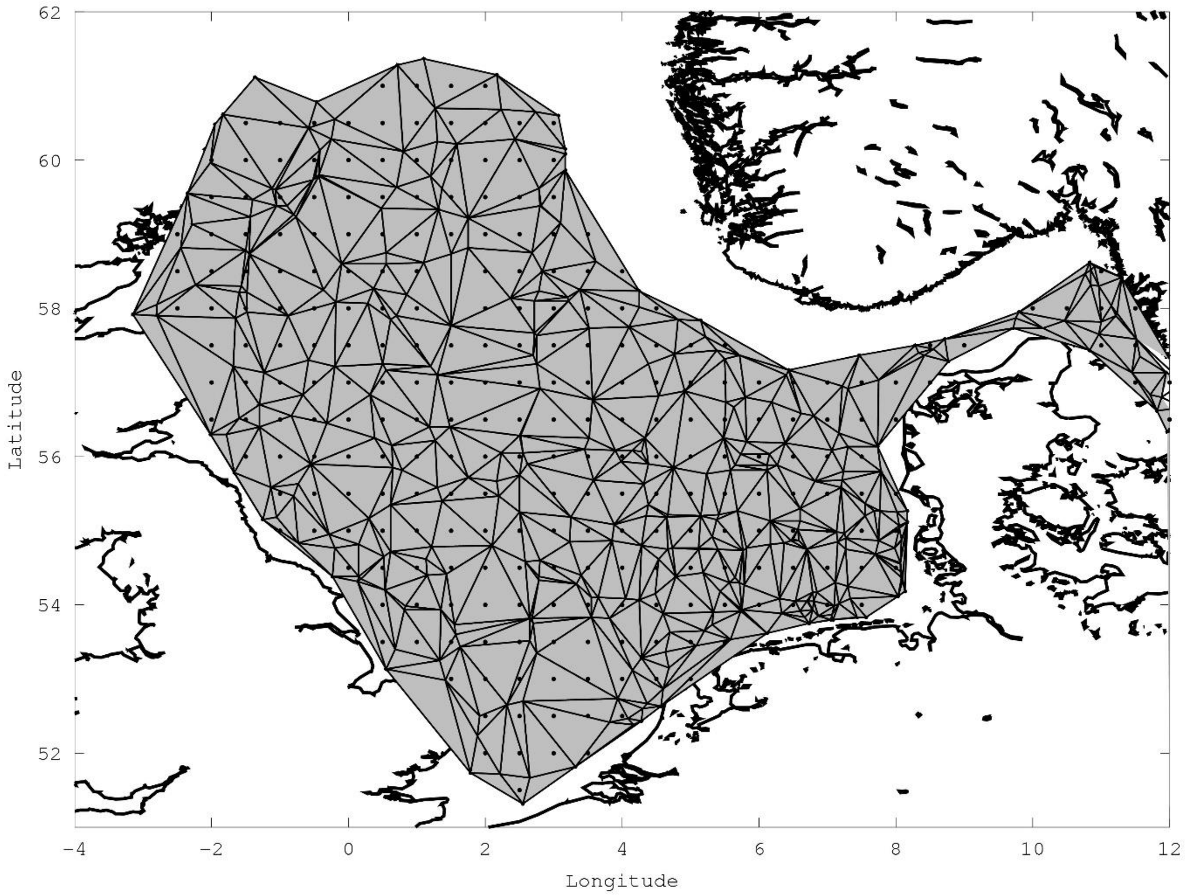

Figure 1. *Study area (the North Sea), showing the positions of the fish hauls (triangle vertices) and the mapping region (grey patches) of annual CPUE maps, Equations 1 and 2, for the arbitrarily chosen year 1984. The evenly distributed black dots are the grid points of both the downsampled hydrography model AHOI and the annual CPUE maps. Lines joining the positions of the fish hauls are edges of Delaunay triangles.*

While the main analysis has been performed with survey data from Q1, they were matched to bottom temperatures of the previous summer (i.e., Q3 with a negative lag of 6 months). A justification of this choice, including a discussion of the potential mechanisms involved, is given in Appendix S1.

2.2.5 Habitat modelling as function of environmental variables

The relation between cod abundance $\hat{y}_T$ and temperature changes T was modelled with a GAM with gamma distribution consisting of smooth functions of space and a parametric part:

$$g(\hat{y}_T) = s_{R1}(lon, lat) + a(Y) \cdot s_{R2}(lon, lat) + \boldsymbol{X} \cdot \boldsymbol{B}, \qquad (3)$$

where $\hat{y}_T = E(s_M(lon, lat))$, i.e., the CPUE expected value from the annual maps $s_M(lon, lat)$ for Q1 (Equations 1 and 2).

The sub-index "T" in $\hat{y}_T$ is for "temperature" and to distinguish this from $\hat{y}$ in Equation 2. The variable $a(Y)$ is abundance of the complete North Sea cod stock in year Y from the ICES stock assessments (ICES, 2017) for each fish length class.

$\boldsymbol{X}$ is the row vector of T:

$\boldsymbol{X} = (1, T, T^2)$ (4)

and $\boldsymbol{B} = (b_0, b_1, b_2)^T$ is a column vector of coefficients to be determined. Smoothers s_{R1} and s_{R2} are similar to s_M. s_{R1} accounts for the relation between CPUE and cod's long-term habitat, i.e., environmental variables which do not change on the time scales of this study. This "geographical attachment" (Planque et al, 2011) can be sediments, bathymetry, spawning grounds (for $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$), end points of larval drift and nursery areas (for $LC_{0\text{-}25}$) and the distribution of prey and predators.

Using $a(Y)$ as explaining covariate accounts for local CPUE variations due to the size of the entire fish stock following population dynamics (fishery, recruitment, etc.). Note $a(Y)$ depends only on year Y and not on lon, lat. Therefore, the scalar $a(Y)$ is matched each year to local CPUE(lon, lat), allowing the other covariates (for instance T) and model terms to explain the remaining variance. This approach is similar to Pinsky et al (2013), who used annual average biomass as explaining covariate. The interaction with the spatial smooth s_{R2} through the term $a(Y) \cdot s_{R2}(lon, lat)$ is intended to account for population density effects on spatial distribution of cod, i.e., displacements of fish towards less suitable regions during times of large population. In these "geographic regression models" (Hastie and Tibshirani 1993; Wood, 2017), each covariate is assumed to have a linear influence on the linear predictor for the response, but the slope parameter of that linear dependence varies smoothly with geographic location. $\boldsymbol{X} \cdot \boldsymbol{B}$ accounts for regional variations of abundance due to temperature alone.

$s_{R1}(lon, lat)$, $s_{R2}(lon, lat)$ and $\boldsymbol{B}$ are determined from $s_M(lon, lat)$, the positions *lon*, *lat* of the AHOI grid points, the AHOI Q3 bottom temperatures T and annual abundance a(Y). A logarithmic function for g was chosen because, in combination with the quadratic temperature term in Equation 4, it results in a Gaussian bell-shaped temperature effect (i.e., a smooth curve with a single maximum) when Equation 3 is re-arranged and g moved to the right-hand side:

$$\hat{y}_T = \alpha \cdot \exp(s_{R1}(lon, lat) + a(Y) \cdot s_{R2}(lon, lat) - \tfrac{(T - \beta_T)^2}{2 \cdot \gamma_T}). \qquad (5)$$

where the parameters α, β_T and γ_T depend on the parameters $\boldsymbol{B}$. Further details about the choice for Equation 5 are given in Appendix S1.

Once the habitat model was fitted with the downsampled data, model predictions were performed in the higher resolution of AHOI, i.e., on a 0.2°×0.2° grid. This approach of intentionally reducing resolution to train the model while predicting with higher-resolution has shown good performance in habitat modelling of plant distributions (Thuiller et al., 2005). CPUE changes were predicted for two cases: 1) Past changes 1967-2015, to reproduce the observed historical displacement of North Sea cod, and 2) Changes 2020-2100 from the RCP8.5 climate scenario, to project future changes of the habitat of cod under future climate change.

2.2.6 Partial effects

The partial effect of a particular covariate was calculated by evaluating all other covariates on their sample mean over all observations used to fit the model. For the case of the temperature partial effect, Equations 5 becomes:

$$\hat{y}_T(T) = \alpha \cdot \exp\left(s_{R1}(\overline{lon}, \overline{lat}) + \bar{a} \cdot s_{R2}(\overline{lon}, \overline{lat}) - \frac{(T - \beta_T)^2}{2 \cdot \gamma_T} \right).$$

The overbars denote sample means, i.e., for the case of longitude:

$$\overline{lon} = \frac{1}{n} \sum_{i=1}^{n} lon_i,$$

with lon_i each of the n longitudinal positions used to fit the model and similar equations for *lat*, a and T.

Model terms evaluated on the mean covariates can be expressed as amplitude of the exponential, similar to parameter α in Equation 5, giving a simple function of the single variable *T*:

$$\hat{y}_T(T) = \mathrm{A_T} \cdot \exp\left(-\frac{(T-\beta_T)^2}{2\cdot\gamma_T}\right), \qquad (6)$$

with $\mathrm{A_t} = \alpha \cdot e^{s_{R1}(\overline{lon},\overline{lat})} \cdot e^{\bar{a}\cdot s_{R2}(\overline{lon},\overline{lat})}$.

Because both smooths s_{R1} and s_{R2} depend partially on the same covariates *(lon, lat)*, an average of model terms (instead of covariates) is needed to estimate their partial effects.

Thus, the partial effect $\hat{y}_{R1}(lon, lat)$ for geographical attachment is given by:

$$\hat{y}_{R1}(lon, lat) = \mathrm{A_R} \cdot \exp\big(s_{R1}(lon, lat)\big), \qquad (7)$$

with $\mathrm{A_R} = \alpha \cdot exp\left(-\frac{(\bar{T}-\beta_T)^2}{2\cdot\gamma_T} + \bar{a} \cdot \overline{s_{R2}}(lon, lat)\right)$, with a similar equation for the density-dependent $\hat{y}_{R2}(lon, lat)$.

2.2.7 Suitability index

Following the same reasoning of the previous section, to isolate geographically distributed cod abundance changes due to temperature alone, the population size effect was removed from Equation 5:

$$\hat{y}_T(lon, lat, T) = \alpha \cdot \exp\left(s_{R1}(lon, lat) + \bar{a} \cdot s_{R2}(lon, lat) - \frac{(T-\beta_T)^2}{2\cdot\gamma_T}\right), \qquad (8)$$

A convenient representation for $\hat{y}_T(lon, lat, T)$ was obtained by scaling α with the historical maximum (98th percentile) of $\hat{y}_T(lon, lat, T)$ for all (*lon, lat,T*):

$$S(lon, lat, T) = 100 \cdot \frac{\hat{y}_T(lon, lat, T)}{\max(\hat{y}_E)}, \qquad (9)$$

This yielded a thermal suitability index for North Sea cod defined between 0 (completely unsuitable) to 100 (completely suitable). The few super-optimal values (those larger than the 98th percentile) were adjusted to 100.

2.2.8 Cross-validation

To validate our habitat model we have performed the following 10-fold cross-validation: After fishery and hydrography data were matched (see Subsection "Matching past CPUE and hydrography changes" above), the data-sets were split into 10 subsets containing each randomly selected 10% of the complete data-set. Afterwards, 9 subsets (i.e., 90% of the data) were used to fit the model (Equation 5). Values of the explaining co-variates in the remaining subset were used to predict CPUEs (10% of the data) which were compared with the corresponding observations to estimate residuals. The procedure was repeated with all 10 subsets.

We calculated deviance residuals R_i for gamma distribution following McCullagh and Nelder (1989) (Sections 2.3.1 and 2.4.3):

$$R_i = sign(\hat{y}_T^i - \hat{y}^i) \cdot \sqrt{2 \cdot \left(-\log\left(\frac{\hat{y}^i}{\hat{y}_T^i}\right) + \frac{\hat{y}^i - \hat{y}_T^i}{\hat{y}_T^i}\right)}, \qquad (10)$$

with $\hat{y}^i$ being the ith abundance estimate from Equation 2 and $\hat{y}_T^i$ the corresponding output estimate from the habitat model Equation 5. Note from their definitions that both $\hat{y}^i$ and $\hat{y}_T^i$ are always positive and, thus, the two quotients and the logarithm in Equation 10 are defined in all cases. Similarly, it can be shown that the square root is also always real. To generally validate the model and study also possible regional or temporal biases, deviance residuals have been grouped inside space, time and temperature bins.

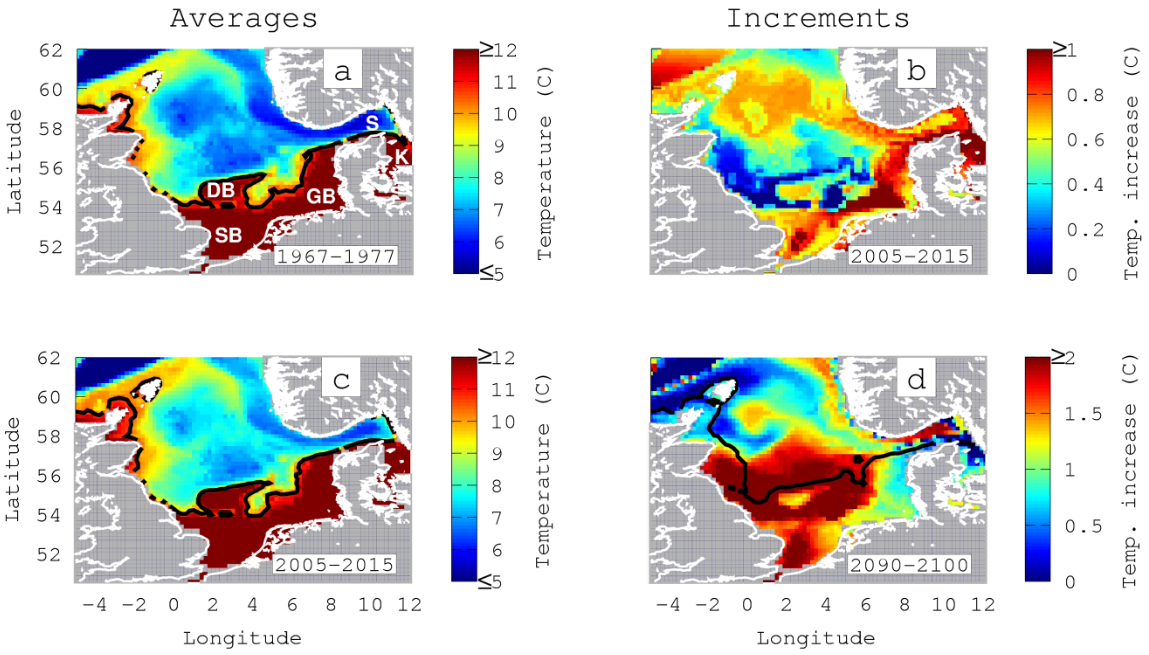

Figure 2. *Average Q3 bottom temperature (°C; left panels) and their increments (right panels) for selected decades: a) 1967-1977; b) Increment between 1967-1977 and 2005-2015; c) 2005-2015; d) Increment between 2005-2015 and 2090-2100 (RCP 8.5 scenario). The black contour is the 10.5°C isotherm. The following geographical locations referred in the text are shown in panel a: Dogger Bank (DB), Southern Bight (SB), German Bight (GB), Kattegat (K) and Skagerrak (S).*

2.3 *Results*

2.3.1 Temperature changes

Q3 bottom temperature increment in the North Sea from 1967 to 2015 (Figure 2ab) ranged between zero for the eastern coast of England and deep central parts of the North Sea to more than 1°C in the western German Bight and Skagerrak. Regions of less than 50 m in depth, mostly south of 56°N (the Dogger Bank, Southern and German Bights and southern Skagerrak; see geographical locations in panel a) show the maximum temperature increase. In regions of more than 50 m in depth, mostly north of 56°N, the temperature increase is moderate (0.7°C in the central North Sea), none or even slightly negative (around the Dogger Bank).

2.3.2 Model validation

Before describing the results of the habitat model, a brief, general validation of the model will be given. Modelled CPUE against observed values (Figure 3abc) are roughly homogenously distributed around the identity line. Only small CPUE values (CPUE<1) seem to be somewhat overestimated by the model. The model explains 43.9% (for LC_{0-25}), 36.2% (for LC_{25-40}) and 58.6% (for LC_{40-140}) of the observed deviance (see Table 1). All model terms are highly significant, with p-values undistinguishable from zero. These notions speak of a reasonable fit and good model performance.

The model term explaining the highest amount of deviance is the population-density effect $a(Y) \cdot s_{R2}(lon, lat)$ with almost 14% for $LC_{0\text{-}25}$ and $LC_{25\text{-}40}$, and with 30% for $LC_{40\text{-}140}$ (Table 1). It is followed by the spatial attachment $s_{R1}(lon, lat)$ with an explained deviance ranging from 9 to 12%. The term explaining the least deviance is the temperature effect, with less than 1% for each of the three length class models.

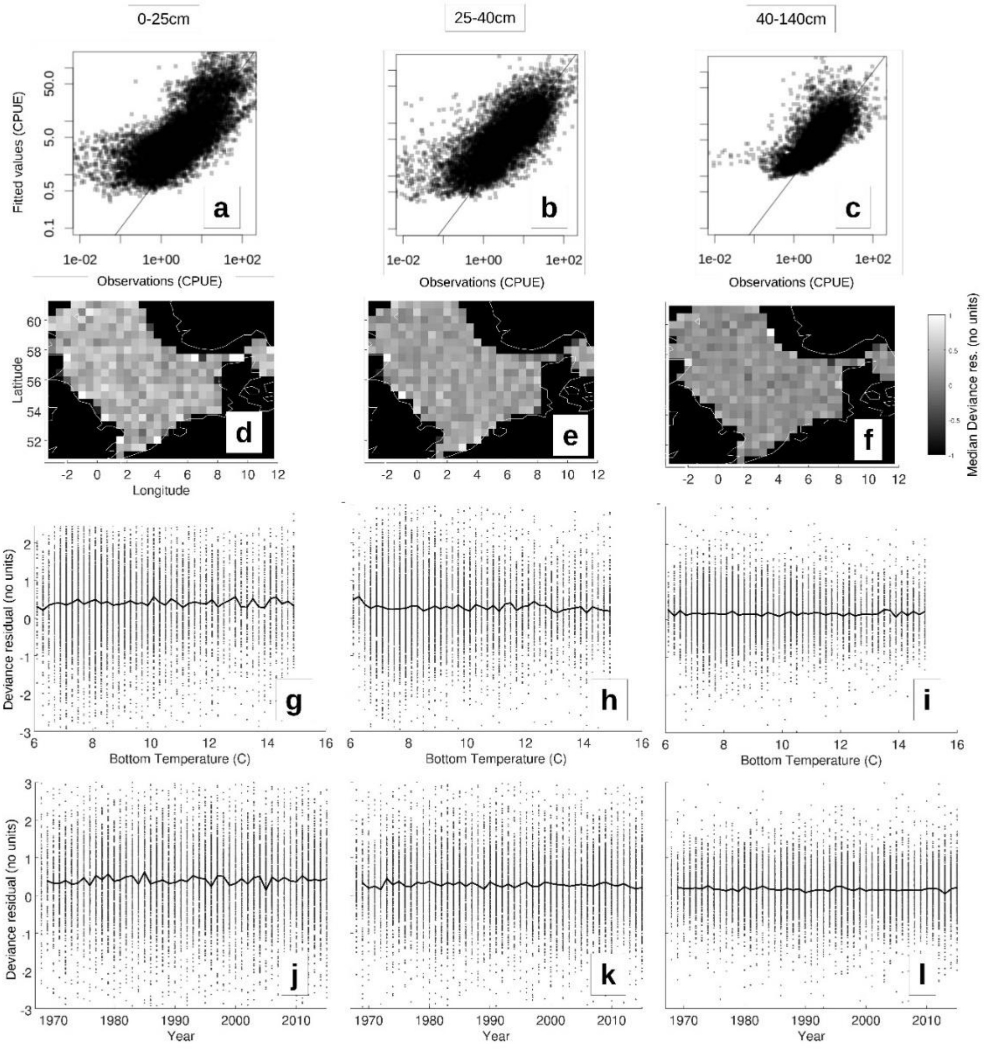

Figure 3. *Validation of the habitat model for $LC_{0\text{-}25}$ (left panels), for $LC_{25\text{-}40}$ (central panels) and $LC_{40\text{-}140}$ (right panels). abc): Modelled CPUE (Equation 5) against observed gridded CPUE (Equation 2). The straight line is the identity line. Both axes are logarithmic. Following panels: Deviance residuals (Equation 10; no units) binned in space (median residuals in each bin are shown; panels def), temperature (dots; panels ghi) and year (dots; panels jkl) bins. The black curves in panels g-l joint the median residuals in each bin.*

Table 1: *Deviance (%) explained by each model term (Equation 5) as calculated by refitting the model excluding each of the terms and comparing with the deviance explained by the full model. Deviance of the full model does not match the sum of individual deviances because the deviance of the intercept is not shown and model terms are commonly not completely independent.*

	Length class		
Model term	**0-25cm**	**25-40cm**	**40-140cm**
Full model	43.9	36.2	58.6
Temperature $\frac{(T-\beta_T)^2}{2 \cdot \gamma_T}$	0.5	0.7	0.7
Spatial attachment $s_{R1}(lon, lat)$	11.2	8.7	12.3
Population density effect $a(Y) \cdot s_{R2}(lon, lat)$	13.7	13.7	30.0

Deviance residuals from the cross-validation (Equation 10) are also roughly centered on zero and homogeneously distributed in space (Figure 3def), temperature (Figure 3ghi) and year bins (Figure 3jkl). There is only a bias of less than 0.5 (black curves in panels g to l), which is small in comparison with the amplitude of the residuals (dots). Most importantly, there are no evident residual patterns in space (panels def), temperature (panels ghi) or year (panels jkl) for all 3 length classes, indicating lack of autocorrelation in the residuals as well as a fair splitting of noise and signal. Therefore, the cross-validation supports the notion of an adequate fit and good representation of thermal habitat.

Further, more specific details relating the model validation (for instance of the temperature partial effect alone) are described for brevity in the Appendix S1 of the Supplementary Material.

2.3.3 Preferred temperatures

Preferred Q3 temperatures for North Sea cod, as given by the maximum partial temperature effects (Equation 6; see Figure S4 in the Supplementary Material, red curves), were roughly 10.0°C for LC_{0-25} and LC_{25-40}, and 11.0°C for LC_{40-140}.

2.3.4 Geographical attachment ($\hat{y}_{R1}$)

Regions in the North Sea showing large geographical attachment $\hat{y}_{R1}(lon, lat)$ (Equation 7) are (Figure 4, light grey areas): The Southern and German Bights, Skagerrak and Kattegat (see Figure 2a for geographical locations) for all three length classes, the eastern coast of England, central and eastern North Sea (east of 5°E) for $LC_{0\text{-}25}$, as well as the central and north-eastern North Sea for $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$.

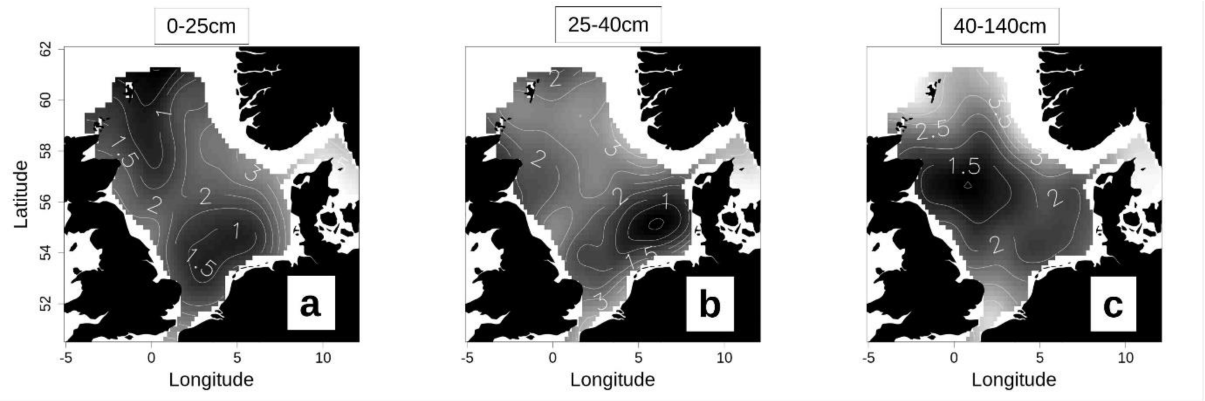

Figure 4. *Geographical attachment* $\hat{y}_{\boldsymbol{R1}}(\boldsymbol{lon}, \boldsymbol{lat})$ *(CPUE per model grid point; Equation 7) for* $LC_{0\text{-}25}$ *(a),* $LC_{25\text{-}40}$ *(b) and* $LC_{40\text{-}140}$ *(c). Lighter shading indicates regions with higher values for geographical attachment.*

2.3.5 Density-dependent habitat use ($\hat{y}_{R2}$)

Regions in the North Sea showing large density-dependent habitat use $\hat{y}_{R2}(lon, lat)$ are (Figure 5, light grey areas): The German Bight for the three length classes, the Southern Bight for $LC_{0\text{-}25}$, the central North Sea (for $LC_{0\text{-}25}$ and $LC_{40\text{-}140}$) and the northern North Sea (for $LC_{40\text{-}140}$).

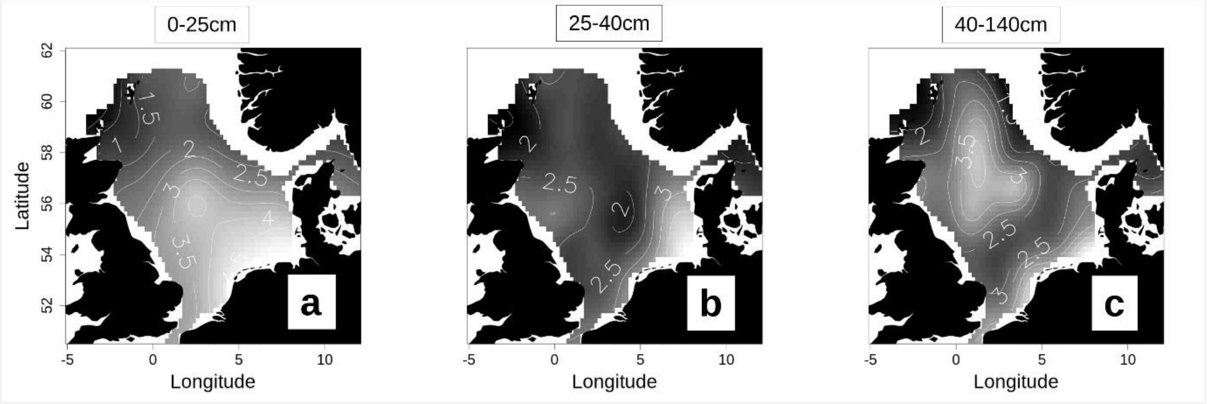

Figure 5. *As Figure 4 but for density-dependent habitat use* $\hat{y}_{R2}(lon, lat)$ *(calculated with an equation similar to Equation 7).*

2.3.6 Changes of suitable habitat

Suitable habitat attributed to historical temperature changes can be divided in 2 regions for all three fish length classes (Figure 6abc): A region of decreased suitability south of 56°N and a region northward (excepting the eastern coast of Scotland) where suitability either remained unchanged (mostly for LC_{0-25}, panel a) or increased (for LC_{25-40}, panel b, and LC_{40-140}, panel c). The region of decreased suitability covered the Southern and German Bights and the Dogger Bank (geographical locations are in Figure 2a). A maximum decrease in suitability of 12% and lower occurred for LC_{40-140} in the Southern Bight. Increase in thermal suitability was roughly 10% in southern Skagerrak for the three length classes. Additionally, LC_{25-40} (panel b) and LC_{40-140} (panel c) showed increased suitability in the northern North Sea and the edge of the Norwegian Trench of 6% or more. In the rest of the North Sea, suitability remained unchanged for LC_{0-25} (panel a), while LC_{25-40} (panel b) and LC_{40-140} (panel c) experienced modest suitability increases of roughly 2%.

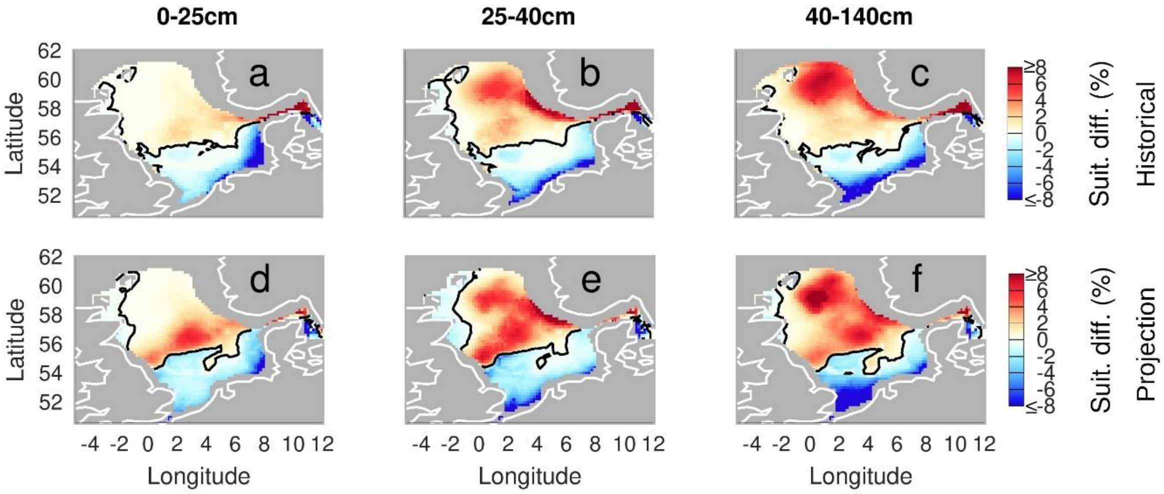

Figure 6. *Changes of thermal suitability (%; Equation 9) of North Sea cod between the decade 1967-1977 and the decade 2005-2015 (abc) and between the decade 2005-2015 and the decade 2090-2100 (RCP8.5; def) for* LC_{0-25} *(left panels),* LC_{25-40} *(central panels) and* LC_{40-140} *(right panels). Red tones represent a suitability increase, blue tones a decrease. Unchanged suitability is stressed with a thick black contour.*

The spatial pattern of suitability changes remained almost unchanged for the future projection under climate change as represented by the climate scenario RCP8.5 (Figure 6def): Suitability further decreased south of 56°N and east of Scotland. For $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$, suitability decreased in the Southern Bight additionally 15%. Similarly, suitability further increased additional 10% in southern Skagerrak for all three length classes and in the central and northern North Sea for $LC_{25\text{-}40}$ (panel e) and $LC_{40\text{-}140}$ (panel f). The only prominent difference in the changes of suitability pattern in the future projection (in comparison to the historical one) is an additional increase of suitability in the central North Sea (ca. 56°N and 3°E) for all three length classes.

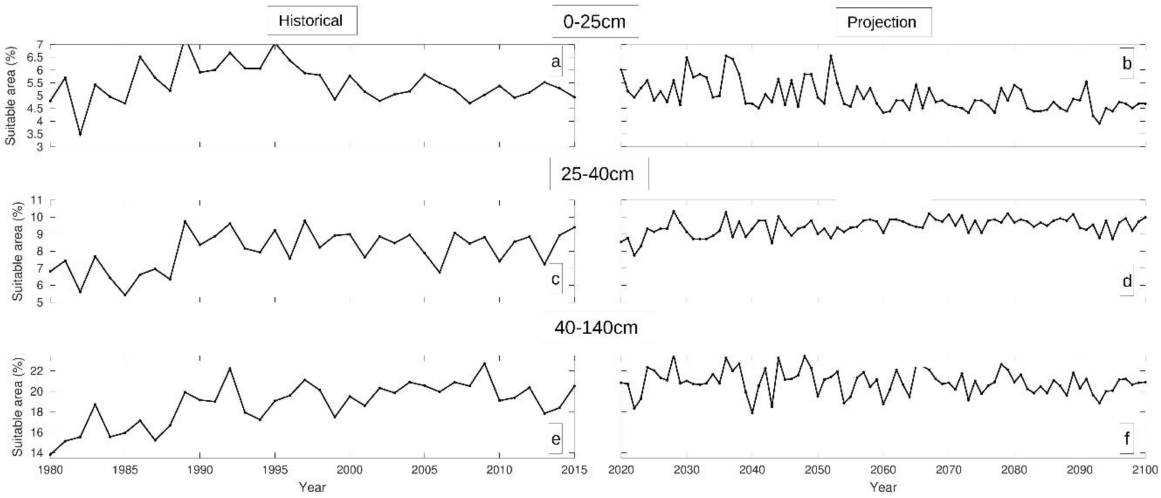

Figure 7. *Changes of the suitable area (suitability Equation 9 of more than 50%) as function of year for the historical (left panels) and projected (right panels) periods, for the 3 length classes $LC_{0\text{-}25}$ (ab), $LC_{25\text{-}40}$ (cd) and $LC_{40\text{-}140}$ (ef). The historical period is plotted after 1980 because before this year the IBTS grid (and thus the total area) was still not standardized (see Section "Spatial biases of IBTS data" in the Supplementary Material).*

Changes of the area of the most suitable thermal habitat (suitability > 50%; Figure 7) indicate an increase of suitable area for North Sea cod from the 1980s until the 1990s for the three length classes (roughly 3% for $LC_{0\text{-}25}$ and $LC_{25\text{-}40}$ and 5% for $LC_{40\text{-}140}$). After the 1990s, the suitable area of $LC_{0\text{-}25}$ (panel a) started to decrease, with $LC_{25\text{-}40}$ (panel c) and $LC_{40\text{-}140}$ (panel e) staying roughly steady. Similar trends for the 3 length classes (decrease for $LC_{0\text{-}25}$, panel b, and steadiness for $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$, panels d and f) continue for the future projection until the end of the century.

2.4 *Discussion*

2.4.1 Bottom temperature increase

Though not focusing on summer temperatures and the same time period than used in this study (1967-2015), some previous studies have also shown significant temperature increases in agreement with the summer bottom temperature changes of Figure 2ab: Hiddink and Ter Hofstede (2008) showed a trend of roughly 2°C in the average winter bottom temperature during the period of 1977-2003. Dye et al (2013) showed spatially resolved trends of satellite sea surface temperature for the period of 1983-2012, indicating changes of 0.5°C in the South (the coast of the Nederland), as well as of winter bottom temperature from *in situ* ICES observations of 0.5°C all over the North Sea (though trends in the south were non-significant due to large inter-annual variability). Using a spatially resolved model-data synthesis, Holt et al. (2012) showed strongest near bottom temperature changes (0.15°C/year) in the shallow southern North Sea during the period of 1985–2004.

2.4.2 Preferred temperature

The temperature partial effect (Equation 6 and Figure S4) reveals a preferred Q3 bottom temperature for North Sea cod of roughly 10.5°C for the three length classes. Because this preference is defined by the previous summer temperature, it is not a direct measure of the temperature experienced by individual cod during the time of the survey sampling. However, the geographical distribution of cod abundance being similar in Q1 and Q3 (Section “Q3 vs. Q1 temperature” in Appendix S1) would indicate a link to the 10.5°C isotherm (though not necessarily physiological). This finding is supported by previous studies, where the preferred temperatures were calculated as those for which the growth rate of cod is maximum; Pörtner et al. (2001) show highest growth rates for cod associated with water temperatures between 10 and 11°C (see Figure 4 therein). Brander (2003) presents a growth-temperature model based on assessment weight-at-age data, which shows that North Eastern Atlantic cod grows fastest for roughly 11°C (for fish roughly 4 kg, i.e., adults; see Figure 6 therein). Butzin and Pörtner (2016) model a physiologically optimal temperature of ca. 11°C for Atlantic cod of roughly 1 kg (i.e. juveniles; see Figure 1a therein). Histograms of frequency of Q3 isotherms occupied by tagged cod in the northern North Sea from Neat and Righton (2007) (their Figure 4c) roughly indicate a preferred temperature of 11.8ºC.

Blanchard et al. (2005) quantified the effect of temperature and fish spatial density on the distribution of the suitable habitat of juvenile cod from 1977 to 2002 using a model of ideal free distribution fed with abundance estimates of a virtual population analysis (ICES, 2004). Based on laboratory experiments from Björnsson and Steinarsson (2002), they support cooler optimal temperatures: 9.1°C for age-1 cod (equivalent to our LC_{0-25}) and 7.4°C for age-2 cod (partially equivalent to our LC_{25-40}). The differences with Blanchard et al. (2005) might lie on the preferred *in situ* temperature for cod differing from its physiological thermal optimum due to food availability or avoidance of predators. In agreement with this notion, Neat and Righton (2007) stated that thermal optima may be inadequately described by laboratory experiments (based on observations of temperature as recorded by tagged cod), with natural variance in thermal tolerance of cod allowing residence in apparently unsuitable areas.

2.4.3 Geographical displacement of cod's habitat

Modelled CPUE as function of temperature alone (Equation 9; Figure 6abc) revealed a geographical displacement of cod's suitable thermal habitat. Hedger et al. (2004) were the first discussing a displacement of cod from the Southern and German Bights in the 1980s to the north-eastern North Sea in the 1990s. Perry et al. (2005) described a long-term northward shift of latitudinal range of North Sea cod (together with other fish species), but they did not consider longitudinal shifts. Based on centre of mass calculations by Engelhard et al. (2014) the stock showed a northward displacement during the period of 1980-2010 based on IBTS survey data (their Figure 3b) and an eastward displacement during the period of 1980-2000 based on commercial data (their Figure 3a). The present study agrees with those notions by reproducing a similar north-eastward displacement until 1997, from the south-western part (the Southern Bight) onto the northern and eastern North Sea, including here part of the German Bight, the western coast of Denmark and southern Skagerrak (Figure 8; compare panel b with Figure 4, upper panels, of Hedger et al 2004). Maximal eastward displacement in 1997 was confirmed by calculating a mass centroid index as biomass-weighted average longitude (similar to Engelhard et al. 2014 and Pinsky et al. 2013; no figure shown). Afterwards, a subsequent northward displacement occurred until 2015 (Figure 6).

Engelhard et al. (2014) used linear models with random effect to examine the impact of temperature, fishery and abundance on the North Sea cod distribution. By correlation analysis, they concluded that the northward displacement of adult cod in the North Sea was due to temperature increase, but the eastward displacement was mostly related to fishing pressure.

While the spatial effect of fishing was not included in the present study, the effect of year-to-year changes of the entire fish stock (whether from recruitment or from total fishery) are included in the term $a(Y) \cdot s_{R2}(lon, lat)$ (Equation 3). The results suggest that the eastward displacement can be explained without involving fishery (i.e., with temperature alone) because its effect is eliminated in (Equation 8) and, yet, an eastward displacement is still evident (Figure 8).

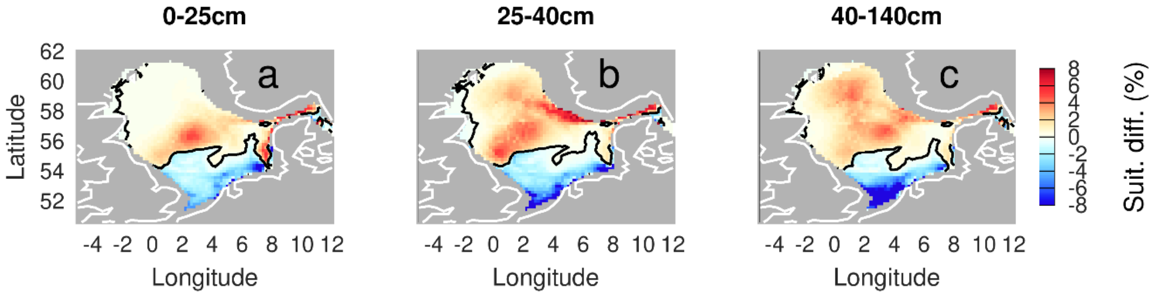

Figure 8. *Similar to Figure 5def, i.e., changes of thermal suitable habitat of North Sea cod (%) but from 1967 to 1997.*

A possible explanation of this disagreement is that the analysis of Engelhard et al. (2014) is based on a single-dimensional time series of temperature, total fishing pressure in the North Sea and longitudinal and latitudinal components of the centre of gravity of the cod stock. The lack of spatially-resolved temperature changes would not have been able to identify the eastward displacement of cod; however, the possibility of differing regional fishery impacts to cod distribution cannot be disregarded. Unfortunately, data on the spatial distribution of fishing effort with sufficient coverage of the North Sea were only available from 2000 onward for the study area, which was deemed insufficient for a robust investigation of its effect on long-term changes to cod distribution. Lack of spatially resolved fishing effort is unfortunately common in fishery studies, independently of the study area (see for another example, Pinsky et al., 2013).

By comparing tag-recorded temperatures with simultaneously sampled ICES CTD data, Neat and Righton (2007) stated that individual cod had access to cooler waters than those they were observed to have occupied. Since individual cod only seldom accessed those cooler waters, Neat and Righton (2007) conclude that the northward shift of cod towards cooler waters (described then by Perry et al., 2005) could have been due to a depletion of cod in the south rather than from increased temperature.

However, the time scale of the habitat displacement indicates that the cod stock only emigrated from a particular region due to warming conditions over decades and generational time scales. Therefore, it may be difficult to draw conclusions from the study due to a small sample size spanning a considerably shorter time period (1999-2005). Results from this and similar studies (Hedger et al., 2004; Perry et al., 2005; Engelhard et al., 2014; Nicolas et al., 2014), suggesting a real shift of cod habitat, are consistent with Neat and Righton (2007) only if the mechanism behind the displacement is not a physiological impairment of temperature for adult cod, but indirect links between temperature and other aspects of the cod habitat (like spatial differences in recruitment and survival, prey availability, etc.; Neat and Righton, 2007; Engelhard et al., 2014).

In line with these notions, the distribution of the zooplankton species *C. finmarchicus* (the preferred and often dominant prey of larval North Sea cod) has displaced northwards in the last years (Olsen et al 2011), probably as consequence of increasing temperatures. Such is inferred by a negative correlation between a plankton index (reflecting quality and quantity of plankton food available for larval cod) and sea surface temperature in the North Sea (Beaugrand et al., 2003; Beaugrand and Kirby, 2010). Furthermore, Olsen et al. (2011) pointed out, that lower larval cod survival rates would in turn lead to difficulties in stock regeneration. The implied spatial changes in survival rate of larval and success of spawning cod in different parts of the North Sea match well the changes in spatial distribution observed in this study, supporting the notion of an indirect (rather than direct) influence of temperature on the cod habitat.

The area of suitable thermal habitat for North Sea cod (Figure 7) could seem intuitively too small in absolute values (ranging from 5% for LC_{0-25} to 20% for LC_{40-140}). However, the spatial distribution of fish, and thus of the size of its suitable area, depends not only on the spatial distribution of environmental properties but also on the stock size (fish density effect). Assuming, as it seems probable, that North Sea cod was mainly underpopulated in the later years of the study period, most cod would have been concentrated only on a relatively small, highly suitable area of the North Sea (see Figure S1). This would lead to an underestimation of the size of the thermal suitable area, explaining the small values in Figure 7. However, the relative values (i.e., the changes) of suitable area are independent of an absolute scale of suitability and, thus, provide evidence of a reduction in area of the thermal habitat for LC_{0-25} and of increase for LC_{25-40} and LC_{40-140}.

This positive impact of the temperature increase on the habitat of for $LC_{25\text{-}40}$ and for $LC_{40\text{-}140}$ in a large region of the North Sea (Figure 6bcef) is contrary to Blanchard et al. (2005) who concluded that the suitable cod habitat in the complete North Sea has reduced from 1977 to 2002 (their Figure 5). An explanation for this disagreement may again be due to an underestimation of preferred temperature for North Sea cod by Blanchard et al. (2005) (physiological thermal optimum based on laboratory experiments might differ from preferred *in situ* temperatures due to food availability or avoidance of predators).The small amount of deviance explained by temperature alone (less than 1%) in comparison to all other terms (Table 1) should not be misunderstood as climate change having only a small influence on the spatial distribution of North Sea cod. Temperature changes at the climate scale explain so little variance because spatial variations of temperature or time variations at shorter time scales (like daily, annual or interannual variations) are one order of magnitude larger than climate change signals. Yet, the magnitude of those changes alone says nothing about their impact on an ecosystem. For instance, while typical variations of temperature at daily basis can be as large as 12ºC and have no negative influence on an ecosystem, a much smaller increase of temperature at climate scale of 1ºC can cause important well-documented changes (see for instance Table SPM.A1 in IPCC, 2014, for a summary of observed impacts attributed to climate change reported in the scientific literature in the last years). In addition, a large degree of abundance variability is associated with changes in overall historical population size and other spatial habitat preferences. Only after careful consideration of these influences, as accounted for by the other model terms, can the residual thermal habitat signal be identified.

Even though some previous studies have considered temperature changes as the major mechanism behind the north-eastward displacement (Hedger et al., 2004; Perry et al., 2005; Engelhard et al., 2014; Nicolas et al., 2014), or as an explanation of a general decline of the cod habitat (Blanchard et al., 2005), none have quantified the changes of suitability due to temperature alone, spatially-resolved at scales smaller than hundreds of kilometres. Therefore, the present maps of suitability changes as function of temperature alone (Figure 6) represent a step forward in our understanding of the processes driving changes to cod habitat.

2.4.4 Relation to distribution of temperature and spatial smooth terms

As described above in Materials and Methods, $\hat{y}_{R1}(lon, lat)$ (Figure 4) should represent geographical preference of non-variable environmental properties like bathymetry and sediments because it explains the geographical distribution of cod abundance only as function of space (Equation 7). $\hat{y}_{R2}(lon, lat)$ (Figure 5) depends on an interaction with abundance which modifies the effect of total population depending on location (Equation 5). Therefore, $\hat{y}_{R2}(lon, lat)$ should represent the use of habitat as function of population density or, alternatively, a density-dependent geographical preference. Large values of this term indicate the regions which North Sea cod inhabits during times of higher population sizes (the German Bight, for instance, see Figure 5). Such regions would be indicative of less-preferred habitats, but possibly still acceptable during periods of higher competition. The spatial pattern for these density-dependence terms generally shows higher values around the margins of the positive regions of the geographical attachment term. This result is consistent with the observation that fish stocks will often reduce their spatial distribution to a core, preferred habitat during periods of low population size when competition is low, which often results in higher fishing selectivity in terms of catch-per-unit effort. Thus, the geographic attachment term is likely also identifying core habitat areas that are associated with higher abundances across the entire time period.

$\hat{y}_{R1}(lon, lat)$ and $\hat{y}_{R2}(lon, lat)$ have different spatial distributions, with $\hat{y}_{R1}(lon, lat)$ having maximum mostly in Skagerrak and $\hat{y}_{R2}(lon, lat)$ in the Southern Bight (for $LC_{0\text{-}25}$), the German Bight (all length classes) and the central North Sea ($LC_{40\text{-}140}$). In the present analysis, both terms are considered as contributing to the regional changes of thermal habitat of North Sea cod in the last decades (Figure 5abc) as described by Equation 8. A qualitative discussion of which is the role of each term follows.

Because of the exponential function in Equation 8, temperature changes have a larger contribution to suitability in regions where $\hat{y}_{R1}(lon, lat)$ and $\hat{y}_{R2}(lon, lat)$ are large (for instance, the Southern Bight, the German Bight, Skagerrak and Kattegat; see Figures 4 and 5). In agreement, these regions showed strong changes of cod abundance throughout the decades in this and previous studies, indicating they are particularly sensitive to temperature changes (Hedger et al., 2004; Kempf et al., 2013 and Nicolas et al., 2014). Those changes can be geographically divided in two groups:

1) Regions of decreased suitability. These are regions of less than 50 m in depth, mostly south of 56°N (the Dogger Bank, Southern and German Bights and southern Skagerrak) and the eastern coast of Scotland. In these regions, Q3 bottom temperature was at the identified preferred level of 10.5°C or above in 1967-1977 (Figure 2a; black contour curve) and increased by roughly 1°C during the period of 2005-2015 (Figure 2b). This increase beyond the preferred temperature reduced the thermal suitability for cod for the three length classes (see Figure 6). For the LC_{40-140} class, the Southern Bight stands out with a reduction in suitability of more than 12%, which is due both to a large positive increase in temperature and a high geographical attachment ($\hat{y}_{R1}(lon, lat)$) for this length class (Figure 4c). In agreement with these findings, Hedger et al. (2004) argued that temperatures during the 2000s in the southern North Sea might have already become too warm for cod. Similar strong changes of thermal habitat in the German Bight for the three length classes (particularly LC_{0-25}) seem to be related to a large $\hat{y}_{R2}(lon, lat)$ in that region (Figure 5).

In this case, a reduction of cod population might be partially responsible (together with the temperature increase) for the strong abundance decrease in the German Bight. Such a reduction in population would had led to a concentration of cod in the most suitable region of Skagerrak (see Figure S1, bottom panels).

2) Regions with increased suitability. These are regions of more than 50 m in depth, mostly north of 56°N. From 1967-1977, these regions were considerably below cod's preferred temperature of 10.5°C (6 to 9°C; Figure 2a), while temperature increased during the last decades by roughly 0.7°C (Figure 2b). The large geographical attachment ($\hat{y}_{R1}(lon, lat)$) in these deep, cool regions of the central and northern North Sea for LC_{25-40} (Figure 4b) and LC_{40-140} (Figure 4c) renders the temperature increase (onto the preferred temperature) as particularly favourable for cod's habitat. Suitability improved up to 8% in northern Skagerrak for all length classes (Figure 6abc), the central and northern North Sea, as well as the edge of the Norwegian trench for LC_{25-40} (Figure 6b) and LC_{40-140} (Figure 6c). Therefore, these regions seem to become key zones for suitable thermal habitat for North Sea cod. This general displacement of North Sea cod habitat onto the central deep regions of the North Sea is in agreement with Dulvy et al. (2008), who observed distribution shifts into deeper waters by demersal fish assemblages as reaction to climate change. The temperature increase in the central and northern North Sea had virtually no impact on the thermal suitability of LC_{0-25} because this is a region of small geographical attachment ($\hat{y}_{R1}(lon, lat)$) for the length class (Figure 4a).

2.4.5 Future projection of cod habitat suitability

The projected changes in suitability for 2020-2100 (Figure 6def) indicate that the geographical pattern of past changes of thermal suitability (Figure 6abc) are likely to continue under the scenario RCP8.5, with a further decrease in suitability south of 56°N and an increase north of it. An examination of the geographical attachment $\hat{y}_{R1}(lon, lat)$ (Figure 4) and temperature changes (Figure 2cd) can again explain these patterns in suitability changes.

At the end of the present century, water temperature in the southern regions of the North Sea, shallower than 50 m in depth, are projected to increase by roughly 1.5°C as compared to present conditions; i.e., reaching and exceeding the preferred temperature of 10.5°C (black contour in Figure 2d). As a result, these regions are projected to further decrease in suitability in the decades to come (Figure 6def).

The regions north of 56°N were still below the preferred temperature of 10.5°C during the period of 2005-2015 (Figure 2c). Under RCP8.5, most of these regions are projected to increase in temperature by 1.5-2.0°C in the following decades (Figure 2d); for example, increases from 7 to 8.5° in the central North Sea (56°N, 5°W) are still considerably below the preferred temperature of 10.5°C. The key zones of thermal habitat remain geographically unchanged but further increase in suitability (particularly for LC_{25-40}). Roughly one half of the North Sea is projected to still be at or below the preferred temperature at the end of the century (black contour in Figure 2d). RCP8.5 represents the most pessimistic scenario regarding increase of atmospheric CO_2 (Cubasch et al., 2013) and the large range of tolerated temperatures of cod (see “Q3 vs. Q1 temperature” in Appendix S1) suggest that the central and northern North Sea will still remain, from a thermal tolerance perspective, habitable for cod till the end of the century.

Following ideas put forward by Queirós et al. (2016), such observations render the regions of increased suitability (Figure 6) as important for planning and protection policies during the following decades. These identified regions of improved habitat for cod are consistent with the findings of Queirós et al. (2016) (their Figure 1) for the north eastern North Sea and east of Scotland. However, contrary to our findings, Queirós et al. (2016) consider the north-eastern coast of England (see Figure 6def) a region where the North Sea ecosystem will become more vulnerable to increasing environmental temperature. Similarly, this study identifies the German and Southern Bights as regions of strongly decreased suitability, which were not identified as vulnerable regions to climate change by Queirós et al. (2016).

Such mismatches may be explained by the fact that Queirós et al. (2016) did not focus particularly on cod, but considered the more complex North Sea ecosystem as a whole. While this approach is helpful for a general understanding of the ecosystem, generalizing the preference of various fish species does not allow drawing conclusions about a specific fish like cod. Additionally, while focusing on the North Sea, Queirós et al. (2016) projections are based on outputs from global climate model (GCMs). A main weakness of GCMs is the neglect of tides, known to be important in the seasonal stratification of the water column in the tidally mixed areas of the southern North Sea, which induces an artificial vertical temperature gradient (Mathis et al., 2017). The regional climate model used in this study should be better able to resolve temperature increases at the spatial scales addressed by this study due to its higher grid resolution and simulation of tidal waves (Mathis et al., 2015).

Currently it is well known that most geographical regions, species, ecosystems and countries will be harmed by climate change, while others (even if to a lesser extent) are benefitting (see for instance IPCC, 2014). From a fisheries standpoint, fish habitat shifts have already caused losses to some countries while benefitting others, which has already led to conflicts and are expected to continue in the decades to come (Pinsky et al. 2018). The past changes and projections of thermal suitable habitat for North Sea cod has the potential for a similar outcome; for example, the Economic Exclusive Zones (EEZ) of Belgium, Netherlands, Germany and Denmark are completely inside regions of projected habitat suitability decreases (Figure 6), indicating greater impacts from cod displacement in the future independent of sound management. The situation for the United Kingdom remains relatively unchanged, with a portion of its EEZ decreasing on suitability but another one increasing. Norway seems to be the only country definitively winning on North Sea cod suitability, with its complete EEZ in a region of increment. This has potential major implications for management, since relative stability in quotas (each country gets a constant share of the total allowable catch) could be questioned under such circumstances.

An increasing thermal suitability in the Skagerrak and Kattegat could support mixing between North Sea cod and local cod stocks increasing the potential competition between North Sea cod and local populations. Especially juvenile cod has been proofed to drift into the Skagerrak and Kattegat from where it currently moves back to the North Sea when becoming adults (Knutsen et al., 2004).

An interesting follow-up study relating the projected displacement of North Sea cod could be to model its geographical expansion into areas outside the present survey area. This demands expanding the domain of AHOI as well or, alternatively, integrating another hydrography product with a larger domain (for instance, an ocean reanalysis) into the habitat model. Additionally, geographical attachment should be represented not with the proxy-variables longitude and latitude but with model terms depending on, for instance, bathymetry and sediments.

2.4.6 The influence of increasing temperatures on the biology of cod

The results of the analysis suggest that the suitable thermal habitat of cod has generally improved in the northern areas and decreased in southern areas of the North Sea, and these trends are predicted to continue in the coming decades under climate change scenarios (Figure 6). However, the overall net gain of roughly 3 and 6% area for the most suitable habitat of $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$ (Figure 7c and e) is opposing the observed decline in North Sea cod population (Figure S2). This apparent contradiction arises from the fact that yearly biomass changes ($a(Y) \cdot s_{R2}(lon, lat)$) explain a considerably larger amount of variation than that attributable to temperature-induced regional variations ($\frac{(T-\beta_T)^2}{2 \cdot \gamma_T}$; see Table 1). Thus, the findings must be taken within the context of other factors that have strong effects to overall abundance, such as fishing mortality and recruitment. Decreased recruitment survival has also been associated with increasing temperature (ICES WGNSSK 2018). This work has taken care to remove the influence of these confounding factors on overall population size by focusing on post-recruitment dynamics in distribution as influenced by thermal habitat changes. In this section, we draw attention to the complexity of the ecosystem cod inhabits and briefly discuss how climate change directly and indirectly affects cod through aspects other than thermal suitability, like pre-recruitment dynamics. Note, however, that this topic is beyond the scope of the present study and, thus, only a short overview can be given.

Several studies (O'Brien et al., 2000; Olsen et al., 2011; Akimova et al., 2016), have shown a negative relationship between water temperature and cod recruitment in the North Sea. Cod seems to need relatively low temperatures to spawn: During a tagging experiment, Righton et al. (2010) found preferred temperatures of around 6.02°C (±1.09) during spawning season (late winter – early spring) in the southern North Sea and 7.56°C (±0.48) in the northern North Sea, while a peak in abundance for spawning cod in the North Sea was identified for low temperatures, ranging between 5 and 7°C (González-Irusta et al., 2016).

Based on the results of the Southern Bight, which showed interannual variability in the use of spawning grounds, González-Irusta et al. (2016) imply an active avoidance of spawning grounds with winter temperatures >8°C for cod. In line with this notion, Nicolas et al. (2014) pointed out that the redistributions of adult cod in the North Sea (due to shifts of its thermal suitable habitat) could possibly lead to local failures in recruitment. They further argue that, considering that environmental temperature will continue to rise in the North Sea, the impact of temperature would further reduce the cod stock regardless of any management measure. It is important to reiterate that these observed optimal temperatures are likely to be associated with optimizing recruitment success rather than habitat suitability for the spawning cod themselves.

Climate change may evoke different responses of species, which influence their survival rate and abundance of the stock (Kingsolver et al., 2009). A change of distribution in time and space may lead to a mismatch between prey and predator, which in turn affects the connectivity and therefore the ecosystem in its vulnerability and resilience (Hollowed et al., 2013). Pörtner et al. (2016) imply that cod in the southern North Sea is already at the edge of its thermal window, limiting oxygen uptake in higher temperatures. To adapt to higher temperatures, especially in summer, cod would need to adjust their thermal window by adjusting their oxygen supply capacity and therefor their aerobic metabolism (Pörtner and Knust, 2007). Perhaps as a consequence of this limitation, and the time required for such adaptation to occur, North Sea cod has been observed over decades to be limited in its distribution by a relatively constant summer thermocline threshold, as shown by this study.

Summarizing, while the rising temperatures can have an overall positive impact on the thermal habitat of North Sea cod, they can also lead simultaneously to a general decrease of the total fish abundance because of differing physiological constraints during specific processes, like spawning, or during specific life stages, i.e. larvae. Further modeling considering all effects of temperature on North Sea cod is needed to obtain a profound understanding of the complete consequences of climate change on cod. Such understanding is indispensable for adapting management to the effects of climate change.

2.5 *Summary and Conclusions*

Previous studies have identified changes in habitat temperature as a major factor for a geographical displacement of North Sea cod in the last decades. However, none of those studies have quantified the impact of temperature on this displacement in a spatially resolved manner at scales smaller than 100 km (for instance, Nicolas et al., 2014). In the present study, the spatial distribution of different life stages of cod was modelled from 1967 to 2015.

The model was fit point-to-point with realistic past temperature changes spatially resolved at scales of 20 km. The results (Figure 6abc) show that, following observed temperature increases in the North Sea from 1967 to 2015, suitability has decreased south of 56°N (more than 12% in the Southern Bight) and increased north of it (with maximum of roughly 10% in southern Skagerrak). Because our study considers density-dependent effects associated with overall changes in population size (through the term $a(Y) \cdot s_{R2}(lon, lat)$; see Equations 5 and 8), our results indicate that the decadal displacement of North Sea cod can be explained with temperature changes alone. However, the density-dependent use of habitat (Figure 5) indicates that population decline would have been perceived stronger in the Southern Bight than in Skagerrak, giving the impression of an eastward displacement of habitat. This notion is in partial agreement with Engelhard et al. (2014) who attribute an eastward displacement of cod mostly to fishery.

Future changes to suitability were estimated throughout the century using temperature projections from a regional climate model under the most pessimistic IPCC scenario (RCP8.5). The projection (Figure 6def) shows further suitability decrease south of 56°N and increase north of 56°N, with exception of east of Scotland where suitability is predicted to decrease.

An additional 15% decrease of suitability is projected for the Southern Bight and an additional 10% in southern Skagerrak. Together with the latter region, the central and northern North Sea, as well as the edge of the Norwegian trench, will most probably remain thermally suitable for North Sea cod throughout the century in spite of strong temperature increase due to climate change.

Supplementary material

Supplementary material with an appendix describing in detail choices and additional validation criteria of our model, as well as additional figures (S1 to S6) and tables (S1 and S2) is available at ICESJMS online.

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3. *Publication 2*

Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea

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Abstract

One of the most applied tools to create ecosystem models to support management decisions in the light of ecosystem-based fisheries management is Ecopath with Ecosim (EwE). Recently, its spatial routine Ecospace has evolved due to the addition of the Habitat Foraging Capacity Model (HFCM), a spatial-temporal dynamic niche model to drive the foraging capacity to distribute biomass over model grid cells. The HFCM allows for continuous implementation of externally derived habitat preference maps based on single species distribution models. So far, guidelines are lacking on how to best define habitat preferences for inclusion in process-oriented trophic modelling studies. As one of the first studies, we applied the newest Ecospace development to an existing EwE model of the southern North Sea with the aim to identify which definition of habitat preference leads to the best model fit. Another key aim of our study was to test for the sensitivity of implementing externally derived habitat preference maps within Ecospace to different time-scales (seasonal, yearly, multi-year, and static). For this purpose, generalized additive models (GAM) were fit to scientific survey data using either presence/absence or abundance as differing criteria of habitat preference. Our results show that Ecospace runs using habitat preference maps based on presence/absence data compared best to empirical data. The optimal time-scale for habitat updating differed for biomass and catch, but implementing variable habitats was generally superior to a static habitat representation. Our study hence highlights the importance of a sigmoidal representation of habitat (e.g. presence/absence) and variable habitat preferences (e.g. multi-year) when combining species distribution models with an ecosystem model. It demonstrates that the interpretation of habitat preference can have a major influence on the model fit and outcome.

3.1 *Introduction*

Habitat preference of species is a widely known concept in ecology; first defined as the tendency of a species to choose one resource over another if both are equally available (Johnson et al., 1980). Since then, multiple definitions and extensions of the concept have been suggested (e.g. Rosenzweig and Abramsky, 1986; Hall et al., 1997; Aarts et al., 2008), next to numerous definitions of habitat itself and whether it comprises only abiotic factors or biotic relationships as well (e.g. Darwin, 1859; Allee et al., 2000; Valentine et al., 2005). These different interpretations of habitat and habitat preferences or lack of a common definition might lead to miscommunication between and misinterpretations by scientists (Hall et al., 1997). Additionally, there are still ongoing discussions about how to quantify habitat preferences in the light of their use and availability (Beyer et al., 2010). Modelling these preferences faces certain problems, such as an unequal access of individuals to all habitats and areas as well as variations of habitat availability and quality over time (Garshelis, 2000). Combining a spatially resolved trophic ecosystem model with habitat preference maps based on single species distribution models (SDM) can be a solution to better account for habitat preferences within the ecosystem model.

In the recent years, spatially explicit ecosystem models are increasingly being applied to study the effects of climate change, spatial fisheries management or to support marine spatial planning (e.g. Romagnoni et al., 2015; Alexander et al., 2016; Bossier et al., 2018). Therefore, it is necessary to establish best practices when it comes to working with spatially explicit ecosystem models as well as protocols on how to best combine these ecosystem models with SDMs. A popular ecosystem modelling approach with an increasing number of models worldwide is implemented in the Ecopath with Ecosim software (EwE, Christensen et al., 2004; Colleter et al., 2015; Heymans et al., 2016). EwE encompasses three modelling components: the static, mass-balanced Ecopath that is used to construct a ‘snapshot’ of the trophic food web of individual species or functional groups (FGs), originally proposed by Polovina (1984) and further developed since (Christensen and Pauly, 1992). The temporal simulation module Ecosim uses the Ecopath parameterization as a baseline to assess ecosystem dynamics over time, with the main goal to evaluate the impact of environmental stressors and fisheries on the ecosystem (Walters et al., 1997, 2000).

Ecospace adds the spatial dimension to the model (Walters et al., 1999; Christensen et al., 2014), providing a routine which allows for impact analysis of spatial management measures such as marine protected areas and physical structures like wind farms (Christensen and Walters, 2004). Many Ecopath and Ecosim models have been published in the past, while publications applying Ecospace are comparably rare, but increase in appearance recently (Colleter et al., 2015).

In recent releases of the EwE software, the options to inform Ecospace about habitat preferences have become very flexible. One of the first possibilities was to assign absence/presence preferences connected to static habitat layers implemented in the basemap. To include multiple environmental stressors, a new habitat foraging capacity model (HFCM) was implemented that allowed the user to implement continuous rather than binary habitat preferences (Christensen et al., 2014). The foraging capacity of a cell is based on the foraging arena theory implemented in Ecosim, defining the capacity of a cell for a predator to forage on a prey (Ahrens et al., 2012). It is used as a multiplier to the search area (A) in the foraging arena equation (Christensen et al., 2014). From here on, multiple, cumulative environmental drivers could also affect the computed foraging capacity of the FGs in a given cell, implemented via environmental preference functions. This increased the variation between the cells to distribute the FGs over the map where they are most likely to occur (Christensen et al., 2014). Furthermore, it opened the opportunity to close the gap between SDMs and ecosystem models, by allowing the user to implement environmental response functions derived from SDMs (Grüss et al., 2016). One of the most recent improvements to relate FGs' distributions in Ecospace directly to scientific surveys, is the possibility to implement scaled habitat preferences predicted by external SDMs directly as foraging capacity maps into Ecospace (Figure 1). This increases the interchangeability between different model types further.

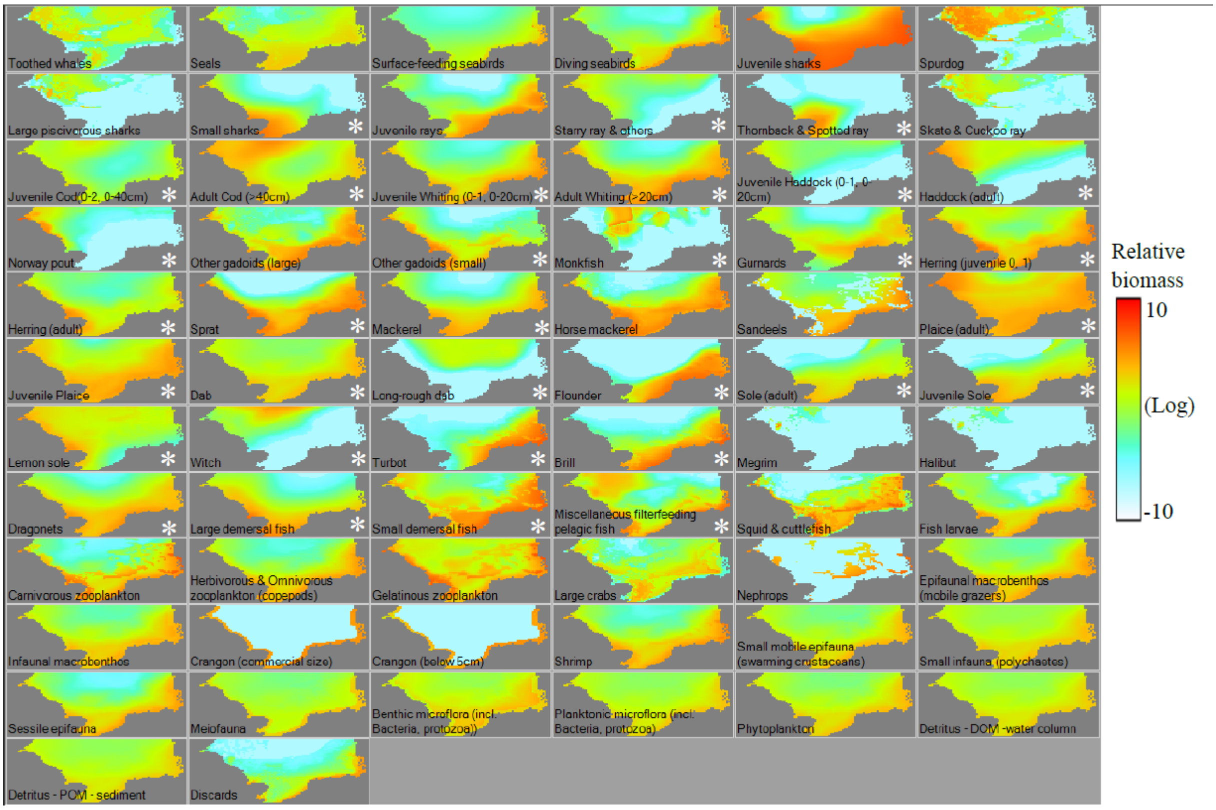

Figure 1: *Biomass maps created within the southern North Sea Ecospace model for all FGs. Colors depict high (red) to low (blue) relative biomass. Thirty-two of these functional groups were driven via external foraging capacity maps based on habitat preferences derived from species distribution models (SDMs), indicated by the white star.*

Thus far, temporal abundance changes of each FG in Ecosim are reproduced in each grid cell of Ecospace. The new spatial-temporal data framework allows for time-dynamic inclusion of geospatial data such as habitat maps during each Ecospace run (Steenbeek et al., 2013). Including dynamically changing environmental driver maps, and a dynamic redistribution of biomass based on species environmental preferences allows for a better representation of changes in the physical habitat (Christensen et al., 2014). This also allows implementing time-dynamic foraging capacity maps based on external SDMs during the Ecospace run. This enables the modeler to bypass the necessity to enter environmental preference functions in Ecospace. Implementing these maps can be done, just like the environmental driver maps, in different temporal frequencies, e.g. seasonally, annually or once every few years. To integrate them with the computed foraging capacity and to account for shifts in habitat preferences over the period of the model run increases the realism in distributing the biomass of FGs over the grid cells.

Combining the single species distribution modelling approach with a trophic ecosystem model in this way bears potentials to increase our knowledge on impacts of changes in biotic and abiotic factors on species and fisheries yield. This increases Ecospace usefulness as a support tool for spatial management decisions. The application of this approach to many FGs simultaneously in a strongly exploited ecosystem like the North Sea has so far not been reported. Neither has the test for the sensitivity of different implementation frequencies of external foraging capacity maps, which might show how inertia and sensitivity of the ecosystem model differs with forcing frequencies.

Therefore, this study aims to analyze which representation of habitat preference best serves to create foraging capacity maps and is capable to interact with the information contributed by the tropho-dynamic model. Furthermore, the sensitivity of the updating frequency of foraging capacity maps (e.g. seasonal, annual, multiannual) on Ecospace's biomass and catch predictions compared to the empirical data is being evaluated.

3.2 *Material and Methods*

3.2.1 Ecopath with Ecosim model of the southern North Sea

Our Ecospace model is based on a previously published EwE model (Stäbler et al., 2016), representing the ecosystem of the southern North Sea in the base year 1991 up to 2010 (statistical areas IVb and IVc, defined by the International Council for the Exploration of the Sea (ICES)). The southern North Sea model has a focus on commercially important species and higher trophic levels, and comprises 68 groups of which 35 represent multi-species groups and 30 single species. Particulate organic matter, dissolved organic matter and discards are represented in three additional groups. Life history changes are implemented for seven commercially important species, cod (*Gadus morhua),* whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), sole (*Solea solea*), plaice (*Pleuronectes platessa*) and brown shrimp (*Crangon crangon*) through the multi-stanza approach (Walters et al., 2010).

These stanzas characterize juvenile and adult life stages of the fish species, while brown shrimp was split according to the body size they need to reach to be targeted by the fishery. Fishery exploitation is implemented in the model through twelve fleets, representing the diversity of the fishing sector in this region.

There have been several adaptations to the original Ecopath and Ecosim model of the southern North Sea. These were changes in the diet matrix and the addition of off-vessel prices in Ecopath, as well as some changes to the reference time series in Ecosim. For more detail, see Appendix A. To account for these alterations in Ecopath and Ecosim, we used the new stepwise fitting routine to fit predator/prey vulnerabilities and primary production anomaly splines that resulted in the lowest discrepancies between the model and the observed time series (Scott et al., 2016). The fitting routine automatically repeats the sensitivity search and Ecosim runs with an increasing number of vulnerability parameters. These different parameterizations towards reference time series were fitted; the resulting measures of fit include residual sum of squares (SS, log-scaled biomass, catches) and Akaike information criterion (AIC; Akaike, 1974). The Ecosim settings with the lowest AICs (AICs that differed more than 2 compared to the lowest AIC were excluded) were then tested for their model efficiency (see Table 2, Stow et al., 2009) in reproducing the reference time series of biomass and catch. For further information on this Ecopath and Ecosim model of the southern North Sea, see Stäbler et al. 2016, 2018 and 2019 and Appendix A.

3.2.2 Ecospace of the southern North Sea

The software used to construct the Ecospace model is EwE version 6.6, professional edition, and fit to time series for the period 1991 - 2010 and run in monthly time steps. As a basis for distributing biomasses simulated by Ecosim in space, a basemap of the study area was constructed as a georeferenced Esri American Standard Code for Information Interchange map (Esri ASCII), with a resolution of 0.125° per edge length of each grid cell. The bounding box for the study area ranged from -4° to 9° longitude and from 51° to 57.25° latitude. We assigned static habitats to the basemap encompassing various sediment structures, a distance to coast measure and fishing habitats. All habitat maps were binary, defined by 1=present and 0=not present. Sediment types were derived from the European Marine Observation and Data Network (EMODnet, 2017) using a seabed substrate map that includes five substrate classes (mud to muddy sand, sand, coarse sediment, mixed sediment, rock and boulders).

To account for seabirds living close to the coast to breed on land, the habitats “near coast” and “marine” were added. The 12 nautical mile zone representing territorial waters of each surrounding country was used as a proxy to separate coastal from offshore areas. Additionally, depth was included as an environmental driver, ranging from 0-100 m. Data used to reproduce the bathymetry of the study area was retrieved from the General Bathymetric Chart of the Oceans (GEBCO, 2017). These have a higher resolution than Ecospace; therefore, within each grid cell the mean depth was taken and then classified into ten discrete depth categories in ten meter intervals, starting with 5 m.

Fishing effort allocation across the grid implements the effect of spatially explicit exploitation (Christensen et al., 2008; Christensen and Walters, 2004; Walters et al., 1999). Usually, fishing fleets are assigned simply to the same habitats as FGs targeted in order to distribute fishing effort on the basemap. We attempted a more realistic representation of the spatial dynamics of the fisheries using spatially resolved effective fishing effort data (STECF, 2017). However, for a few fleets that have very specific target FGs (like sandeel and nephrops trawlers) the fleets follow the distribution of these FGs, while all others were assigned to the before mentioned habitat structures. Mean annual primary production was added to the basemap as a static layer, based on Moderate Resolution Imaging Spectroradiometer (MODIS) ocean color data; from 2002 to the present (Behrenfeld and Falkowski, 1997; http://www.science.oregonstate.edu/ocean.productivity/index.php) and was kept constant over time to solely examine the influence of varying foraging capacity.

Ecospace takes a habitat preference approach and allocates Ecosim’s biomass dynamically over a basemap of grid cells with respective preferred and non-preferred habitats. The spatial allocation of the biomass is based on the foraging capacity for each FG within a cell. Within cells with preferred habitats, FGs have increased feeding rates (allowing for increased growth rate) and survival rates. Outside of these cells, dispersal rates, which depict random movement within the model area, may be higher to escape the non-preferred habitats (Christensen et al., 2008). In the HFCM, the computed foraging capacity within Ecospace can be overwritten by external foraging capacity or multiplied by cell specific habitat capacity and environmental capacity. As external foraging capacity, scaled habitat preference maps predicted by SDMs can be integrated into Ecospace directly. These maps have the same spatial extent and resolution as the Ecospace basemap and each grid cell has a specific foraging capacity between 0 and 1 assigned to.

From here on, habitat preferences refers to the predicted results of the SDMs, while they are referred to as external foraging capacity as soon as they enter Ecospace to overwrite the computed foraging capacity. In addition, Ecospace can calculate foraging capacity from FGs affinity for given habitats and from FGs functional responses to environmental conditions. Habitat capacity is based on the habitat layers implemented in the basemap (here sediment and distance to coast). Each habitat type gets a proportion assigned of how suitable the habitat is for a certain FG. Environmental capacity is based on environmental driver maps (here depth). It is being ascertained by applying an environmental response function specific to each FG to the environmental driver map. All aforementioned possibilities within Ecospace can be applied individually or combined (Figure 2).

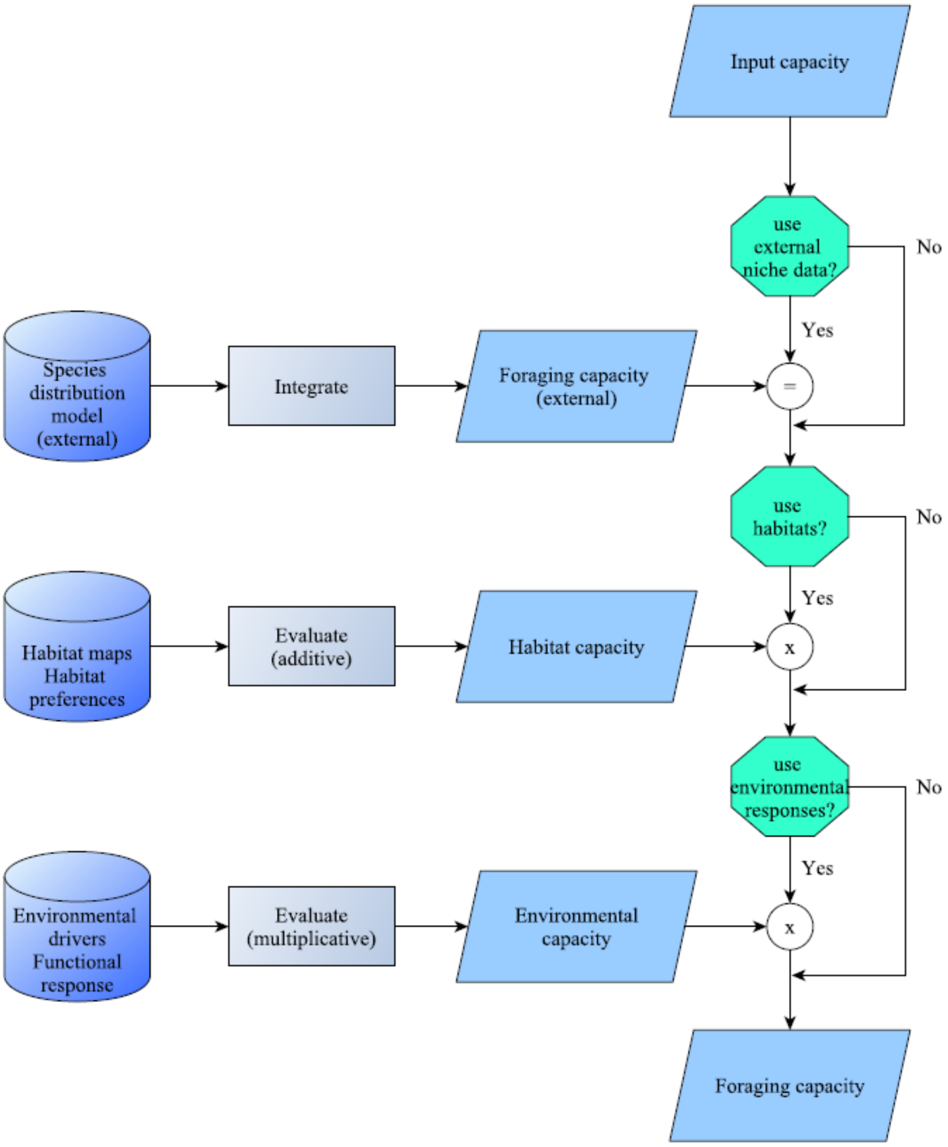

Figure 2: *Foraging capacity options in Ecospace*

In this study, foraging capacity for most FGs was pre-defined by external foraging capacity maps, while for some FGs the foraging capacity was calculated from affinity for habitats and/or environmental preferences. Distributions for six FGs were affected though habitat affinities, while for eleven FGs an environmental response function depending on depth was implemented. Foraging capacity maps for 32 FGs were driven from external habitat preferences through the spatial-temporal data framework (see Figure 1). The multi-stanza modus of Ecospace computes the distributions of multi-stanza groups to be highly correlated within each group, which sometimes leads to a better fit if only one of the stanzas is distributed by temporarily changing the foraging capacity. We followed this approach for the FG plaice, where only the distribution of the juvenile stanza was driven by its foraging capacity. The adult stanzas distribution was a result of the distribution of juveniles as well as presence of predators and prey. For crangon, the stanza smaller than commercial catch size followed the distribution of the stanza targeted by fisheries.

In Ecospace, biomass is time-variant within a cell even if no external forcing occurred since a fraction of biomass is always dispersing randomly around the basemap, represented by the dispersal rate (km/year). The base dispersal rate set as default within Ecospace is 300 km/year, except for detritus (Christensen et al., 2008). For our model, we chose five different dispersal rates to represent the mobility of FGs based on their life form, i.e. 1000 km/year for fast top predators, 600 km/year for pelagic FGs, 300 km/year for faster moving demersal fish FGs, 30 km/year for mainly flat fish and zooplankton FGs, 3 km/year for nearly stationary or sessile groups (primarily benthic FGs). These dispersal rates were chosen based on the general “300-30-3” rule (similar to Chen et al. 2009), expanding the classes for more differentiation in speed. Using a custom built plug-in for EwE, each Ecospace run was started with a 10-year spin-up (or burn-in) period to stabilize FG distributions. For more details about the Ecospace structure, see the Appendix A.

3.2.3 Species distribution models

The new spatial temporal data framework within Ecospace allows for the implementation of time dynamic foraging capacity maps. These are habitat preferences generated by SDMs prior to implementation and then applied directly as foraging capacity, with a range of 0-1. This method was applied for thirty-two FGs, representing most single species FGs, including six multi-stanza groups, and eleven multi-species FGs (see Appendix A).

These groups represent mainly commercially important species and also groups that were well represented within the scientific surveys that sampled the data used for the SDMs. Data on species abundance for this analysis was gathered from two different surveys, due to the different catchability of the surveys for certain groups. Catch-per-unit-effort data (CPUE, number_per_hour) from quarter 3 (Q3, only sampled quarter) of the ICES Beam Trawl Survey (BTS) from 1991-2010 was used for juvenile and adult sole (*Solea solea*), brill (*Scophthalmus rhombus*) and turbot (*Scophthalmus maximus*), long-rough dab (*Hippoglossoides platessoides*) and monkfish (*Lophius piscatorius*). For the remaining 25 FGs, CPUE data was used for quarter 1 (Q1) and Q3 of the ICES International Bottom Trawl Survey (IBTS) from 1991-2010 (see Appendix A). For the chosen timeframe, Q1 and Q3 are the only two quarters that were sampled continuously.

One of the major aims of this study is to identify the best representation of habitat preference when combining an SDM with a trophic food web model. We tested two representations in this study: a more general representation based on binary data (presence/absence model) versus one that accounts for gradations in quality by considering abundance (hurdle model). The idea is to identify if a sigmoidal or an exponential response is best suited when combined with the trophic model. The hurdle model contains binary (presence/absence) and continuous response (abundance) sub models that are applied to the data separately and the predicted distribution resulting them are being multiplied at the end (Cragg, 1971; Maunder and Punt, 2004). A hurdle model approach is widely used in SDMs due to its ability to deal with data sets that contain a high number of zeros (i.e. 'zero-inflated').

In their recent published paper, Coll et al. (2019) used Bayesian models (integrated nested laplace approximation; INLA) to create single FG distribution maps. We tested the applicability of INLA for our study against the fitting method commonly used for generalized additive models (GAM; Hastie and Tibshirani, 1986), i.e., PIRLS (Penalized Iteratively Re-weighted Least Squares). The GAMs were created using the ‘mgcv’ package (Wood, 2009), while INLA was applied with the ‘R-INLA’ package (Rue et al., 2009). Due to high computational costs, we modelled only key groups with either high commercial importance or a small sample size (cod (adult), whiting (adult), starry ray & others, sole (adult) and plaice (adult)). Both modelling approaches were fitted to presence/absence (PA) data and a combined hurdle model.

For the hurdle model, a GAM was fitted to CPUE (with CPUE>0) data using the classical approach (PIRLS) and using INLA and the resulting predictions were subsequently multiplied with the results of the PA model. To consider time dependency, both the GAM and R-INLA were run for each year separately. A k-fold cross-validation approach with 4 folds was applied to compare the predictive skill of the different model types. The fit was assessed with the area under the response curve (AUC; Swets, 1988) for the presence/absence and with the root mean squared error (RMSE) for the hurdle model. The results of this assessment showed that for this study, INLA does not outperform the less time-consuming fitting method used in a GAM. Therefore, GAM was chosen and will be described in more detail in the following paragraph. For more information about the comparison of these two SDMs, see Appendix 1.

Presence/absence data were modelled using a GAM with the canonical link logit. For the hurdle model, also CPUE data was modelled with a non-zero abundance GAM ($\widehat{CPUE}$=CPUE>0) using the gamma distribution with a log link to assess the abundance:

$$logit\left(\widehat{PA}\right) = s(lat, lon, k = 10), \qquad (1)$$

and

$$log\left(\widehat{CPUE}\right) = s(lat, lon, k = 10), \qquad (2)$$

with *lat* and *lon* representing sampling locations, $\widehat{PA}$ and $\widehat{CPUE}$ being the modelled dependent variables, respectively. The s(lat, lon) smoother is a thin plate regression spline (Wood, 2003), using the basis dimensions k (Wood, 2017). The results were then used to predict the occurrence and the presence in survey catches on a spatial grid implemented in Ecospace (i.e., 0.125° x 0.125°). Consequently, the hurdle model (*hurd*) was applied, combining the resulting predictions of the two models, $\widehat{PA}$ and $\widehat{CPUE}$:

$$hurd = \widehat{PA} \times \widehat{CPUE}. \qquad (3)$$

Finally, all model predictions were standardized between 0 and 1, dividing all predictions by their annual maximum for the later use in Ecospace. In some cases the annual CPUE was n<=10 and could not be modelled for these specific years (pertains six FGs) even though over all the species were well represented within the data. In these cases, maps from the previous year were taken (see Appendix B).

3.2.4 Ecospace scenarios

Eight scenarios were tested to evaluate the influence of the different habitat preferences representations (PA versus hurdle) and to address the second aim of the paper, the analysis of the best input frequency. Each representation was applied at each frequency (Table 1). The baseline scenario was used to compare the originally static version of Ecospace to the time dynamic foraging capacity.

Table 1: *Scenarios of implementing habitat preference maps at different temporal frequencies. Each frequency was tested twice, once with habitat preference maps based on the presence/absence model, once with maps based on the hurdle model.*

SDM	*Scenario name*	*Frequency*	*Data Input*
presence/absence	Seasonal	Every 6 month, implemented in January and July	IBTS FGs: maps for Q1 and Q3 BTS FGs: maps only for Q3, starting map for the first half of 1991
presence/absence	Annual	Annually, implemented in January	IBTS: Mean map of Q1 and Q3 BTS: map of Q3
presence/absence	Multi-years	Every 5 years (1991, 1996, 2001, 2006)	IBTS and BTS: Mean map for 5 years (1991-1995, 1996-2000, 2001-2005, 2006-2010)
presence/absence	Baseline	Once before the run	IBTS: Mean map of 1991 BTS: Q3 map of 1991
hurdle	Seasonal	Every 6 month, implemented in January and July	IBTS FGs: maps for Q1 and Q3 BTS FGs: maps only for Q3, starting map for the first half of 1991
hurdle	Annual	Annually, implemented in January	IBTS: Mean map of Q1 and Q3 BTS: map of Q3

hurdle	Multi-years	Every 5 years (1991, 1996, 2001, 2006)	IBTS and BTS: Mean map for 5 years (1991-1995, 1996-2000, 2001-2005, 2006-2010)
hurdle	Baseline	Once before the run	IBTS: Mean map of 1991 BTS: Q3 map of 1991

For each scenario, skill assessments for the model predictions of biomass and catch have been conducted for all FGs that have been fitted to time series in the underlying Ecosim (Table 2, see Appendix B for a list of FGs used for the skill assessment). Before calculating fit statistics, these biomass and catch time series were smoothed by applying a GAM to represent general trends. Furthermore, since the reference time series of biomass and catch are relative measures only, they were scaled to the absolute values resulting from Ecospace (for more information see Appendix B). We used a set of measures for the skill assessment. They inform about either the temporal, the spatial or the spatial-temporal fit of Ecospace. The root mean square error (RMSE) describes the distance between simulated and observed time series. Model efficiency (MEF) is a measure of model skill with respect to the range of natural variations. A value >0 indicates a close match between the time series, while values <0 indicate that a constant value would be a better predictor than the simulations (Stow et al., 2009). In this study, for biomass and catch the MEF was calculated in relation to the biomass or catch value of the base year 1991. To assess the spatial fit of the different scenarios, the Schoener's D index was used. It serves as a metric to calculate spatial niche overlap, and therefore enabling the spatial comparison between the SDMs and Ecospace. It is based on the probability of occurrence, ranging from 0 (no match) to 1 (maps are identical; Schoener, 1968; Warren et al., 2008). Here we applied the hurdle-based habitat preference maps from the SDM models a second time. Not as input maps into Ecospace, but as a reference of observed habitat preferences. We used the hurdle maps rather than the PA maps, because they include species abundance (here: survey-based CPUE) and not just presence/absence and the resulting maps in Ecospace are representing biomass rather than just presence/absence distributions. To avoid confusion with the hurdle scenarios, it will be called *abundance reference* from here on.

The overlap was therefore calculated between the Ecospace biomass distributions at the end of every year and the abundance reference. Spatially resolved catch data for the entire time period in this study was not available. Therefore, a comparison between observed fishing distribution and spatially disaggregated Ecospace catch results was not an option. We calculated the Pearson correlation (PEAR) between reference time series used in Ecosim for catch and catch results derived from Ecospace as an additional metric to evaluate the fit of the model in terms of spatially aggregated catch.

Thresholds were applied to assess the number of FGs that achieve a good fit in relation to a satisfactory threshold. Some of the thresholds were chosen ad hoc, others were defined based on their general range (like Schoener's D index). Additionally, a Taylor diagram (Taylor, 2001) was created between the abundance reference and the scenario outputs, to directly evaluate the spatial-temporal fit. Each grid cell of each year for each FG was compared between observation and scenario output to account for differences in space and time.

Table 2: *Skill assessment metrics. Thresholds mark the breaking point above which the results were classified as satisfying. Sim represents the smoothed mean biomass or catch results of Ecospace extracted at the end of each year; obs refers to the equivalent time series implemented in Ecosim. Except for Schoener's D, all values were log-transformed. psim represents probability values in the annually extracted Ecospace results for each cell and pobs probability values in each cell of the reference maps.*

Metric	*Formula*	*Threshold*
Root mean squared error (RMSE)	$\sqrt{\frac{\sum_{i=1}^{N}(\mathrm{sim}-obs)^2}{N}}$	RMSE<=0.25
Model efficiency 1991 (MEF)	$\frac{(\sum_{i=1}^{n}(obs-obs_{1991})^2-\sum_{i=1}^{n}(sim-obs)^2}{\sum_{i=1}^{n}(obs-obs_{1991})^2}$	MEF>0
Pearson correlation (PEAR)	$\frac{Cov(sim,obs)}{\sqrt{Var(sim)}*\sqrt{Var(obs)}}$	PEAR>=0.75 PEAR<=-0.75
Schoener's D	$1-\frac{1}{2}\sum_{i}\lvert psim-pobs\rvert$	Schoener's D>=0.5

3.3 *Results*

3.3.1 Comparison of Ecospace scenarios – Biomass

The model fit of Ecospace was evaluated for three aspects (temporal, spatial and spatial-temporal fit) and for two variables (catch and biomass). Results for the skill assessment metrics evaluating the temporal fit of the mean biomass revealed, that scenarios forced with capacity maps from PA GAMs provide better fits than the scenarios that were forced with capacity maps from the hurdle model (Table 3). Among the PA forced scenarios, the multi-year scenario achieved the best results for MEF and RMSE, while the static baseline scenario performed worst in terms of RMSE. In contrast to the PA scenarios, the temporally variable hurdle scenarios performed worse than the static baseline scenario in the case of metrics that evaluate the temporal fit. The seasonal hurdle scenario had to be excluded from all following skill assessments, since it resulted in the depletion of the FG mature herring, implying a bad fit already within the Ecospace run.

Table 3: *Model efficiency (MEF) and root mean squared error (RMSE) were used to assess the temporal fit, and Schoener's D index was applied to evaluate the spatial fit. All metrics show the skill assessment based on biomass averaged over all FGs for each scenario. Results marked with * represent the best results in terms of the overall mean. The numbers within the brackets display percentage of functional groups that exceeded the thresholds (MEF threshold= 0, RMSE threshold= 0.25, Schoener's D index= 0.5).*

Scenario\Skill	*MEF biomass*	*RMSE biomass*	*Schoener's D biomass*
PA Seasonal	0.497 (92.2)	0.4123 (33.3)	0.6695 (96.9)
PA Annual	0.5358 (94.1)	0.4065 (33.3)	0.6734 (93.8)
PA Multi-years	0.5719 (92.2)*	0.3986 (37.3)*	0.6587 (93.8)
PA Baseline	0.5421 (96.1)	0.4145 (29.4)	0.6214 (87.5)
Hurdle Annual	-0.2413 (70.6)	0.5466 (17.6)	0.7503 (93.8)*
Hurdle Multi-years	0.0518 (70.6)	0.5198 (19.6)	0.7182 (93.8)
Hurdle Baseline	0.551 (94.1)	0.423 (31.4)	0.5454 (68.8)

When comparing the spatial distribution of the abundance reference with the Ecospace maps, the Schoener's D index showed the best results for the temporally variable hurdle scenarios. All PA scenarios followed this and the worst fit was achieved with the static hurdle baseline scenario. Evaluating individual Schoener's D indices on FG level revealed only small differences within the PA or hurdle scenarios. Therefore, in the following, only the example of the PA annual scenario is discussed in detail (see Appendix B for the other individual results). Only two of the thirty-two FGs with foraging capacity maps displayed medians below the threshold of 0.5 for the individual Schoener's D indices (Figure 3). Gurnards and herring (adult) had the worst fits in all PA scenarios with time dynamic maps. Some FGs showed a large range of values in between years (e.g. monkfish, norway pout, thornback and spotted ray), while others showed 'outliers', identified by the boxplot. There was no evident correlation between the trophic level and the fit of the model. In addition, there was no evident difference between FGs for which the foraging capacity was forced by habitat preference maps based on data of the IBTS and the BTS survey. Due to sampling design, the former were forced by a mean map between Q1 and Q3, while maps based on data collected in Q3 only forced the latter. Multi-stanza FGs displayed no pattern within these results.

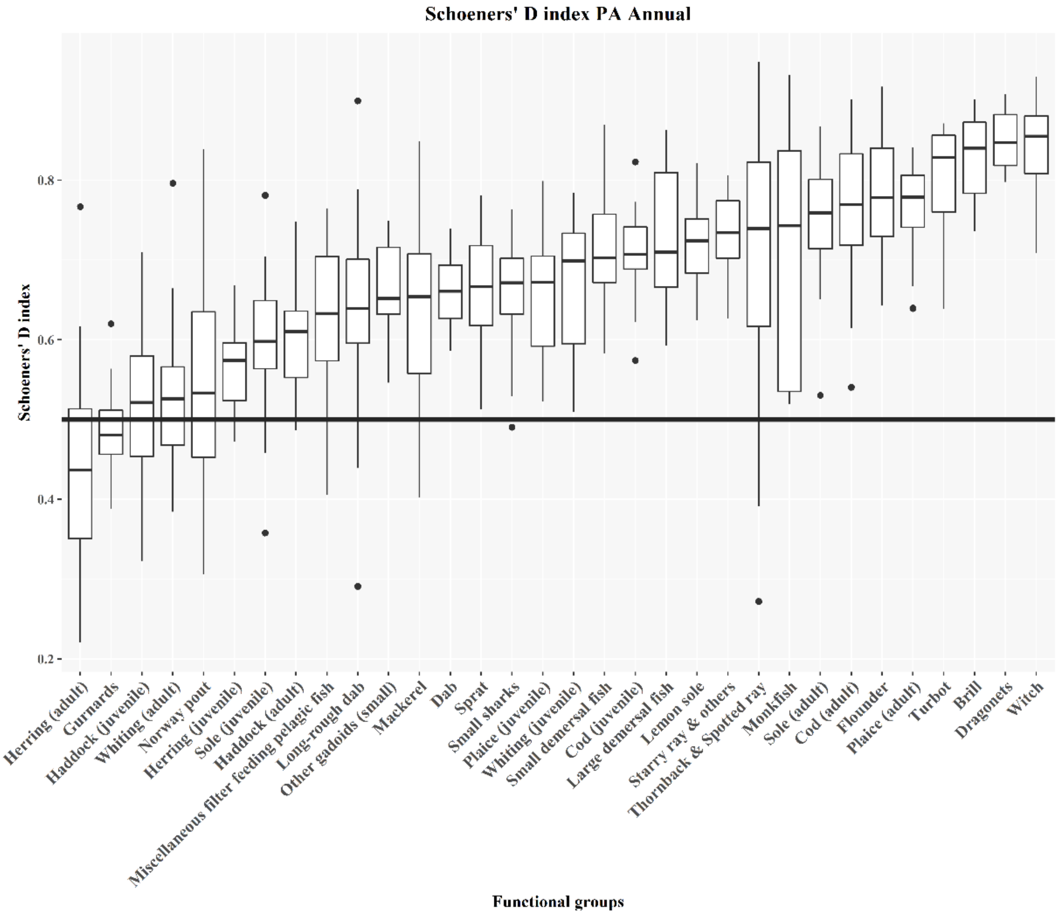

***Figure 3:** Schoener's D index as a measure of niche overlap from 1991-2010 for each functional group forced with annually changing PA habitat capacity maps. Thick black line marks 0.5, the threshold above which the fit was considered acceptable. The boxplot indicate median, upper, and lower quartile for each group. Lines below and above the boxes indicate values outside the middle 50% range while dots represent outliers.*

Ranking MEF of all scenarios (1 – best to 7 – worst) for the different FGs individually revealed differences in the best fitting scenarios (Figure 4). The PA multi-years scenario showed the worst fit for only two FGs, which also reflected the general trend towards the multi-year scenario as the one with the best fit for biomass. FGs for which this scenario had the worst fit were nephrops and sandeels. For most FGs, the temporally variable hurdle scenarios ranked lowest among the MEF, as expected based on the summarized results over all FGs. Nevertheless, some FGs seemed to benefit from these scenarios, the majority being mostly FGs with quite low trophic levels. The PA baseline scenario also showed fifteen ranks five and higher, while the hurdle baseline scenario shows twenty-three ranks five and higher. This indicates that adding variability in the foraging capacity during the run by updating the habitat maps increases the MEF. Overall, the preference for scenarios between the different FGs was quite diverse.

There was no evident pattern or clustering based on trophic levels or ecological niches. What became apparent was the dominance of the PA scenarios over the hurdle scenarios when condensing the FGs into larger groups and calculating the mean rank for the MEFs of the scenarios. The hurdle baseline or the hurdle multi-year scenario have a positive effect only on other demersal fish and crustaceans, the latter being the only group where solely a hurdle scenario is beneficial.

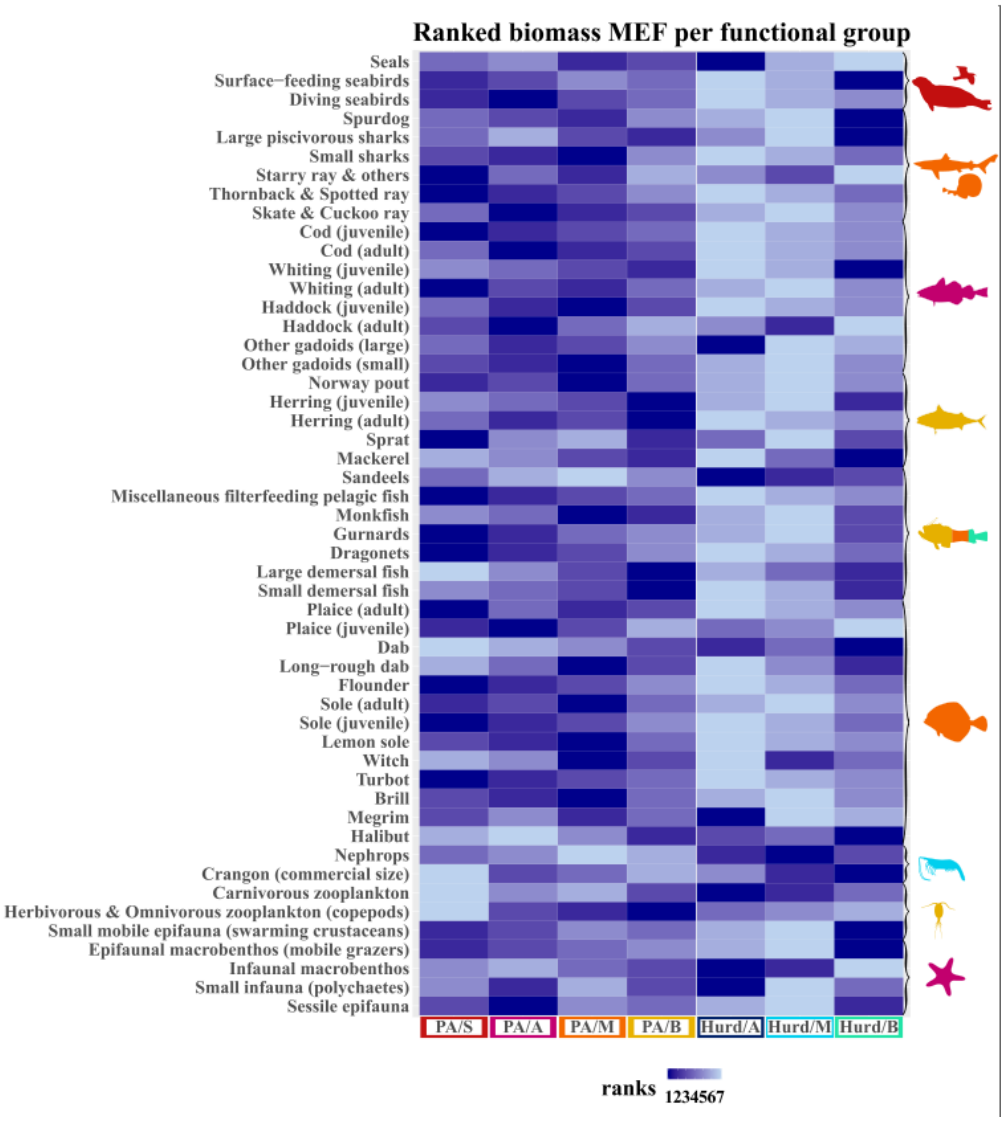

Figure 4: *Ranked model efficiency for biomass per functional group per scenario with the best (1) to worst (7) fit, from dark to light blue. Scenarios from left to right: S= Seasonal, A= Annual, M= Multi-years, B= Baseline. Functional groups are sorted by trophic level. Species silhouettes represent different ecological groups, colors represent the scenario with the best fit (mean rank over all functional groups within the group). From top to bottom: marine mammals & birds, elasmobranches, gadoids, forage fish, other demersal fish, flatfish, crustacean (commercially important), zooplankton and benthos. If a group has multiple colors, it points to multiple best fits.*

Mean biomass over time evaluated for four commercially important FGs (mature cod, whiting, sole and plaice) as examples, revealed distinctive patterns for each scenario (Figure 5). These displayed FGs were subjected to different kinds of spatial-temporal forcing. The foraging capacity of cod (adult) and whiting (adult) was based on the IBTS survey; thus, the maps varied for Q1 and Q3. They were therefore the class of FGs that were directly influenced by changing foraging capacity within the seasonal scenario. For sole (adult) on the other hand the distribution was based on the BTS survey, so solely on Q3. Plaice (adult) is shown as an example of FGs, which was only forced by the distribution of the connected stanza plaice (juvenile) and a static basemap. Therefore, within these four FGs there was an increase in complexity of forcing. All four revealed that the hurdle scenarios, which represented the abundance-based maps, underestimated the biomass for these FGs in most cases, especially in the beginning of the run. Only in the case of cod (adult) the annual and multi-years hurdle biomass exceeded the reference time series after 2000. In most cases for the PA scenarios, the trend depicted in the Ecospace scenarios matched those of the time series and with increased periodicity of map input, the peaks of the reference time series were being matched. What did become apparent, especially in the case of PA scenarios, was that steep and abrupt changes in biomass were not accounted for in all Ecospace scenarios. The steep decrease of cod (adult) biomass beginning in 1998 was not represented. Additionally, there was a lack of biomass decrease for plaice (adult) and sole (adult) in the beginning of the time series.

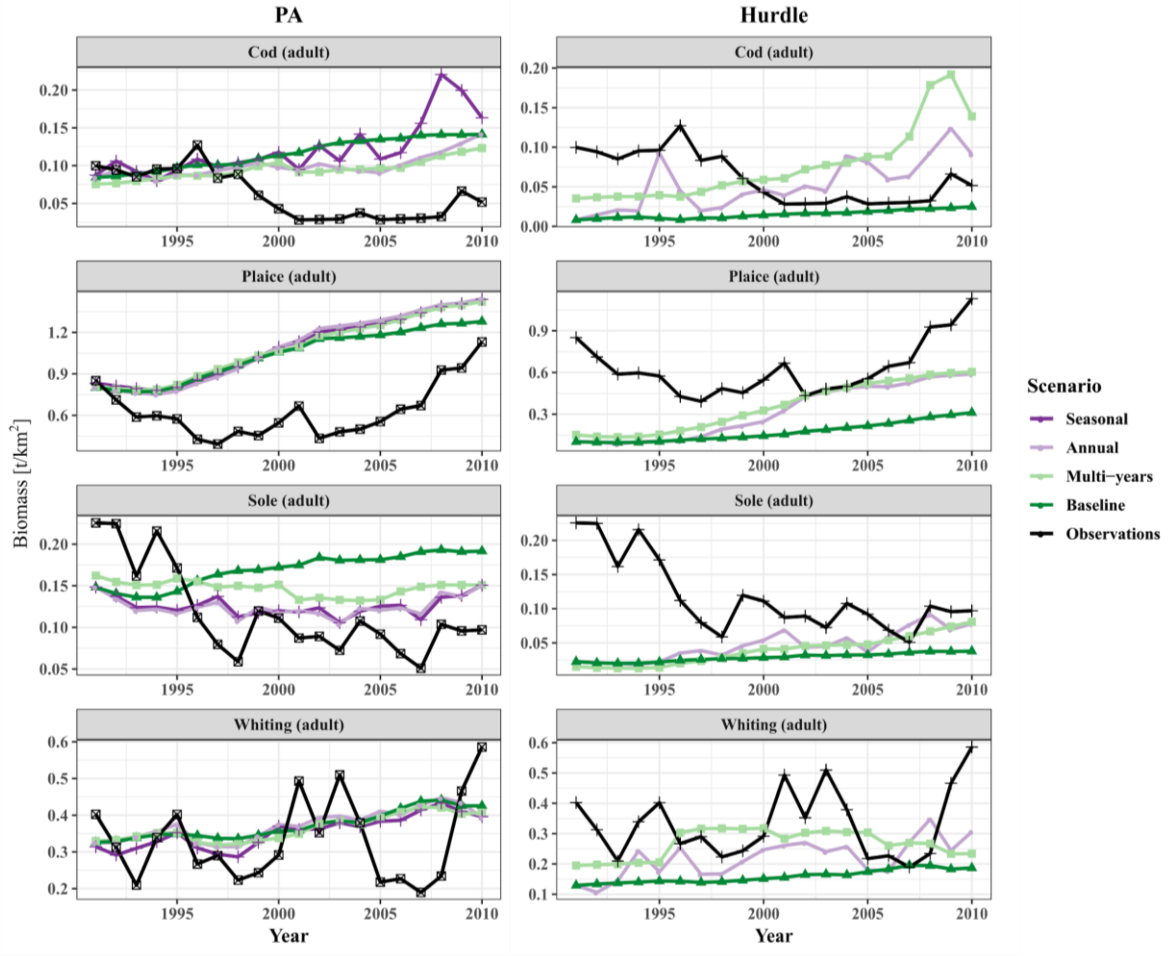

Figure 5: *Mean biomass [t/km^2] over all cells per year for selected commercially important functional groups. Left: PA scenarios, right: Hurdle scenarios. Different colors represent the different scenarios, while the black line represents the observations scaled by the FGs biomass entered in Ecopath.*

To evaluate the temporal and spatial fit in combination, the correlation and the centered root mean squared error (RMSE) between Ecospace biomass layers and the abundance reference for all scenarios were evaluated with a Taylor diagram (Figure 6). Within this diagram, the abundance reference is represented by the circle labeled “observation”. Therefore, the closer a symbol for the scenario is to the observation, the better the fit. For this analysis, the variation between the standard deviation of the Ecospace output and the observed abundance reference was smaller for the hurdle scenarios. This was to be expected, since the abundance reference is the output of the hurdle SDM. Therefore, the spatial overlap is closely related. Yet, the PA scenarios result in better RMSE and correlation than the hurdle scenarios. Within the hurdle scenarios, the annual scenario had the best correlation and RMSE, which were quite similar for the other two scenarios. Yet these two scenarios (hurdle multi-years and hurdle baseline) perform better in terms of standard deviation.

For PA, the three temporally variable scenarios reached quite similar results, while the static baseline scenario had a better standard deviation but a worse correlation and RMSE.

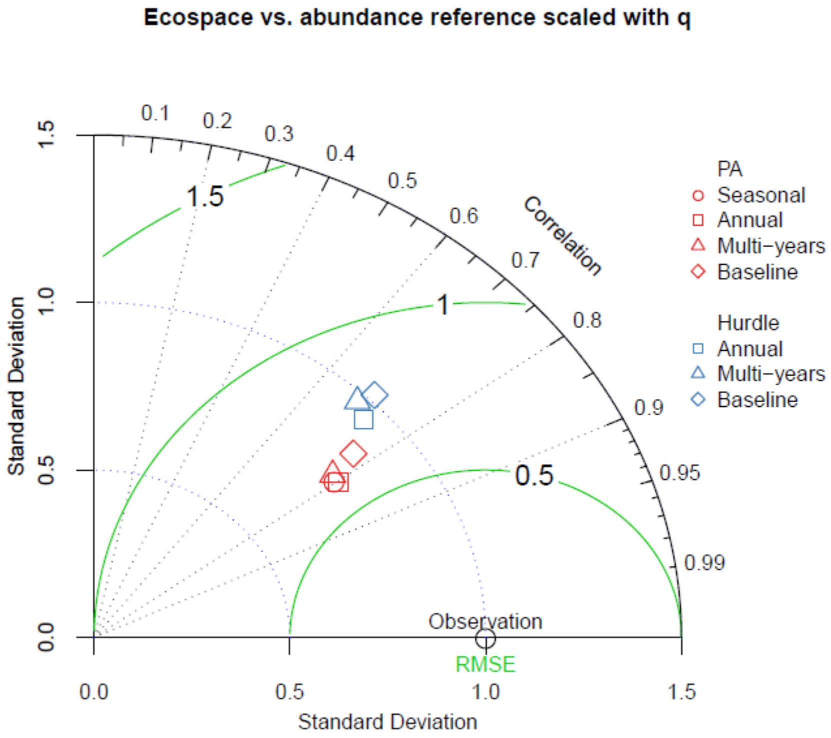

Figure 6: *Ecospace-simulated biomass vs. observed abundance (CPUE) by scenario in terms of correlation (right arch), RMSE (green arch) and Standard Deviation (x and y axis). Both biomass and abundance data are log-transformed, and log-abundance values were re-scaled with a parameter q, derived for each unique scenario and FG. Comparisons were made per cell per year per functional group.*

3.3.2 Comparison of Ecospace scenarios – Catch

Since the distribution of catch was not based on a GAM and has therefore no spatially resolved maps to compare to, the catch skill assessment only evaluates the temporal fit. It is based on a comparison between the observed relative time series included in Ecosim and the mean catch values obtained from the different Ecospace scenarios (Table 4). The metrics used to distinguish between the fits of the models shown here were MEF, RMSE and PEAR. Similar to biomass, the time dynamic hurdle scenarios showed the worst fit in all metrics, while the hurdle baseline scenario comes close to the results achieved with the PA scenarios. Overall, the seasonal as well as the multi-years PA scenario showed the best fit, supporting once more the decision towards a multi-year PA scenario.

Table 4: *Model efficiency (MEF), root mean squared error (RMSE) and Pearson correlation (PEAR) based on catch assessment for each scenario displaying the mean over all functional groups. Results marked with * represent the best results in terms of the overall mean. The numbers within the brackets display percentage of functional groups that exceeded the thresholds (MEF threshold= 0, RMSE threshold= 0.25, Schoener's D index= 0.5).*

Scenario/ Skill	*MEF catch*	*RMSE catch*	*PEAR catch*
PA Seasonal	0.4829 (89.7)*	0.5016 (28.2)	0.478 (64.1)*
PA Annual	0.4664 (89.7)	0.4931 (33.3)	0.4289 (64.1)
PA Multi-years	0.4489 (89.7)	0.4885 (33.3)*	0.4393 (61.5)
PA Baseline	0.4065 (92.3)	0.4937 (30.8)	0.4141 (61.5)
Hurdle Annual	0.1385 (76.9)	0.6043 (12.8)	0.2364 (38.5)
Hurdle Multi-years	0.3182 (79.5)	0.5557 (15.4)	0.2287 (53.8)
Hurdle Baseline	0.428 (89.7)	0.5024 (30.8)	0.4572 (59.0)

A more concise picture emerged based on the ranked MEF for the single FGs (Figure 7). Similar to biomass and expected based on the skill assessment metrics table, the temporally variable hurdle scenarios showed the worst fit for most of the FGs. Only for a few foraging fish, demersal fish and flatfish the fit was better for these scenarios. Especially for the higher trophic levels, the annual hurdle scenario almost always resulted in the worst overall MEF. This was also reflected in the grouped MEF ranks displayed by the FG silhouette in different colors. The PA seasonal and the PA multi-years scenario showed the best fit for most of the ecological groups (three times red (PA seasonal) and four times orange (PA multi-years)). The hurdle baseline scenario had a good fit for three of the ecological groups, but also received the lowest rank seven times. This shows a high variation in model fit for the different scenarios among the ecological groups, especially when it comes to the hurdle scenario. The two annual scenarios and the hurdle multi-years scenario did not achieve the best grouped MEF for any ecological group.

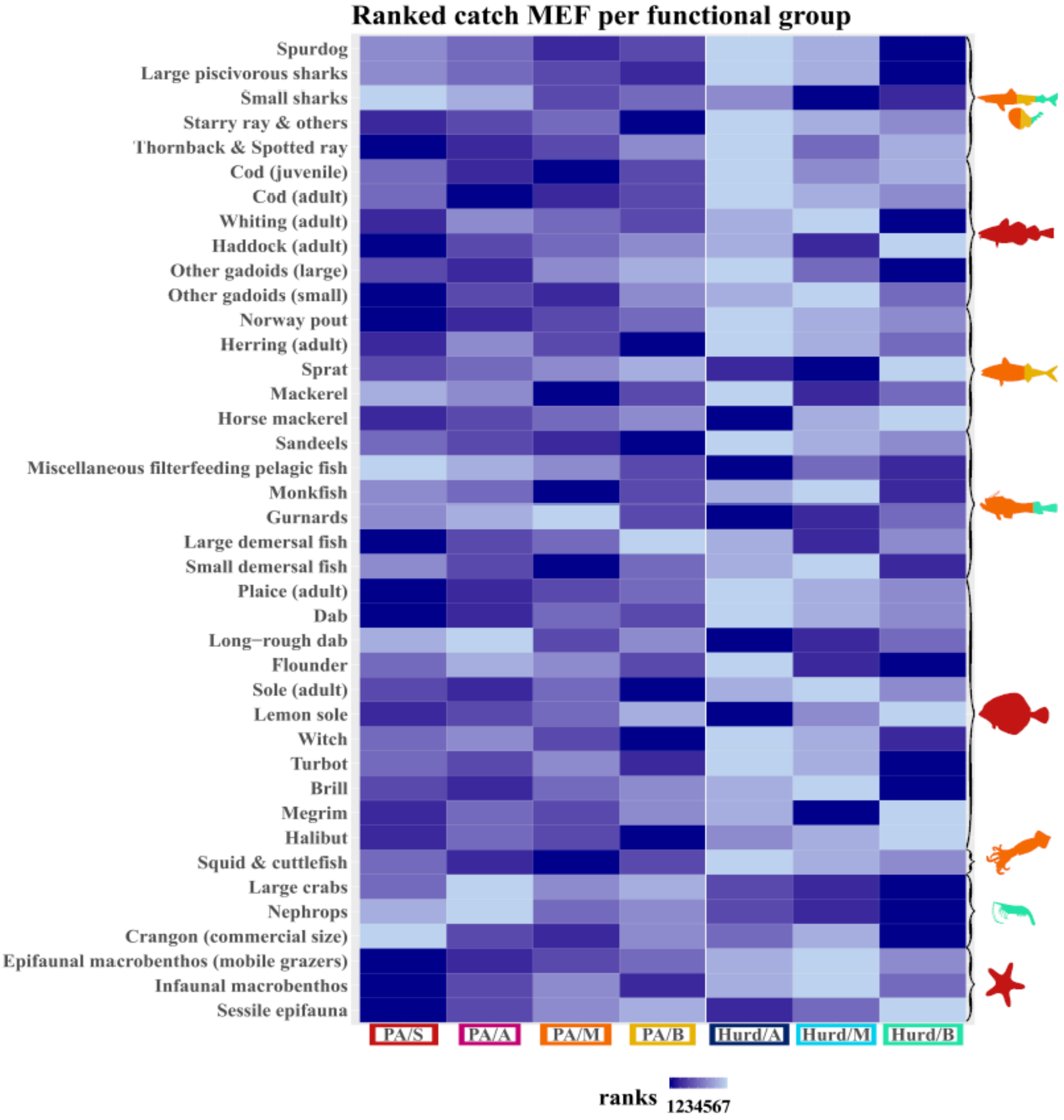

Figure 7: *Ranked model efficiency for biomass per functional group per scenario with the best (1) to worst (7) fit, from dark to light blue. Scenarios from left to right: S= Seasonal, A= Annual, M= Multi-years, B= Baseline. Functional groups are sorted by trophic level. Species silhouettes represent different ecological groups, colors represent the scenario with the best fit (mean rank over all functional groups within the group). From top to bottom: elasmobranches, gadoids, forage fish, other demersal fish, flatfish, squid and cuttlefish, crustacean (commercially important) and benthos. If a group has multiple colors, it points to multiple best fits.*

Mean catch over time was analyzed for the same FGs as for biomass in section 3.1, they therefore underlie the same foraging capacity forcing (Figure 8). The increasing variability over time was visible here as well, but not quite as apparent as for biomass. The PA based scenarios matched the time series especially in trend and in most cases, they matched the observations. Yet, here again the southern North Sea Ecospace model failed to account for strong changes in the catch time series, as it was visible for biomass time series comparison of cod (adult).

The hurdle scenario on the other hand completely underestimated the catch for cod, plaice and sole, especially in the beginning of the time series. In most cases, even the trend was not that precise within the hurdle scenarios.

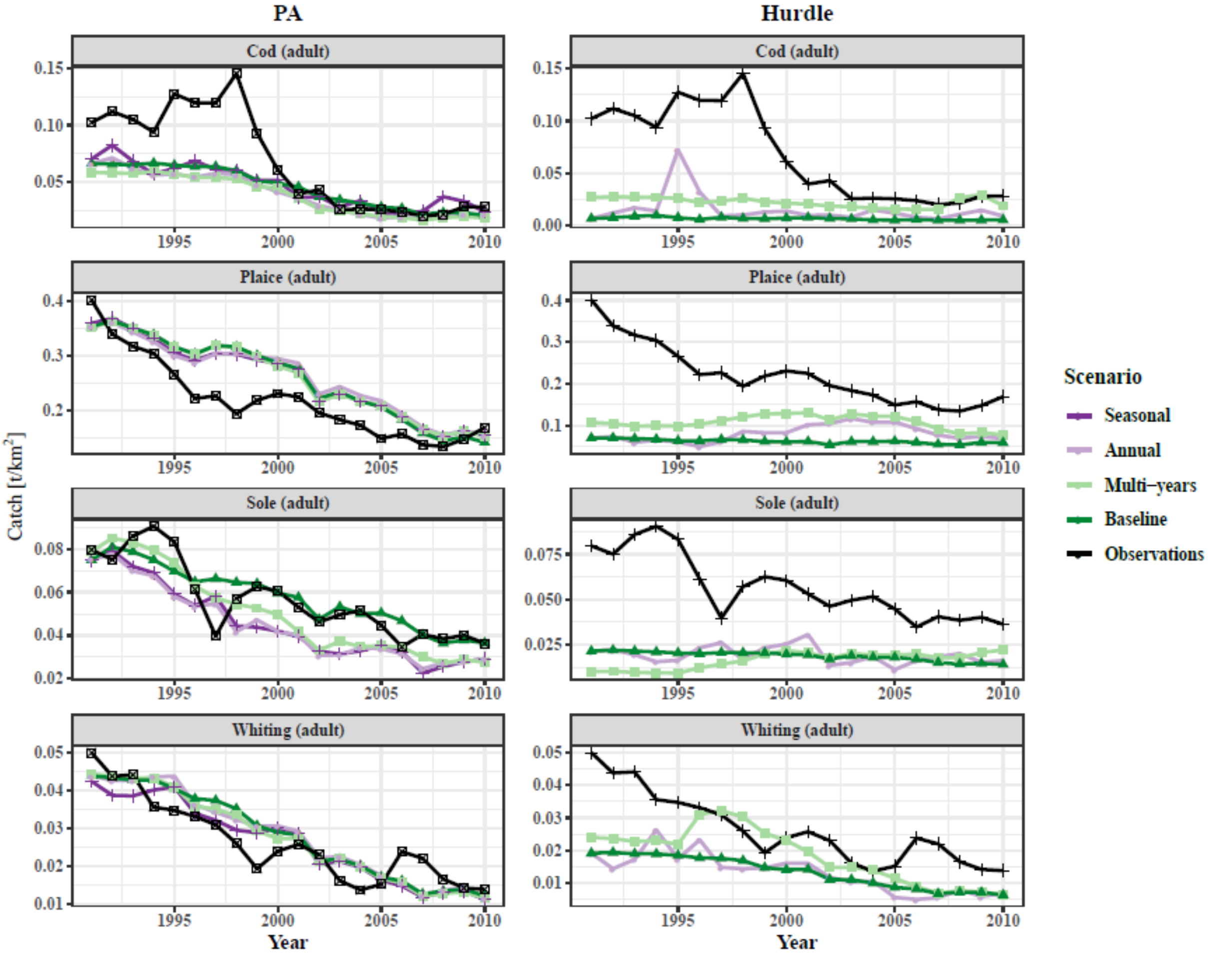

Figure 8: *Mean catch [t/km^2] over all cells per year for selected commercially important FGs. Left: PA scenarios, right: Hurdle scenarios. Different colors represent the different scenarios, while the black line represents the observations.*

Overall, the results showed, that the fit of these scenarios differed between the different metrics applied and that each aspect had to be taken into account, temporal, spatial and spatial-temporal. Even between catch and biomass, the scenarios with the best fit differed. Yet, one concise result was the dominance of varying foraging capacity over time and the necessity of a broader definition of this capacity by applying maps based on presence/absence (Table 5).

Table 5: *Summary of the best fitting scenarios under the different dimensions (temporal, spatial, spatial-temporal). Displayed for biomass and for catch.*

Dimension	*Biomass*	*Catch*
temporal	PA multi-years	PA seasonal
spatial	hurdle annual	-
spatial-temporal	PA seasonal, annual, multi-years	-

3.4 *Discussion*

3.4.1 Goals, insights and uncertainties

Within the spatial-temporal framework of EwE, it is now possible to combine habitat preference maps based on SDMs with Ecospace and update these maps during its execution. One of the main goals of this study was to analyze the effect of implementing either presence/absence or abundance-based maps as habitat preferences into a mechanistic trophic food web model. Our study showed that the interpretation of habitat preference could largely affect model's outcomes and fits. We demonstrate that it is necessary to select SDM settings that can inform habitat preference maps without overly constraining trophic or other processes to be addressed by the food web model. This can be achieved by choosing a model with a sigmoidal response (for instance, the logistic model), which leads to a spatial distribution allowing a broader foraging capacity than with a model with exponential response (as the hurdle model). Furthermore, the aim was to evaluate and illustrate the benefits of accounting for changes in habitat preferences over time. All modelling performance metrics employed showed that accounting for changes over time leads to better fits than static maps. Additionally, we displayed a way of how to assess the performance of an Ecospace model outside of EwE.

This Ecospace model is also subject to structural and parameter uncertainties. Building on two other components, Ecopath and Ecosim, Ecospace already inherits uncertainties introduced by these, like data on diets that stem from a single year only (Stäbler et al., 2016) or missing processes as encountered for the stock dynamics of cod (Figure 5). These uncertainties may increase when combining SDMs and models with trophic interactions.

There is a wide range of species distribution models (Guisan and Zimmermann, 2000), of which we tested two approaches to find the best model for our purposes.

Furthermore, it is an important issue that there is no standard routine to optimize Ecospace parameterizations. While for Ecopath and Ecosim there are implemented routines to evaluate the model fit and uncertainties (Steenbeek et al., 2018), Ecospace models have to be assessed outside of EwE. We tried to overcome this shortcoming by creating a routine outside of EwE to evaluate the fitting performance of different scenarios by temporal and spatial comparisons to empirical data. We were able to give insight into problems and pitfalls when combining SDM based distribution maps with trophodynamic modelling in Ecospace, which is quite a new approach. Therefore, this work may serve as basis for further case studies and developments in this field.

3.4.2 Defining habitat capacity in combination with trophodynamic modelling

Implementing SDMs into Ecospace can be a good asset to make food web modelling more robust. A recently published approach by Coll et al. (2019) implemented results from a Bayesian SDM model, either as foraging capacity maps or as environmental forcing function. For their data-poor case study, the combination of both modelling techniques increased the fit compared to an Ecospace that is not informed via SDM. Before the possibility of implementing foraging capacity maps, SDMs could only be incorporated by applying a response curve to environmental layers based on the SDM results (Chagaris, 2013). For these it has to be decided on which factors to include and all chosen drivers have to be incorporated into Ecospace separately (Grüss et al., 2018). This envelope approach expects a certain mechanistic understanding of the different abiotic drivers that influence habitat preferences, which brings about the possibility that certain influencing factors might be missed by this method. Nevertheless, one advantage of this method is the flexibility of changing abiotic driver maps to existing preference functions to test, for example, climate change scenarios. Also it poses a good approach for models in populations and areas that are data poor (Coll et al., 2019).

For areas with good data availability, like the southern North Sea, the need for previous knowledge about mechanistic processes can be overcome by applying SDMs with latitude and longitude as predictors, bypassing the necessity to include other abiotic factors that drive the distribution. This may be sufficient to evaluate e.g., the impact of a closed area under the assumption of non-changing foraging capacity.

However, the way the single species GAMs were built for this study does not allow to test the influence of different environmental parameters in predictions and forecasts based on varying environmental factors (e.g. analysis of the influence of climate change). However, other environmental factors can easily be incorporated into the GAMs for future endeavors (e.g. Núñez et al., 2019).

Compared to Coll et al. (2019), we used the spatial-temporal framework to update the habitat preferences derived from SDMs directly as foraging capacity maps during the execution of Ecospace, rather than inducing changes in the abiotic driver maps connected to forcing functions. Implementing habitat preference maps within the spatial-temporal framework opens the possibility to account for different influences and their strength over time (Steenbeek et al., 2013). Yet there is no common agreement on what habitat preferences to incorporate (e.g. which abiotic and biotic factors) and there are no clear guidelines on how to include these preferences into a complex ecosystem model where trophic interactions and fishing pressure have to be accounted for. It was demonstrated that presence/absence based habitat preferences overall performed better than the abundance weighted hurdle model based preferences. This might be an effect of the data used, as survey data constitute a representation of spatial abundance distributions in a single point of time, but we would argue that it is rather a general effect of the mathematical profile underlying the models.

The presence/absence model was fitted with a logit link, resulting in a sigmoidal profile, while the presence only model was fitted with a log link, which results in an exponential profile. Combining these two models leads to an exponential profile for the final hurdle model. While the sigmoidal profile allows a more general representation of distribution, the exponential profile highlights the areas with high abundances. Both profiles come with benefits but also restrictions. Combining the sigmoidal profile with a trophodynamic model allows for enough flexibility for further interactions that might influence the habitat preference of a species. Moreover, even though the hurdle scenarios yielded better results for the Schoener’s D index, it showed that the more general approach of implementing the presence/absence maps was able to represent the distribution of the single FGs as well when combined with the ecosystem model. Yet this profile lacks the opportunity to include known hot spots with high interests for the species and good foraging opportunities (example maps in Figure 9). The skill assessment of the hurdle model on the other hand showed, that the implementation of maps based on an exponential profile creates too much spatial restriction.

This constraint can have multiple effects within a spatial food web model. It can induce perfect overlap with the predator and fleets, which leads to high pressure on the FG and not much space to escape. Alternatively, as opposed to this, there can be no or hardly any overlap with predators and fleets, which in turn leads to an uncontrolled increase in biomass. Furthermore, there can be no or just minimal overlap with the own prey, which can lead to starvation.

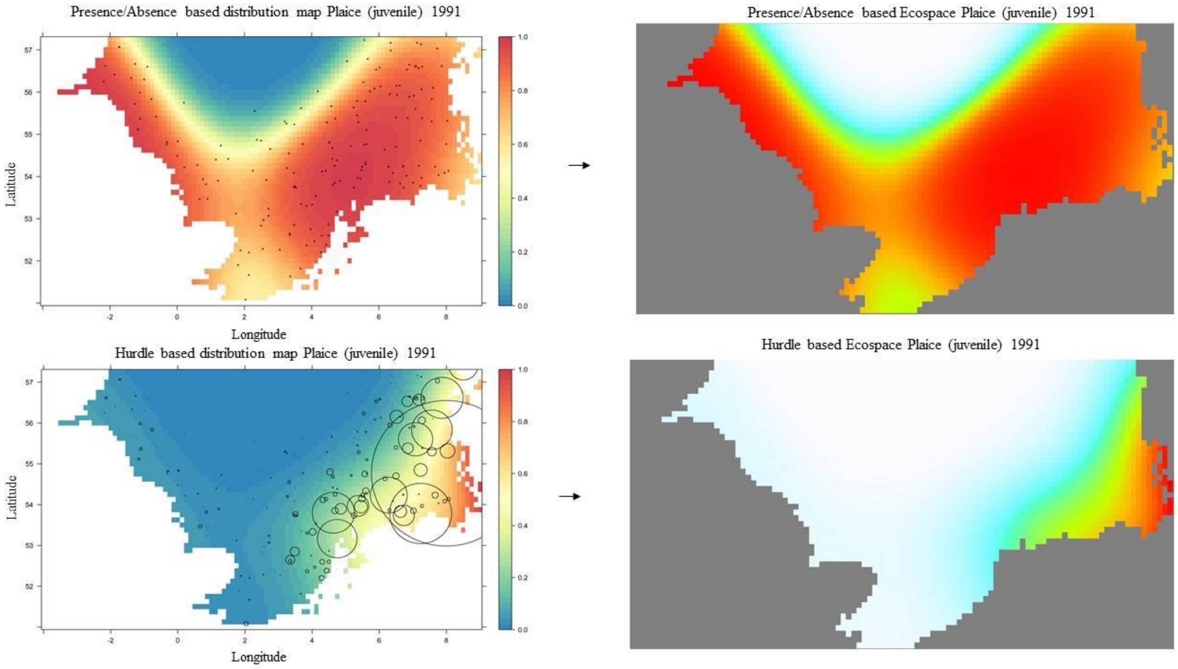

Figure 9: *GAM based distribution maps (left) and how they are incorporated in Ecospace (right). The top row represents presence/absence maps with the sigmoidal profile, while the lower row represents hurdle maps with the exponential profile. Here on the example of plaice (juvenile). The size of the circles in the hurdle map display the different CPUE values.*

Implementing these habitat preferences into Ecospace during the run raised the question on the best periodicity. Our results show that accounting for changes in distribution of species over time increases the overall fit of the model to spatial-temporal data. It could be argued, that the hurdle scenarios with the generally inferior fit implied a different conclusion. Here the static baseline scenario had the best fit. But this was only the case when concentrating on the metrics evaluating the temporal fit. The spatial metric Schoener's D index revealed that the static baseline scenario had the worst fit among all hurdle scenarios. This implies, that even though this scenario is good in reproducing temporal trends, it does so on the cost of spatial redistribution and thus becoming more unrealistic compared to the other scenarios.

For catch, the multi-years scenario and the seasonal scenario displayed the best results. Most fishing habitats were created based on known fishing areas, wide enough to redistribute the effort in case of shifts in habitat preferences. Therefore, adapting to more rapid changes over time might not be as crucial as for biomass.

This is in line with findings by Romagnoni et al. (2015) who also found that changes in different parameters for their Ecospace of the entire North Sea (IV a, b and c) affected biomass and catch differently. This can be justified by the way effort is distributed in Ecospace. Each fleet's effort is proportionally distributed over the cells by a "gravity model", dependent on the sum over the FGs biomass caught by the fleet times the off-vessel prices and the catchability for each FG (Walters et al., 1999). If the fishing area covers enough ground to react to shifts in distribution, it follows the redistribution.

Considering all results, it reveals that in terms of periodicity the multi-years scenario performs best. Yet, the periodicity should support the time period one would like to study (e.g. short period: seasonal might work better, long period: seasonal may not be necessary, annual or even multi-years can suffice) and the research questions the model was built for (e.g. long-term changes in the ecosystem vs. effects of rapid increase of fishing mortality in the distribution of species). Furthermore, changes within the ecosystem during the run were only represented by the changes in foraging capacity. Including monthly, seasonal or annual changes of the chlorophyll-a maps or accounting for changes in water temperature might be necessary to adequately represent the changes over time and to reach a better model fit.

3.4.3 Best practice suggestions for applying a spatial-temporal framework to foraging capacity and shortcomings identified

There are several key best practice suggestions arising from this study for forcing the foraging capacity via the new Ecospace spatial-temporal capabilities. First, when applying scaled habitat preferences predicted with SDMs as foraging capacity, the best performing SDM may not be the best to use in an ecosystem model context. Although the exponential profile of the hurdle model has a better representation of the CPUE data, Ecospace performed worse when fed with its output. This is likely because the sigmoidal profile of the presence/absence maps is more informative as overall habitat capacity measure and additionally more flexible towards further mechanistic structures within the ecosystem model and therefore improving our knowledge on habitat preferences. Implementing time dynamic maps is the preferred option over a constant base map.

Time dynamic maps are an important improvement in Ecospace especially in times of climate change; where in future work the temporal shift in temperature can be accounted for within the foraging capacity maps.The study also identifies a few caveats. First, there is still no automated routine to evaluate the fit of Ecospace. We chose to test the fits using a set of skill assessment metrics and it has proven a good way to find the settings with the best fit. It is important to apply a wide set of different metrics to assess the fit of an ecosystem model, to account for the temporal and spatial fit (Olsen et al., 2016). Model efficiency with the value for the base year 1991, as well as the Pearson correlation (for catch) and root mean squared error served as metrics that informed about the mean temporal fit over the years. Nevertheless, these metrics did not account for spatial dynamics in habitat preference maps over time when compared to the empirical time series. This could be accomplished with the Schoener's D index, which measures the niche overlap, and therefore allows the spatial comparison between the Ecospace output maps and the abundance reference. The combination of the spatial and temporal fit could be achieved with the Taylor diagram, comparing Ecospace and abundance reference standardized maps for all years per grid cell.

One major issue within Ecospace is the current inability to react to situations like partial spatial mismatch between predator and prey by changing vulnerabilities based on occurrences in space. Vulnerabilities are only fitted to Ecosim time series, not taking the amount of spatial overlap into account. As done with this model for brown shrimp, changing single vulnerabilities within Ecosim is possible and justifiable (too much pressure of the adult stanza on the juvenile, while they are both common within a narrow area at the coast). Nevertheless, there is no other way than visibly checking the fit and using skill metrics as done here, to validate the changes. An automated routine, like the automated fitting routine for vulnerabilities and primary production splines applicable to Ecosim (Mackinson et al., 2009; Scott et al., 2016) would be a necessary improvement to account for species overlap in narrow areas. Additionally, as seen in Figure 5, most sharp changes of biomass compared to the observation are hard to meet in this complex ecosystem model. Especially steep downward trends within the time series (as seen for cod, sole and plaice) have proven to be a challenge. There is a need for additional spatial processes, for example by implementing mediation functions or account for biomass accumulation based on spatial conditions, to match these trends and to force a steeper biomass trend in Ecospace.

When fitting Ecospace, multi-stanza groups have to be fitted with caution, as seen in this study for plaice. Distributions of juveniles and adults of the same species are linked through the implementation of multi-stanza group settings (Walters et al., 2010), so it may improve the fit if forcing of stanzas distributions separately were possible. Therefore, the distribution of plaice was driven by forcing the foraging capacity of only the juvenile life history stage over time to avoid overfitting the model. In agreement with the Schoener's D index, the results showed a good niche overlap for the spatial distribution of plaice juvenile and adults, confirming that forcing the foraging capacity of only one of the two multi-stanza was sufficient to drive spatial distributions of both stages. For highly cannibalistic groups however, it might be necessary to force one part of the multi-stanza, e.g. by migration to spawning grounds, to account for changes that only apply to one species life stage. This would be particular relevant when using multi-stanza for species that have very different ecological and trophic ontogenetic changes across their life stages (e.g. eggs, larvae, juveniles and adults).

Even though the Schoener's D index of most FGs surpassed the threshold, there is a difference in variability (Figure 3). The highest variabilities are displayed in pelagic FGs and FGs where the survey coverage might not have been extensive enough. This has two implications. First, it is important to carefully select FGs and the corresponding data when applying SDMs to Ecospace. The smaller the data coverage for the SDM the more variability in the spatial fit. Second, Ecospace seems to perform better when reproducing spatial distributions of more spatially bound FGs than for the fast moving pelagic FGs.

3.5 *Conclusion*

In our study, the new capabilities of Ecospace have proven to be a beneficial asset when reconstructing species' spatial distributions and their shifts over time. It also showed that in an ecosystem model like the one for the southern North Sea, implementing temporally changing habitat preferences maps based on PA on a sigmoidal profile generate better results than an exponential profile based on CPUE. Furthermore, combining SDMs with this trophic model has the potential to further inform about habitat preferences that include biotic interactions introduced by Ecospace. Nevertheless, our knowledge about the best practice in the new spatial-temporal external foraging capacity implementation could benefit from testing further strategies of fitting. In the future, the new capabilities inside Ecospace can be applied to assess changes in ecological indicators over time as well as to test different management strategies within the framework of marine spatial planning.

In the light of climate change, it is possible to test how ecosystems react to temperature driven foraging capacities. Finally, there is not one best practice how to construct an ecosystem model. As with all models, the best model is always the one that best answers your research question in your part of the world's oceans and the best periodicity might differ between models and research questions. However, our study adds insights on the impact of habitat capacity maps on Ecospace results and helps to identify the issues that need to be taken into account when using SDMs as input for ecosystem models like Ecospace.

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4. Publication 3

Tradeoffs between fisheries, offshore wind farms and marine protected areas in the southern North Sea – winners, losers and effective spatial management

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Abstract

Worldwide, ecoregions such as the North Sea suffer from multiple anthropogenic influences, among these intensive fishing, strong shipping traffic and recently a growing number of installations that produce renewable energy as a climate change mitigation measure. In addition to the spatial requirements of these multiple uses, space is needed for conservation measures such as marine protected areas (MPAs) as a requirement to achieve European and international policy goals that require the reconciliation of blue growth (e.g. economic growth in the marine realm) while maintaining a good environmental status. Spatially explicit ecosystem models are crucial tools for identifying trade-offs between these often-conflicting management goals. In this study, we evaluated the influence of MPAs and fishing closures within ocean wind farms on the ecosystem of the southern North Sea with an indicator approach. We additionally tested for the effects of hypothetical spatial management options in line with ecological objectives (such as the protection of biodiversity and endangered species). Our results revealed, that similar to traditional management approaches, spatial management can provide trade-offs between conservational objectives and fishing activities. However, our results suggest that in order to reach conservational management objectives, closures need to be combined with additional spatial management measures, often at a further suspense of overall catches. Furthermore, the size and placement of spatial management options are important factors influencing overall benefits and losses. The implementation of currently designated MPAs in the southern part of the North Sea did not perform as well as hypothetical ones, which were specifically designed with the goal of protecting areas with high biodiversity or endangered species abundance irrespective of national limits within the existing Natura 2000 framework. Although against current political realism, this implicates the possibility to rethink present management to ensure a coherent and target oriented framework for closed areas. The results of the study imply that the implementation of planned MPAs and other closures may not be sufficient to reach their intended objectives and further adjustments to their location and subsequent shifts in fishing effort should be considered.

4.1 *Introduction*

Worldwide, human pressures on marine ecosystems have increased. This is especially true for the North Sea where multiple human impacts cumulatively affect the ecosystem (Halpern et al., 2015) and where especially fish stocks are heavily impacted by climate change (Free et al., 2019). Fisheries, aquaculture, ship traffic, renewable energy installations, oil and gas platforms, as well as tourism, are some of the most noticeable forms of usage of the marine environment (Andersen et al., 2013). The various uses compete for space with environmental protection and conservation interests which can create conflicts among stakeholders and requires the identification and quantification of usage trade-offs (Jennings et al., 2012; Gimpel et al., 2018; Nelson and Burnside, 2019). Solving such trade-offs is a key challenge addressed by the maritime spatial planning directive, which was legally adopted by the European Union (EU) in 2014 (EU, 2014). Important examples are trade-offs between fishing activities and increased ocean space requirements for offshore wind farms (OWFs), but also conservational measures like marine protected areas (MPAs).

The protection of marine ecosystems, especially through MPAs, has moved into the focus of international legislations and commissions (Appendix A Table 1.1A). Within the EU, multiple multinational legislative acts were enforced to regulate and protect the marine environment. The Habitat and Birds Directives address land-based as well as marine protection goals (Council Directive 92/43/EEC, Directive 2009/147/EC). A Natura 2000 MPA network is being developed to protect the species listed in the annexes of both legal acts, promoting a network with good connectivity and including some degree of complete closure to other human activities (Sundseth et al., 2020). In the marine realm, the Marine Strategy Framework Directive (MSFD) was adopted to protect marine ecosystems and to achieve a good environmental status by 2020 (for definition, see Table 1). Furthermore, the MSFD calls for the creation of MPAs in affiliation with the Natura 2000 areas (Directive 2008/56/EC, 2008). Additionally, in May 2020, the EU adopted the new Biodiversity Strategy 2030 as part of the European Green Deal, which requires an increase of EU-wide protected areas and stricter protection measures of at least 30% of the marine area (EU, 2019).

Implementation of MPAs in the North Sea is a stepwise process. By the end of 2018, 496 MPAs were part of the OSPAR MPA network, primarily within territorial waters. At that time, MPAs covered 6.4% of the OSPAR area and 18.6% of the Greater North Sea. Even though these numbers suggest a certain progress, an ecologically coherent implementation of the MPA network is lacking (OSPAR, 2018). The ecological coherence of an MPA is generally evaluated based on five principles, of which on is its ability to support ecological connectivity (OSPAR, 2006). Ecological connectivity was defined by Taylor et al. (1993) as the support or obstruction of animal movement between resources. Currently, spatial connectivity among the Natura 2000 areas is seen as insufficient because MPAs are still too patchy and often lack a common planning process, including the use of protected areas that span country boundaries (Mazaris et al., 2018). Additionally, most OSPAR MPAs have, for example, publicly-documented management information, although only a small percentage of these measures have been implemented (OSPAR, 2018). For example, Belgian Natura 2000 sites are designated and management plans are finalized, yet their implementation and enforcement is still blocked by legal issues (Fraschetti et al., 2018).

OWFs are an important measure for climate change mitigation through substitution of fossil fuel-based energy production. Presently, European OWFs have an installed capacity of 22,072 MW, a majority (77%) comes from the North Sea. In 2019, 502 grid-connected offshore wind turbines were installed in 10 OWFs, and 99% of the turbines were built in the North Sea (WindEurope, 2019). While restricting or rearranging fishing activities, OWFs have the potential to affect ecosystem structure and functioning in diverse ways (Lindeboom et al., 2011, Floeter et al., 2017). Positive impacts can include increased nursery areas for key species supporting the fish community (Reubens et al., 2014; Stenberg et al., 2015; Hooper et al., 2017; Raoux et al., 2017). In contrast, OWFs can potentially have a negative impact on the seabird community through collisions or as habitat loss by avoidance (Busch et al., 2013; Brabant et al., 2015; Garthe et al., 2017). Furthermore, they also likely modify the ecosystem through structural changes by adding hard substrate that can potentially increase the abundance of epifauna, like the bivalve *Mytilus edulis*, which in turn may impact ecosystem functioning (Slavik et al., 2019).

Modern ecosystem-based management (EBM) reconciles the multiple interests people have in using and protecting the ocean and has more recently expanded to include information on potential trade-offs in the equitable use of the marine space (Long et al., 2015; Dolan et al., 2016). Indicator systems are important means for the evaluation of goals within EBM and may include single species measures, group indicators (e.g. pelagic vs demersal or invertebrates vs fish species), ecosystem-level indicators (e.g. trophic-level based indicators) or conservation-based indicators (like species richness or conservation status; Greenstreet and Rogers, 2006; Blanchard et al., 2010; Coll and Steenbeek, 2017, Rita et al., 2017, Otto et al., 2018). The evaluation of many of these indicators requires specialized tools, such as trophic models that consider spatially explicit ecological processes. The models can be large ecosystem end-to-end models (Abdou et al., 2016; Raoux et al., 2017; Grüss et al., 2018) and multi-model ensembles (Shin et al., 2018) that can be utilized to support spatial management (Steenbeek et al., 2020),

In this work, we used an existing spatially explicit trophic model of the southern part of the North Sea to characterize spatial ecosystem structures and effects of changes in spatial management. Following the description of the ecosystem without any spatial closures, we evaluate the effects of area closures on fisheries by implementing existing and planned MPAs and OWFs. Various biomass and catch-based indicators are therefore compared among different closure types to identify changes in the state and functioning of the ecosystem. Based on the intention of achieving an MPA coverage of up to 30%, as it is proposed in the new Biodiversity Strategy 2030 (EU, 2019), we created two additional hypothetical protected areas that exclude fisheries, to test additional spatial management options that are not impacted by national constraints as in the current Natura 2000 framework. One of the two additional closure scenarios is based on the core distribution of endangered species on the International Union for Conservation of Nature’s Red List of Threatened Species (IUCN red list), while the second aims to protect an area with high biodiversity. Furthermore, we test the necessity of additional effort reductions to counteract the effect of effort re-allocation due to closures. Our results provide insights into possible trade-offs and win-win situations in the spatial implementation of conservation measures, fisheries management and renewable energy production.

4.2 *Material and Methods*

4.2.1 Modelling approach

One modelling software that is increasingly being used to evaluate anthropogenic influences on ecosystems is Ecopath with Ecosim (EwE) that comprises three interdependent modules representing (i) the static, mass-balanced Ecopath model, (ii) the temporal simulation component Ecosim, and (iii) the spatial implementation Ecospace (Christensen et al., 2008; Christensen and Walters, 2004). All three model components were developed for the southern part of the North Sea in previous studies (Stäbler et al., 2016, 2018; Püts et al., 2020), representing International Council of the Sea (ICES) management areas 4b and 4c.

Sixty-eight functional groups (FGs) were defined, with a focus on commercially important higher trophic level species. Nonetheless, the 35 multi-species and 30 single-species FGs comprise all trophic levels: mammals and birds (4), elasmobranchs (8), fish (35), crustaceans (4), benthic invertebrates (8), zooplankton and phytoplankton (6). Additionally, three groups represent particulate / dissolved organic matter and fishery discards. Different life stages with specific trophic needs were implemented for several commercially-important species applying the multi-stanza approach (Walters et al., 2010). Exploitation is depicted by twelve fishing fleets, which represent the most prominent fisheries in the southern North Sea.

The EwE Ecospace component is a two-dimensional model to test spatial management measures. It is partitioned into grid cells in which temporal dynamics derived from Ecosim are executed (Christensen et al., 2008; Walters et al., 1999). To determine the spatial distribution of FGs, habitat suitability's and dispersal rates can be defined for model grid cells. Dispersal rates represent the fractions of biomass of each FG dispersing at a given rate (km/year), with a base dispersal rate of 300 km/year (Christensen et al., 2008). For the model of the southern part of the North Sea, five different dispersal rates were chosen 1000-600-300-30-3, based on the FG's life form (for a detailed list see Appendix A of Püts et al., 2020). Furthermore, a habitat foraging capacity model (HFCM) allows for the definition of the degree of habitat suitability in each cell. Habitat suitability for the most important and common FGs were driven by distribution maps created with species distribution models. These were implemented and updated during simulation of historical years to account for shifts in species distribution over time. Distributions of FGs for which insufficient data existed to create species distribution models were driven by habitat properties based on sediment structures, distance to coast and water depth (Püts et al., 2020).

Model spin-up (burn-in period) was conducted for 10 years and run to equilibrium for 40 years followed by an additional 20 years used for evaluation. For a more detailed description of the Ecospace model used in this study as well as changes that were applied to the model, please see the Supplementary material and Püts et al. (2020).

4.2.2 Spatial closures and scenarios

4.2.2.1 Existing and planned closures

Ecospace allows for implementation of MPAs to test varying management strategies. We integrated in our model thirty-three currently designated MPAs that are located within the study area (retrieved from The European Marine Observation and Data Network, 2020, Figure 2). Details on these MPAs including their legal basis (e.g. Habitat Directive, Birds Directive, MSFD), are listed in Annex I. Specific management objectives were applied to each MPA individually, which can be fleet and time specific closures (year-round closures or just certain months). The majority of the MPAs lack an enforced management and some even defined restrictions completely. Hence, we defined closure options based on the goods they aim to protect (Table 1) and translated these into the exclusion of specific gears in the MPAs: 1. all bottom-contacting gears (to avoid seafloor disturbance), 2. all static gears posing a threat to birds and mammals (drift/fixed nets and gears using hooks) or 3. both gear groups. Fleets fishing mainly within the water column, i.e. pelagic fisheries or low impact gears like pots were allowed to continue fishing, as they do not pose an imminent danger to the protected goods listed in Table 1. A detailed list of the protected goods for each MPA is presented in Appendix A Table 1.2A, which is based on the European Nature Information System (EUNIS) and the declared protected habitats and species of the Habitats Directive (Council Directive 92/43/EEC).

Table 1: *Goods protected by MPAs differentiated between habitat types and species groups. Last column shows the fleets that were excluded from fishing in the spatial management scenarios.*

Type of protected good	**Protected good**	**Gears and associated Ecospace fleets excluded**
Habitat	Sandbanks/Mud flats and Sand flats	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)
Habitat	Reefs	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)
Species	Birds	Drift and fixed nets, Gears using hooks
Species	Cetaceans	Drift and fixed nets, Gears using hooks
Species	Benthic community	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)
Species	Fish (including lampreys)	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)
Species	Mammal protection site	Drift and fixed nets, Gears using hooks

The closure of OWFs is regulated differently within the Exclusive Economic Zones of Denmark, Germany, Belgium, Netherlands and the United Kingdom (UK). While Belgium, Germany and the Netherlands prohibit fishing within the OWFs (Lukic et al., 2018), Denmark and the UK exclude trawling but allow other gears. Yet, it is reported that fishers generally try to avoid the OWFs (Groenendijk, 2018).

For testing the effectiveness of OWFs as marine protection sites, we closed all OWFs for the entire year for all fishing gears. We tested two developmental stages of OWFs based on data retrieved from OSPAR (OSPAR, 2020). One includes the currently operational OWFs (from here on referred to as OWF_{op}) the other one planned and designated OWFs (OWF_{pla}; status in the beginning of 2020, Figure 2).

The implementation of OWFs not only causes changes in spatial usage. OWF installation also alters habitats and creates additional hard substrate. Hard substrate has the potential to act as an artificial reef, likely affecting the ecosystem and, in particular, benthic functional groups (Dannheim et al., 2020). To consider these impacts in our model, we developed specific habitat layers based on OWF_{op} and OWF_{pla}, whereby each grid cell contains the percentage of gained hard substrate based on turbines relative to the entire area of each cell.

Unfortunately, detailed information on the type of turbine substructures were not available for all OWFs. Yet, since the majority of turbine substructures in the North Sea are monopiles (The European Wind Energy Association, 2016) we used the mean diameter of monopiles in the North Sea for calculating the lateral surface of the turbines (Negro et al., 2017). Studies have shown that the biggest increase in biomass at the turbines can be found within 1 m above ground and among the riprap, i.e. protective rubble at the base that is used to prohibit erosion from scour (Krone et al., 2013). We aggregated the lateral surface of 1 m of the turbine with the area covered by riprap, multiplied this with the numbers of turbines in the area and calculated the percentage gained in comparison to the area of the entire grid cell. FG affinities to these new habitats were assigned to five groups: (i) large crabs, (ii) epifaunal macrobenthos (mobile grazers), (iii) shrimps, (iv) small mobile epifauna (swarming crustaceans) and (v) sessile epifauna. This is in line with Lynam et al. (2017), which was also used as reference for the affinity of these benthic groups towards different sediment types (see Appendix A1 Table 1.3A for detailed information).

4.2.2.2 Additional ecological-based closures

We additionally tested two hypothetical closures as alternatives to the presently planned MPAs. A first closure had the aim to protect areas of highest ecosystem diversity (i.e. Kempton’s Q). This version of the Kempton’s Q index was modified for use with EwE output to represent diversity among FGs rather than on species level (Ainsworth and Pitcher, 2006). Ecosystem stability is assumed to increase with higher diversity, therefore the core area of the Kempton’s Q index should identify the region with a higher stability that should be protected (McCann, 2000). A second hypothetical closure aimed to protect highest biomass of endangered species, as defined by the IUCN "Red List", which includes species categorized as “near threatened”, “vulnerable”, “endangered” or “critically endangered” (IUCN, 2012). This category applies to 21 species within our model, most of which are birds, elasmobranches and some fish species (for a complete list see Appendix A, Table 2.1A). Based on the spatial patterns derived from the equilibrium baseline run, regions with values in the 75th percentile were identified as core areas for the Kempton’s Q-based as well as the IUCN-based MPA. In order to meet the 30% protection goal formulated by the Biodiversity Strategy 2030, a buffer zone was created around the core areas until 30% of the model domain was achieved (Figure 1). For both closures, bottom contacting gears and static gears were excluded, similar to the designated MPAs.

Kempton's Q index as diversity indicator displayed a slightly fractured pattern. This fragmentation is especially apparent in the northwestern part of the study area near the British coast, where high biodiversity was found around the 50 m depth line (compare with depth isolines in Figure 2). The area is located off the northern coast of England and the south of Scotland and spans all the way over to the Danish coast. In contrast, the biomass of the IUCN-endangered species showed highest concentrations in the German Bight and along the British coast below 53° N towards the English Channel, similar to the pattern of total biomass. Small demersal fish (e.g. *Cyclopterus lumpus*), bird groups (e.g. *Larus argentatus*) and turbot were the main contributors to high biomass concentrations of IUCN-endangered species in the German Bight while elasmobranch groups (e.g. *Raja clavata* and *Squalus acanthias*) and toothed whales (*Phocoena phocoena*) were the main contributors along the British coast. With the exception of one small outlying area, this core area is one continuous area that serves as outline for the IUCN-based MPA.

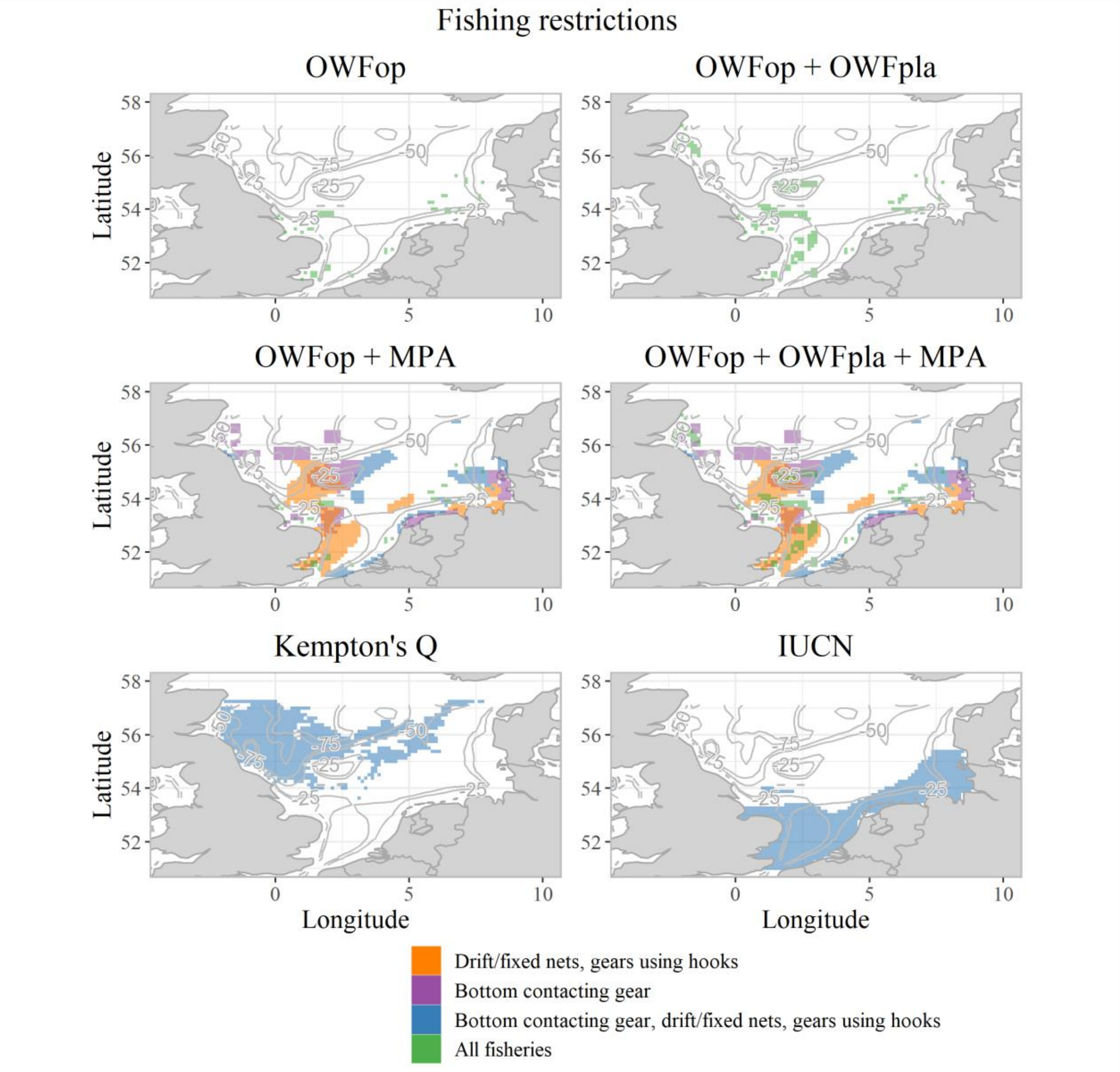

Figure 1*: Six different closures tested in this study. Each closing state contains the existing OWFs since they are currently the only closures that are in place. Color type depicts the type of fishery that was excluded. Green was closed for all fisheries, which affected up to 6.31% of the total area when operational and planned wind farms were closed. Marine protected areas were closed based on protected goods. Three types of exclusion: i) all bottom contacting gear (11.4% closure), ii) all bottom contacting gear as well as passive gears (6.73% closure), iii) all passive gears (14.4% closure). Kempton's Q and IUCN areas were closed for bottom contacting and passive gear.*

Scenarios in fishing effort reduction

Closing areas to fisheries does not change the total effort in the model, but rather redistributes it among the remaining fishing locations. In Ecospace, effort is allocated via a "gravity model", where effort is distributed in relation to the net benefits gained by exploitation of a certain region. Hence effort increases substantially along the edges outside closed areas (Christensen et al., 2008), especially if up to 30% of the entire area is closed.

We tested for the effect of an additional effort reduction in scenarios with closures >= 30% of the total area (OWF_{op} + OWFpla + MPA, Kempton's Q and IUCN). The effort reduction was achieved by decreasing the overall effort in the temporal model Ecosim for each fleet individually by the fraction of total fishing grounds lost to fishing restrictions, rather than the fraction of effort associated with that closure (list of percent losses per scenario see Appendix A3, Table 3.1A). Overall, we tested a set of nine scenarios combining closure types and effort levels (Table 2).

Table 2: *Scenarios defined by closure type, excluded fisheries and gears, with different closure states and size of closure (abbreviations given in the text)*

Closure type	Excluded fisheries and gears	Size of the closure (% of study area)
1. OWF_{op}	All fisheries	1.78
2. OWF_{op} + OWF_{pla}	All fisheries	6.31
3. OWF_{op} + *MPA*	All fisheries (OWF) + bottom contacting gear, passive gear or both (MPA)	30.3
4. OWF_{op} + OWF_{pla} + *MPA*	All fisheries (OWF) + bottom contacting gear, passive gear or both (MPA)	31.6
5. *Kempton's Q*	Bottom contacting and passive gear	30.8
6. *IUCN*	Bottom contacting and passive gear	30.3
7. OWF_{op} + OWF_{pla} + *MPA* + *Effort reduction*	All fisheries (OWF) + bottom contacting gear, passive gear or both (MPA) + Effort reduction equal to lost fishing ground	31.6
8. *Kempton's Q + Effort reduction*	Bottom contacting and passive gear + Effort reduction equal to lost fishing ground	30.8
9. *IUCN + Effort reduction*	Bottom contacting and passive gear + Effort reduction equal to lost fishing ground	30.3

4.2.3 Trait-based indicator approach to evaluate trade-offs

We evaluated our spatial management scenarios using a trait-based indicator approach (Beauchard et al., 2017). The EwE ECOIND plug-in provides the opportunity to calculate ecosystem indicators based on FGs included in the model (Coll and Steenbeek, 2017). Prior to applying ECOIND, traits needed to be assigned to the species in each model FG.

The entire species list includes the 410 species that were used to construct the FGs in the original model (Mackinson and Daskalov, 2007). We focused on traits related to ecology, conservation and exploitation (Table 3). Biomass contribution of each species to the FG were then calculated based on their mean relative occurrence in the ICES International Bottom Trawl Survey (IBTS) and the ICES Beam Trawl Survey (BTS) in the period 1991-1995. For FGs that were not represented sufficiently within the surveys, like benthic or planktonic groups, the biomass contribution was kept equal for all species. Catches were assumed to have the same relative species contributions inside the FGs as in the food web.

Table 3: *Traits assigned to the species in the EwE model for the southern part of the North Sea.*

Trait	**Categories**
Organism type	Mammals, birds, fishes, invertebrates, algae
Ecology	demersal (bathydemersal, benthic, benthopelagic), pelagic (bathypelagic, pelagic-neritic, pelagic-oceanic), land-based
IUCN status	Not evaluated, data deficient, least concern, near threatened, vulnerable, endangered, critically endangered

Indicators calculated via ECOIND can be split into five groups, of which four were tested in this study: 1) *Biomass-based indicators* representing the standing stock in the ecosystem including total biomass, but also separate biomass per species group (i.e. fish and invertebrates), habitat (i.e. pelagic vs. demersal) and exploitation status (i.e. commercial species). 2) *Catch-based indicators* representing catch and consequent discards, similarly to biomass for total catch or to subgroups like organism and ecology. 3) *Trophic-level based indicators* that refer to the position of the species in the food web. 4) *Species-based indicators*, of which some refer to the International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015). *Size-based indicators* were excluded in this study due to the course resolution of EwE with regard to length and age.

For each biomass-based and catch-based indicator the mean values for the entire area, within closures, and outside closures were calculated and changes relative to the baseline run were evaluated. Furthermore, a comparison of effort distribution was conducted to assess the effect of each closure on fishing activity. Eventually, trade-offs and gains/losses in biomass- and catch-based indicators were evaluated (Equation 1).

For this, all indicators (*ind*) were summed up per scenario (*s*) and trend (*t*, positive or negative change compared to the baseline scenario) and the relative difference among the scenarios was calculated:

$$Impact_{s,t} = \left(\sum_{ind=1}^{n} \frac{rel\_change_{s,t}}{\max\_change_{s,t}}\right) \quad (1)$$

with $Impact_{s,t}$ representing the relative positive or negative impact an indicator had, the sum of all relative changes per scenario in relation to the baseline run, trend and indicator, divided by the scenario with the maximum sum over trend and indicators.

4.3 *Results*

4.3.1 Characterizing the ecosystem in the southern part of the North Sea

Prior to assessing the effects of closures on the ecosystem, we provide an overview of the composition and spatial structure of the food web in the southern part of the North Sea based on ecological indicators derived from the Ecopath mass-balance in 1991 (Table 1.1B in Appendix B includes all indicators). The vast majority of the total biomass (606.5 t/km^2) was composed of invertebrates (525.4 t/km^2) and only 3.6% was fish biomass (21.5 t/km^2). Over 90% of the total catch (5.9 t/km^2) in the system was certainly composed of fish species (5.3 t/km^2).

Spatial patterns for the various indicators were derived from a baseline run without fisheries closures (Figure 2). All indicators including those shown in Appendix B, displayed lower values for deeper, central and northern parts of the study area. Total biomass followed the depth pattern in the southern part of the North Sea with highest values at the coasts of Denmark, Germany, Belgium and the Netherlands as well UK in the south towards the English Channel. Fish biomass was similarly distributed to total biomass, although patchier. Total catch was also concentrated along the coastlines following the biomass distribution.

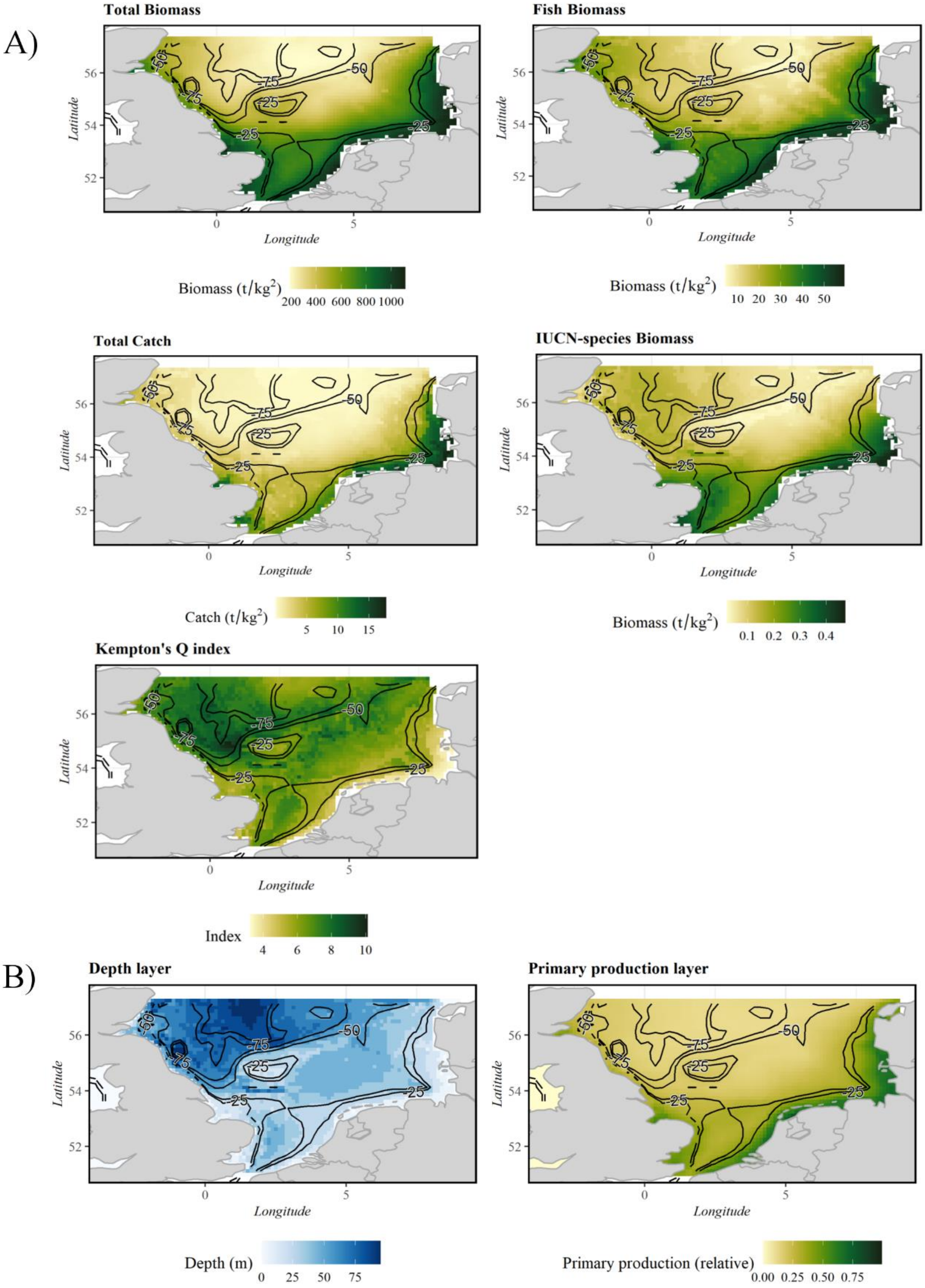

Figure 2: *Baseline spatial distribution of A) selected ecological indicators and B) depth and primary production in the southern part of the North Sea according to the Ecospace model.*

4.3.2 Evaluation of closure scenarios– biomass-based indicators

Overall, excluding fisheries from pre-defined areas induced only small, but negative changes in biomass-based indicators (Figure 3). Negative impacts outside outweighed the positive effects inside the closed areas. Across the entire area, the IUCN scenario seemed to have the strongest impact, followed by the scenarios OWF_{op} + MPA and OWF_{op} + OWF_{pla} + MPA. Overall, total biomass and Shannon diversity hardly changed in any of the scenarios, mammals and bird's biomass are most negatively affected, especially by the closures implemented in the IUCN scenario. Inside the closed areas the most notable increase was displayed for fish biomass in the IUCN scenario (approx. 13%). Next to the fish biomass, the predatory biomass and the biomass of IUCN-endangered species increased inside closed areas in most scenarios, but not with the closures of the designated MPAs. Outside the closed areas biomass-based indicators generally showed negative impacts, with the largest impacts in the IUCN scenario (decreases up to -18%). Only the IUCN scenario produced a minimal increase in overall biomass (~ 2%) and predatory biomass (~ 1%). Changes in trophic levels of the community were so small (maximum 0.2% change) they are not discussed further, but the plots can be found in Appendix B2.

The strong negative impact of the scenarios on mammals and bird's biomass is counter intuitive at first sight. The reason for the negative development of this indicator is the inclusion of the functional group "surface-feeding seabirds". For this functional group, a majority of the diet is based on discards. When reducing fishing opportunities, this decreases the prey availability for this group, which has a negative effect on this indicator. This is also the reason why this indicator decreased inside the closed areas in nearly all scenarios, since fisheries are excluded and the associated discards are not available as prey. This side effect also influenced the results of the indicator for biomass of IUCN-endangered species, which includes surface-feeding birds as well.

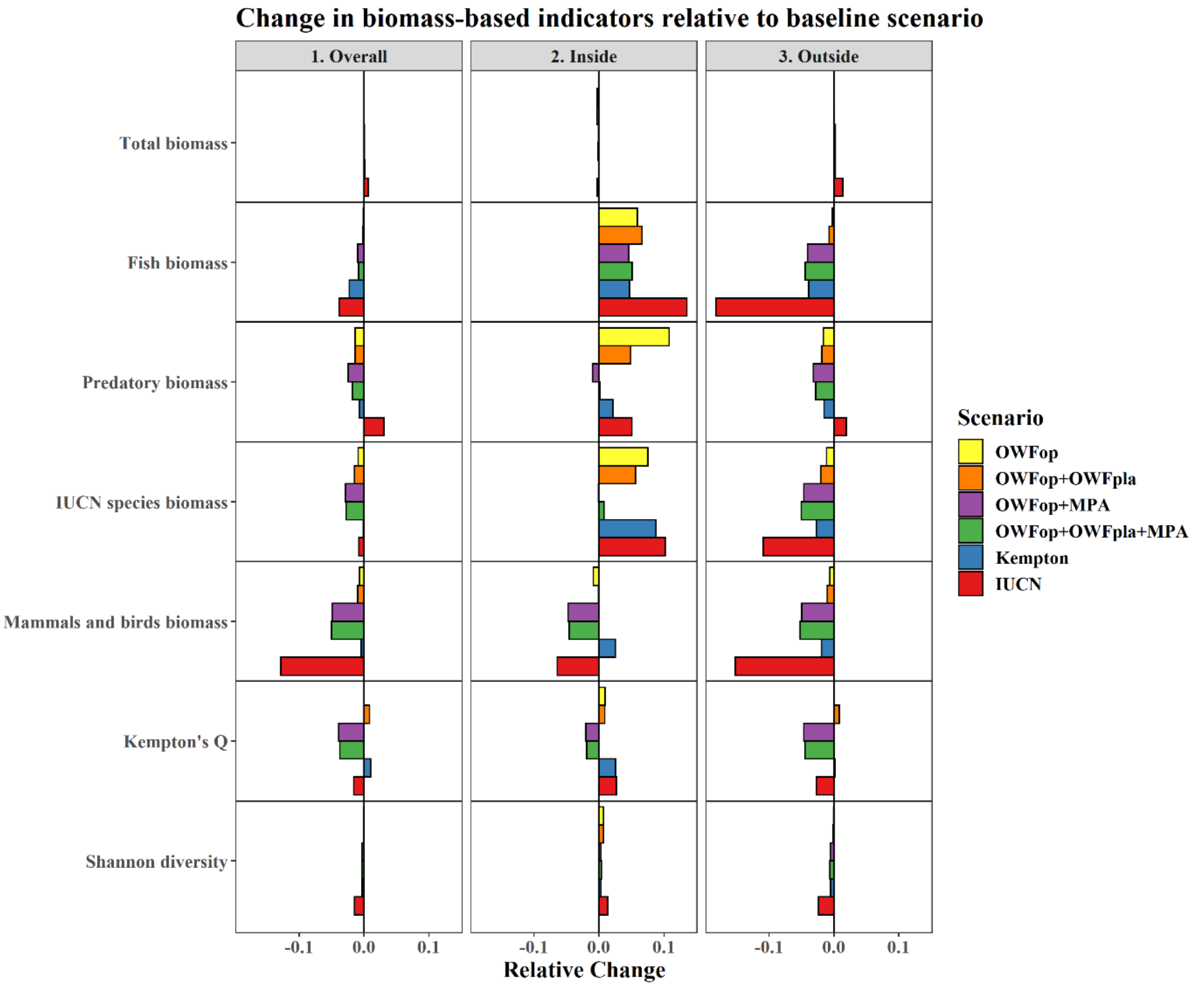

Figure 3: *Change in selected biomass-based indicators relative to the baseline scenario for the different closure scenarios. Left: Results for the entire southern part of the North Sea. Middle: Results inside areas with fishing restrictions in the different scenarios. Right: Results outside the areas with fishing restrictions in the different scenarios.*

Shifts in spatial distribution patterns were detected for most biomass-based indicators (for all indicators see Appendix B). The distributions of the overall biomass (primarily invertebrates) and fish biomass showed contrasting patterns, reflecting trophic effects associated with the decreased predation mortality of invertebrates by fish as their biomass was reduced (Figure 4). While the fish species increased inside the closed areas while decreasing outside, the total biomass increased outside the closed areas. When closing areas to fisheries, the total effort is re-distributed among the remaining fishing areas. This leads inevitably to an increased effort outside the closed areas, which primarily decreases the biomass of commercially targeted fish species. However, this has a positive effect on the invertebrates outside the closed areas. Within the closed areas, the reduced fishing pressure led to an increase in fish biomass and therefore predatory biomass, which in turn reduced the invertebrate biomass.

Size, coherence and location of the closed areas influenced the spatial distribution of fish and total biomass. While the effect of closure was almost undetectable in the OWF_{op} scenario, it became visible by just closing the other areas of the planned OWFs (Figure 4). Additionally, closing MPAs increased the impact on these biomass-based indicators.

Moreover, the evaluation of the scenarios based on the designated MPAs revealed that only the MPAs that at least excluded bottom-contacting gears had a larger impact on biomass distribution patterns in contrast to MPAs closed to passive gears only. Despite an equal size, the impact of the two hypothetical scenarios varied strongly. While the effect of the Kempton's Q scenario is comparable to the scenarios including MPAs, the scenario based on the distribution of IUCN-endangered species had a much stronger impact. Removing the fishing pressure in the area of the IUCN scenario led to a strong increase in fish biomass inside the area and a strong decrease outside, due to the re-distribution in effort, which in turn affected the prey biomass visible via trophic cascades (increasing outside and decreasing inside the closed area).

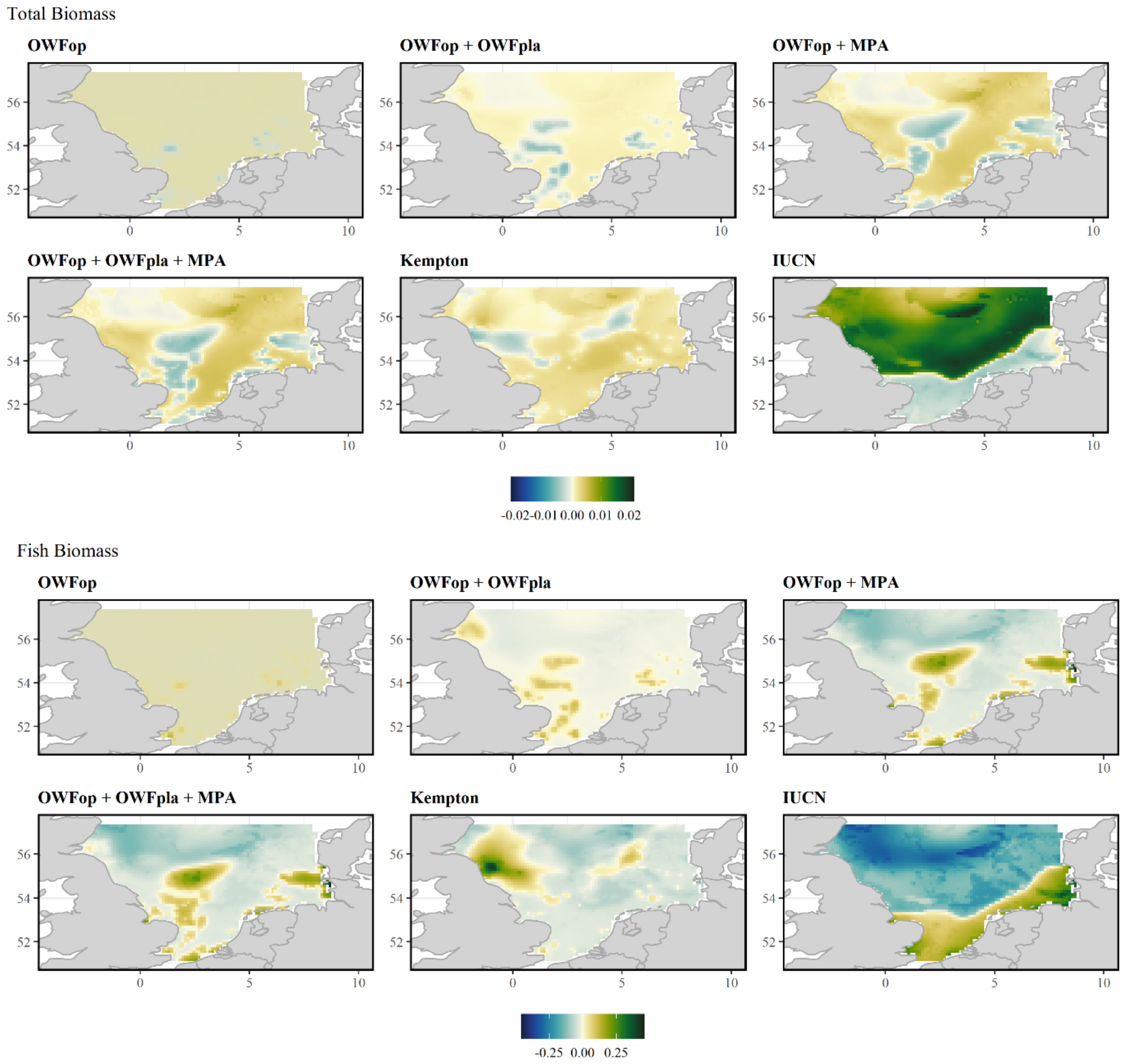

Figure 4: *Changes in the distribution of total biomass (top) and fish biomass distribution (bottom). Changes are relative to baseline scenario with no closures with increases displayed by yellow to greenish colors and a decrease displayed by blue.*

4.3.3 Evaluation of closure scenarios – catch-based indicators

The closure of fishing areas led to an overall decrease in catch, despite the same fishing effort as in the baseline scenario (Figure 5). For the entire study area, the strongest decrease was detectable for the IUCN scenario followed by the two scenarios OWF_{op} + MPA and OWF_{op} + OWF_{pla} + MPA (similar to the biomass-based indicators). For the IUCN scenario, the total catch decreased in the entire area by around -30% and discards decreased by -53% compared to the baseline scenario. The scenarios including MPAs decreased -7%, while the overall decrease was marginal in the scenarios dealing with OWFs only. Comparing indicators, the catch of predatory species was impacted most with a simultaneous reduction in the trophic level of the catch.

When splitting the model area into inside and outside closed areas, almost all depicted catch-based indicators increased outside the closed areas in most scenarios. Only the trophic level of catch did not change noticeably in comparison to the baseline run. Again, the IUCN scenario shows the strongest increase in total catch (~ 18%), predatory catch (~ 46%) and discards (~ 38%). For fish catch, the scenarios based on designated MPAs had a stronger increase then the IUCN scenario (~ 9% and 15%). Indicator values inside the closed areas reflected the applied closures, for example a 100% decrease for the OWF scenarios due to closures for all fisheries.

These results showed that the size and location of the closed areas is crucial to reach a certain overall impact without the addition of measures to reduce fishing effort outside the closures. While all three scenarios, OWFop + OWFpla + MPA, Kempton's Q and IUCN close the fishing grounds up to 30%, the impact on catch-based indicators is quite diverse, highlighting that also the location and coherence of the closed areas is an important factor. Especially the difference between the IUCN and the Kempton's Q scenario is striking. While IUCN had a strong overall impact on the catch-based indicators, the effect of the closures in the Kempton's Q scenario had a much smaller impact.

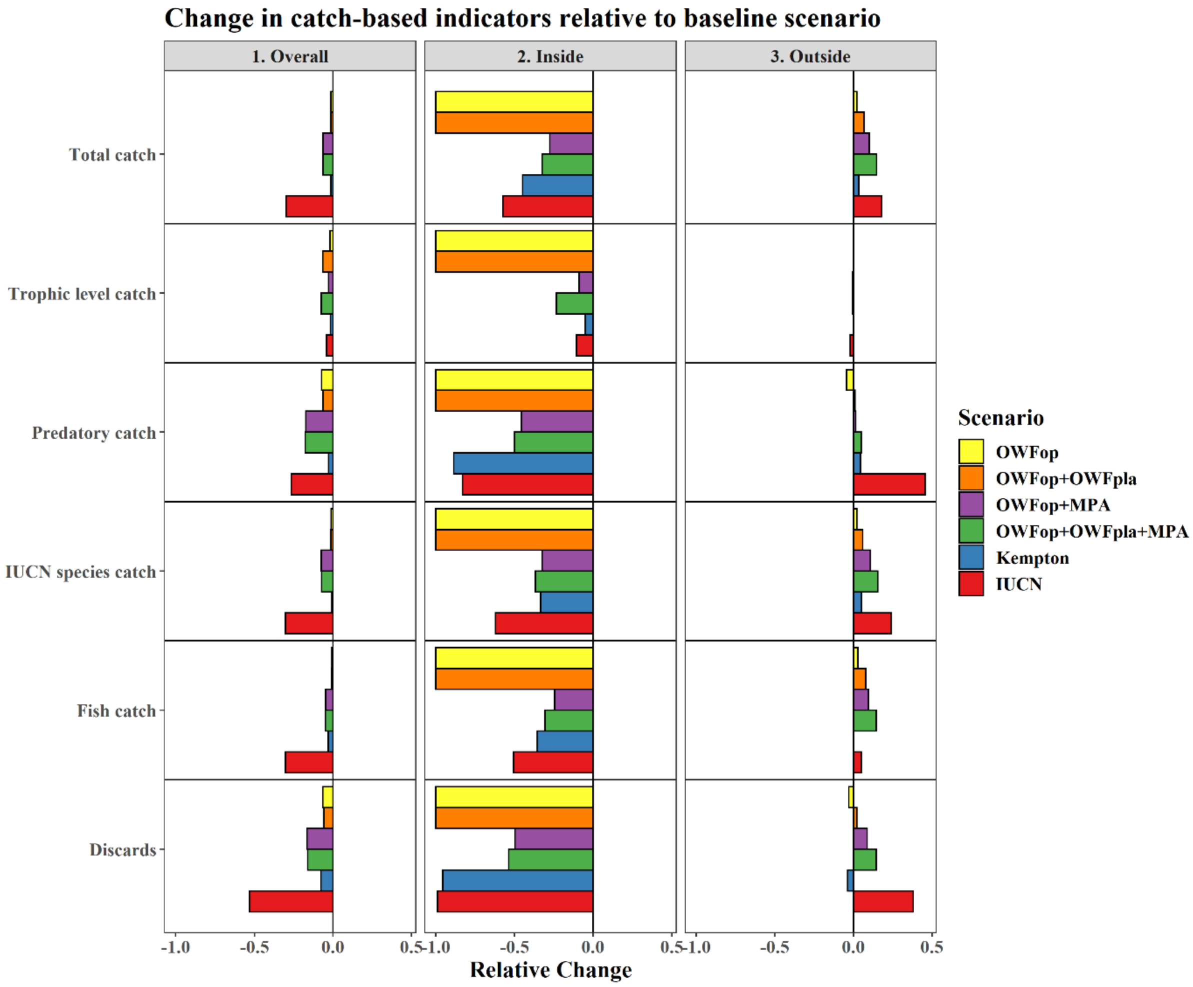

Figure 5: *Changes in selected catch-based indicators relative to the baseline run for the different closure scenarios. Left: Results for the entire model area. Middle: Results inside the closed areas. Right: Results outside the closed areas in the different scenarios.*

The distribution of fish catch shifted depending on the different scenarios. Fish catch increased especially around the borders of the closed areas. Scenarios with larger area closures (closures including MPAs and the IUCN scenario) displayed areas with decreasing catch even outside the closed areas (Figure 6). Overall, this shift in catches displayed the effect of effort reallocation. Outside the closed areas the fishing pressure increased, which led to a decrease in fish biomass, which in turn resulted in a lower catch in equilibrium. Furthermore, the effect of the closures applied to bottom contacting gears were more apparent than for the MPAs that only excluded passive gears.

The same shift is detectable when comparing the distribution of catch to one of the fleets using bottom-contacting gear, i.e. demersal trawls and seiners. Fishing effort is increasing around the edges of almost all closed areas, especially in the central and southern part of the modelled area. Again, the IUCN scenario stands out with the strongest shift in effort. In this scenario, the region with the greatest total catch values in the baseline equilibrium is being closed off, therefore the area where the majority of the fleet effort was concentrated. Hence, this effort needs to be re-distributed, which resulted in the largest overall changes among scenarios.

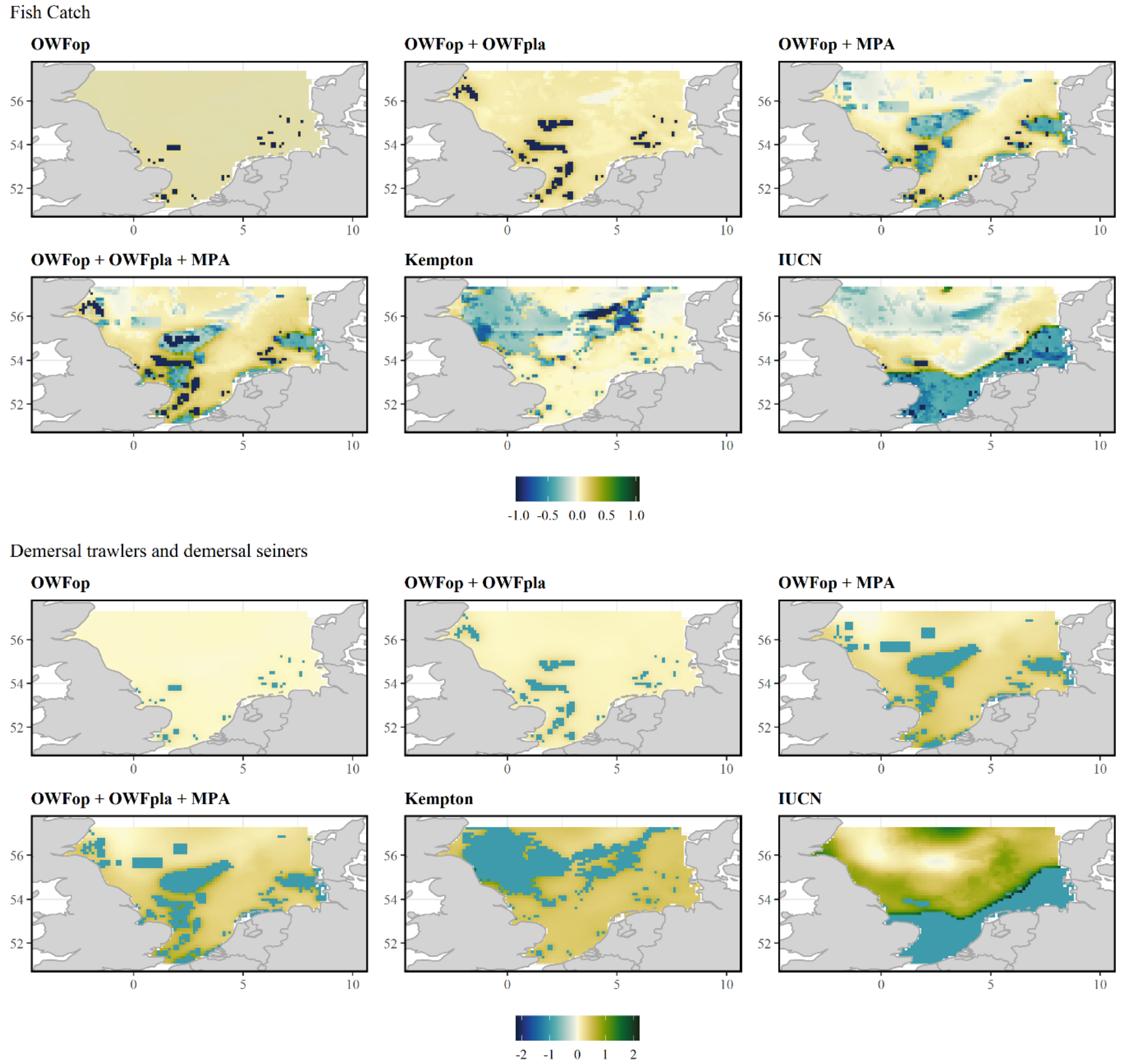

Figure 6: *Shift in fish catch distribution (top) and the distribution of effort of demersal trawlers and seiners (bottom). Changes are relative to baseline scenario with no closures with increases displayed by greenish to yellow colors and a decrease displayed by blue.*

4.3.4 Closure scenarios with additional effort reduction

Especially fish biomass, as the group primarily targeted by the fishery, increased inside and overall for two scenarios due to the additional reduction in effort (Figure 7). For the Kempton and OWFop + OWFpla + MPA scenario, an overall reduction in fish biomass compared to the baseline scenario was turned into a small overall increase. For all scenarios, fish biomass decreased less outside the closed areas then their corresponding scenarios without effort reduction. Similar, the biomass of IUCN species increased for two scenarios (IUCN and Kempton) and decreased less in the OWFop + OWFpla + MPA scenario with reduced effort.

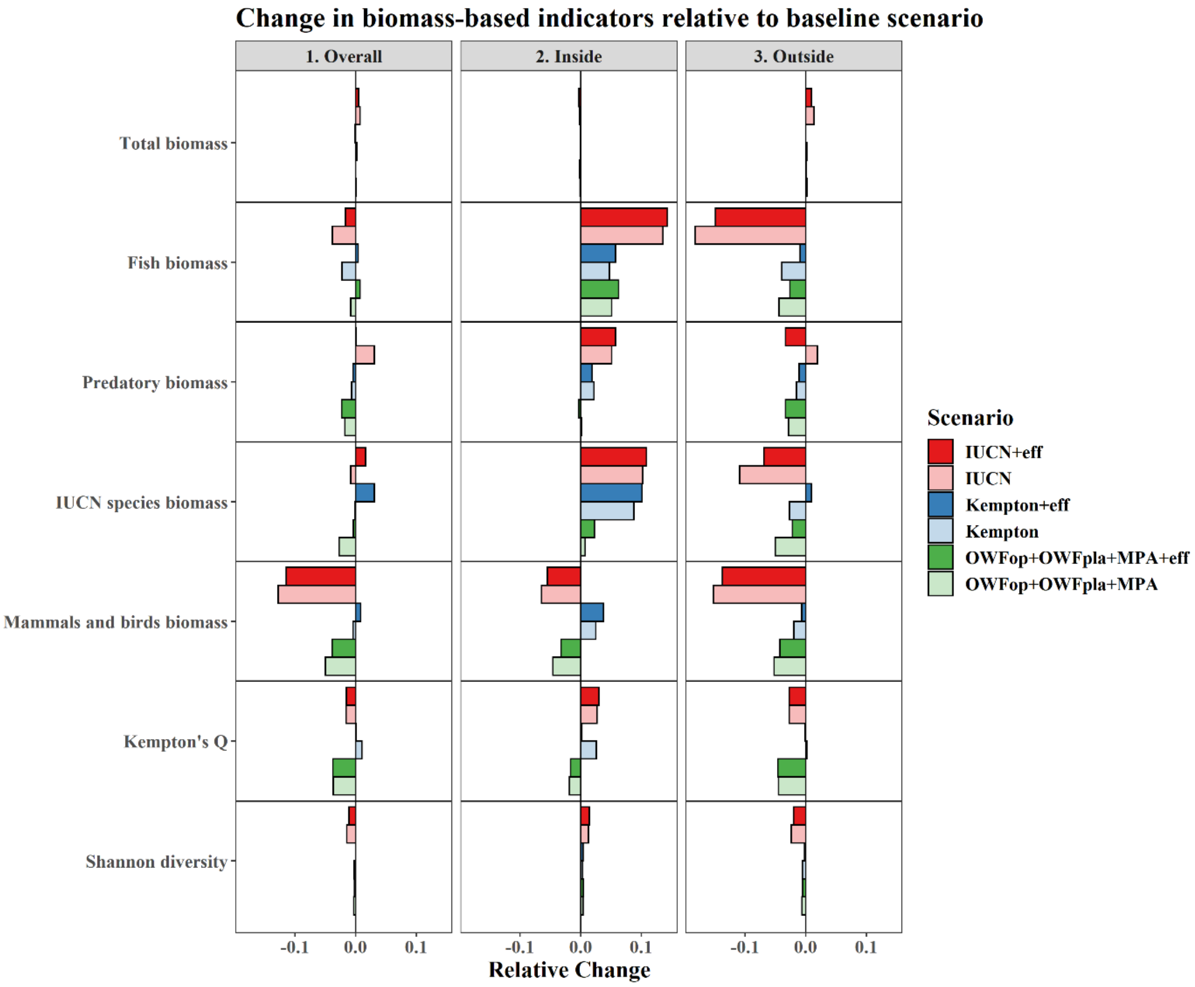

Figure 7: *Biomass-based indicators for the three scenarios that were run with an effort reduction. Darker colors display the effort-reduced scenarios, the lighter shaded colors the scenarios that were executed with the original effort as comparison.*

In terms of catch, the decreased effort led to an expected decrease in total catch comparison to their associated scenarios (Figure 8). The difference to the associated scenarios is of different magnitude, while the total catch in the IUCN scenario only decreased by additional 6%, the other two scenarios decreased by additional 11% and 13%. Trophic level of the catch was not affected by the additional effort reduction. While the IUCN scenario was the scenario with the highest values for the catch-based indicators outside the closed areas, the indicators decreased down to baseline level or even below due to the effort reduction. Reducing the effort also led always to a decrease in discards.

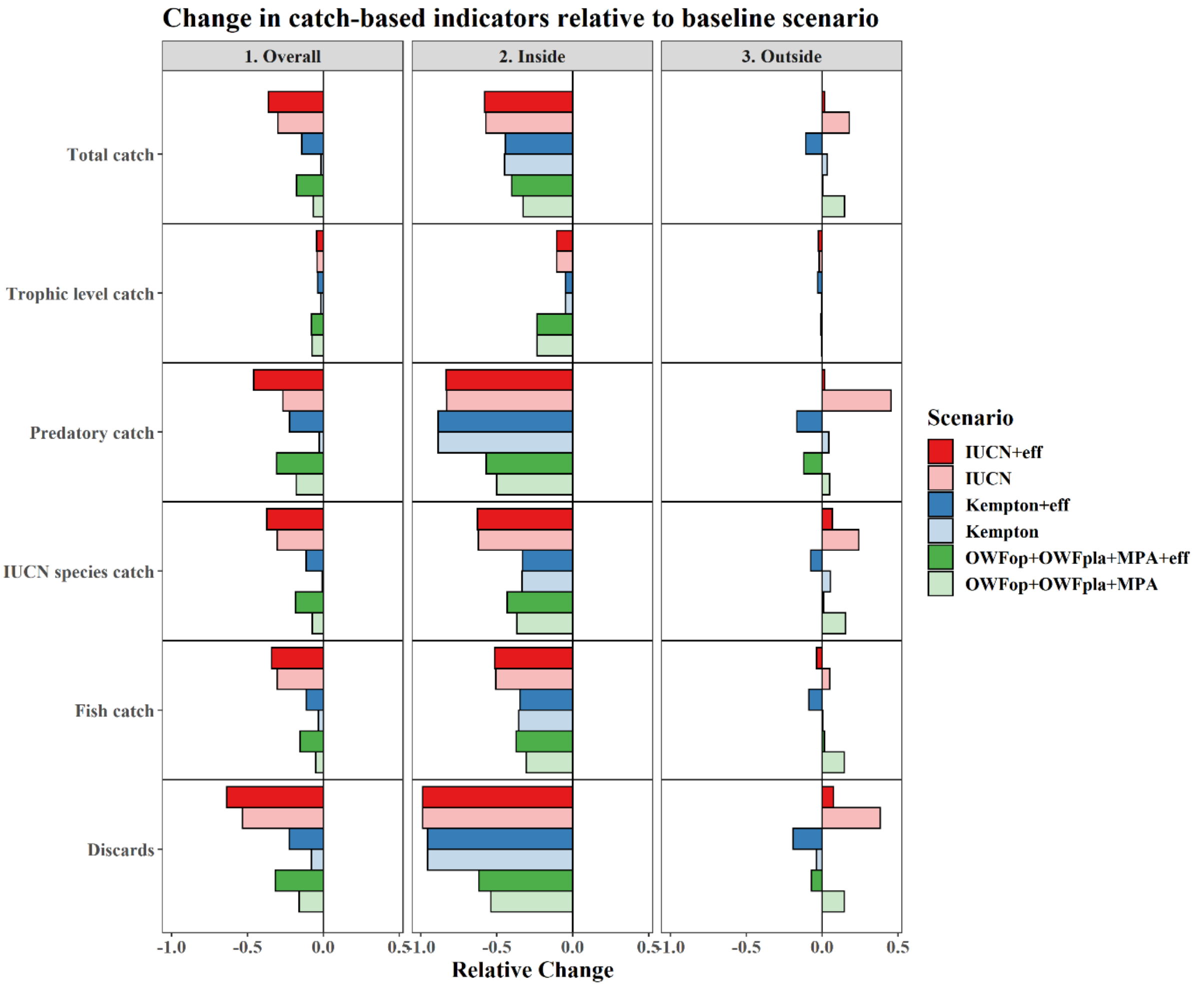

Figure 8: *Catch-based indicators for the three scenarios that were run with an effort reduction. Darker colors display the effort-reduced scenarios, the lighter shaded colors the scenarios that were executed with the original effort as comparison.*

4.3.5 Trade-offs

Summarizing increases and decreases of all indicators (including the ones only presented in Annex B2) for each scenario in relation to the baseline run enabled us to compare the overall impact of all scenarios (Figure 9). Evaluating the overall trade-offs, the great difference between the IUCN scenario with and without effort reduction and all other scenarios is displayed again. While they achieved the maximum sum in overall decreases compared to the baseline run, they also had the most positive impact on biomass and catch-based indicators. One important indicator that influences this are discards. For this evaluation, discard reduction is seen as a positive effect. Under both IUCN scenarios, the fisheries reduced their discards the most, from which the overall effect of these scenarios benefitted. The least negative impacts were calculated for the Kempton's Q scenario, but at the same time, the positive impact was equal to the MPA scenarios. The scenario with closures to all OWFs and MPAs with an additional reduction in fishing effort performed most poorly, as the gains could not outweigh the losses in terms of yield compared to the other scenarios. Furthermore, it became apparent, that additional closures of planned OWFs to the currently existing ones did not have an impact on the overall trade-off.

Considering only the biomass-based indicators, the overall picture is changing. Now the IUCN scenario without the effort reduction seems to have the greatest impact, positive and negative. At the same time, the Kempton's Q scenario with effort reduction has the least losses and ranked second in terms of gains, implicating a positive overall impact on biomass-based indicators. Unfortunately, all scenarios including MPAs did not seem to have much of a positive effect overall caused by trade-offs inherent in the food web and management decisions (e.g., amount of discards vs sea surface feeding seabirds). When assessing the losses and gains just for the catch-based indicators, the Kempton's Q scenario without effort reduction was the only scenario that indicated an increase in those indicators and therefore a more positive effect compared to the other scenarios. All other scenarios had no positive impacts and were just compared based on their negative impact.

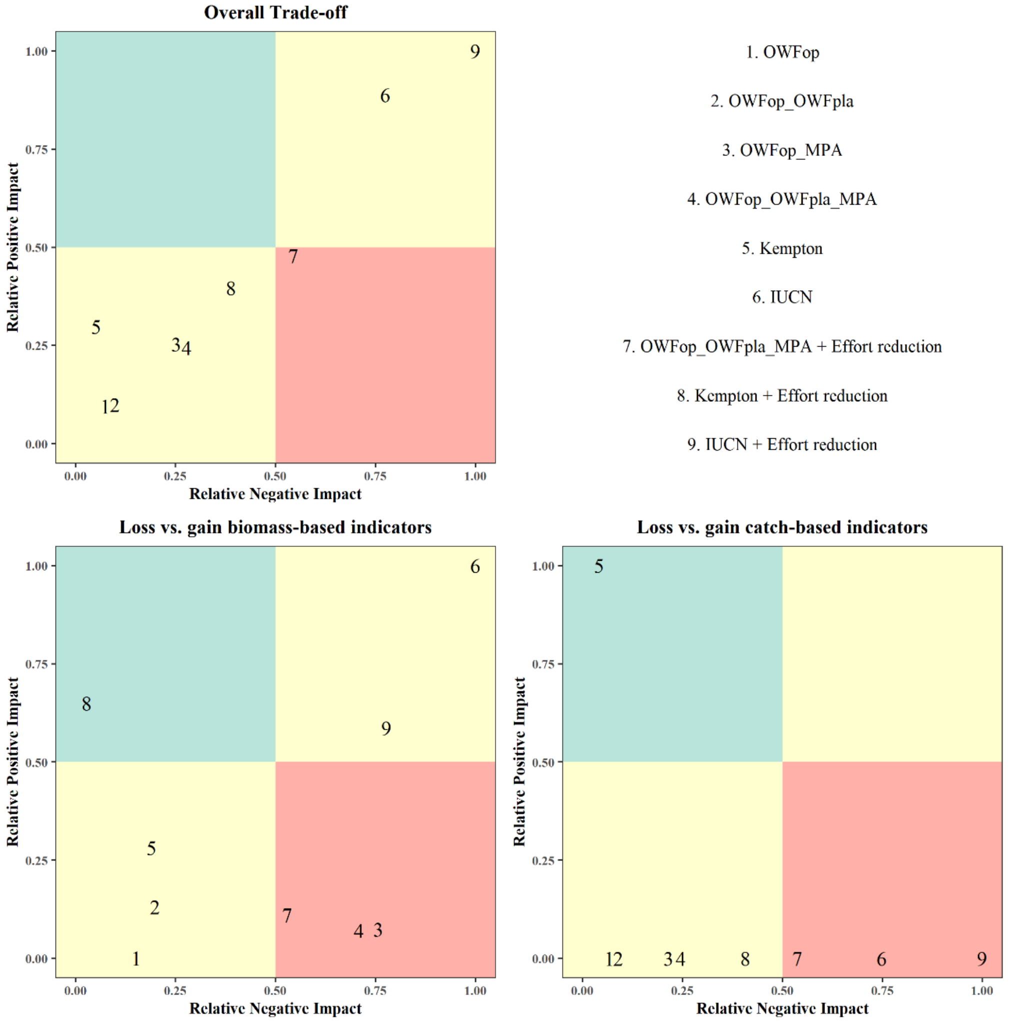

Figure 9: *Top: Trade-offs for all scenarios. Bottom: Losses and gains per biomass and catch-based indicators. For all plots, gains and losses were summed up per scenario and trend (decrease/increase) and the impact relative to the other scenarios was calculated. Color scheme references preferential scenarios (green), neutral scenarios (yellow) and less beneficial scenarios (red) in overall comparison.*

4.4 *Discussion*

We used a spatially explicit ecosystem model for the southern part of the North Sea to evaluate the effects of spatial management measures on this complex ecosystem. Our results show the potential consequences and trade-offs resulting from closing specific areas to fishing. Overall, our study revealed that evaluating the effect of excluding fisheries in certain areas is not straightforward. Effort reallocations as a result from closures, trade-offs within the ecosystem due to trophic interactions and trade-offs between conservational and economic goals complicate any spatial management approach. The impact of closed areas on the ecosystem and fisheries also highly depends on their size and location. Therefore, it is important to predefine management goals, to utilize tools that are able to predict possible outcomes of closure scenarios and to select suitable indicators that are able to measure progress.

4.4.1 Caveats and remarks

Our spatial modelling approach allows to evaluate the impacts of closures to fisheries on the full ecosystem. Even though our model is focused on commercially exploited fish species, all other ecosystem components from phytoplankton up to mammals are represented sufficiently. The rich data availability for the southern part of the North Sea allowed us to reliably model distributional changes of almost half the FGs. Yet, spatial modelling of a large number of FGs required a series of assumptions. For example, dispersal rates were entered based on life form rather than an exact rate of dispersal per year causing potentially some uncertainty about movement patterns. Moreover, fishery exclusions in MPAs in our model reduce catch but does not consider effects of reduced seabed disturbance and a possible recovery of the habitat, likely having positive impacts on the benthic community within MPAs (Langton et al., 2020). We hence consider our modelling results as conservative regarding the effect of closed areas and potentially underestimating spillover effects. Furthermore, we did not assess specific effects of OWFs such as the sensitivity of benthic organisms and other functional groups to noise and vibrations produced by turbines (Dannheim et al., 2020). We also did not make any assumptions of the effects of the construction phase and the removal of the turbines (Lynam et al., 2017) as well as the possibility that artificial structures cause a connectivity sprawl (Bishop et al., 2017).

Within this study, we also assumed an exclusion of fishing gears based on the goods they are aimed to protect (see Table 1). We therefore restricted fishing of bottom-contacting gears from areas with sensitive habitat or areas that were created to protect sensitive benthic communities, to prevent seabed disturbance (Hiddink et al., 2006). Furthermore, static-gears were prohibited in protected areas designed for seabirds and mammals (ICES, 2020). Therefore, not all of the currently implemented MPAs are closed to the same fisheries, some are only closed for bottom contacting gear or passive gear, and some restrict fishing for both types of gears and finally in OWFs all fishing is restricted. This variance in restriction of fishing gears exacerbates the interpretation of the closure effect.

Lester and Halpern (2008) stated that there is a significantly higher density of organisms within no-take areas compared to partially protected areas, which is supported by Hopkins et al. (2016), who state that areas with absolutely no fishing pressure are needed to increase ecosystem resilience in order to persist changes due to climate change. Additionally, fully protected areas with a surrounding buffer zone with partial protection could increase the effectiveness of the MPAs (Vilas et al., 2020). The results presented in this study should therefore be interpreted as general lessons. It allowed us to identify general patterns of ecological indicators in the southern part of the North Sea and reactions of the ecosystem towards different type of closures. Yet, they show trends and relative differences rather than absolute values and cannot be taken as absolute interpretation of the effects of closure. Our assumptions on future MPA management may lead to deviations between the modelling study and reality once management is finally implemented.

4.4.2 Ecological and economic implications

When removing fishing pressure the expected outcome is generally an increase in biomass and a healthier ecosystem (Halpern, 2003). Our analysis largely supports this assumption for biomass-based indicators inside the closed areas. Yet, over the entire study area the positive effect of closures is substantially reduced. This result is in line with previous results showing increased biomass of targeted fish species in MPAs while declining over the entire North Sea (Le Quesne et al., 2008).

We found catch-based indicators to mainly decrease, with strong variability among the scenarios. The overall reduction in total catch is the result of lost fishing areas that is not compensated by the catch outside of the closed areas. Unlike biomass-based indicators that react to shifts in fishing and changes in predator-prey distributions, the influence of the closures on catch-based indicators is a direct effect, which explains a generally greater deviation from the baseline run.

Our study demonstrated that a major consequence of closing fishing grounds are alterations in species distributions. In large enough closed areas a redistribution through dispersal of fish biomass became apparent. Outside the closures increasing fishing pressure and hence reduced biomass of predatory fish species locally caused increased invertebrate biomasses. Such spatial shifts due to altered spatial fishing patterns and modified trophic interactions may lead to trade-offs between management goals. Clearly, trophic interactions need to be better incorporated in the evaluation of fishing restrictions like MPAs, otherwise these food-web effects might be missed and the positive impact of MPAs potentially overestimated (Cabral et al., 2020; Sala et al., 2021).

An important result of our study is the effect of effort redistribution due to fishing restrictions on local fish biomass. In our scenarios without effort reduction fish biomass generally declined, despite of local increases inside the MPAs. Effort redistribution here increased the fishing pressure outside the closed areas and especially at the MPA borders as a consequence of spillover of fish biomass in the model.

The results of our study are in good agreement with Sala et al. (2021) who also implies the necessity of taking effort reallocation and potential decrease in effort into account. We therefore reduced the overall fishing pressure by the same proportion as fishing grounds are lost to test if this decrease would cause positive effects on the ecosystem. In two out of three effort reduction scenarios we found reversed trends with increasing fish and IUCN-endangered species. Therefore, our study shows that fisheries closures need to be combined with other management tools (e.g., Total allowable catch, effort limits) to counteract the effects of effort redistribution. Since additional effort reduction will likely lead to even greater catch limitations, a strong trade-off between fisheries and conservation goals becomes apparent here.

Our model simulations furthermore revealed that closing fishing areas will not only lead to reduced catches but consequently to reduced discards. Generally, less discarding is a benefit to management, supporting the implementation of the landing obligation in the EU (EU, 2018). Yet, we observed that reducing discards might negatively impact parts of the ecosystem such as scavenging seabird species that largely feed on discards (Bicknell et al., 2013). In our model the prey of "surface-feeding seabirds" is composed by a large proportion of discards which reflects the feeding behaviour described in literature. However, in absolute numbers this parameterization has a degree of uncertainty (Phillips et al., 1999; Sotillo et al., 2014) and therefore the effects of lower discards on these birds might be overestimated. Nevertheless, field studies showed seabirds to suffer from reduced discard-based prey availability (Sherley et al., 2020) and hence reducing discards represents another example of trade-offs within an ecosystem that should not be ignored when setting management goals.

4.4.3 Placement, size and connectivity of fishing exclusion

The results of our two theoretical scenarios have shown that the location of a conservational area is as important as the size. The closures had roughly the same extent and were closed to the same fisheries as the previously defined MPAs, yet the outcomes varied significantly. The location of the IUCN scenario covers sea areas along the Danish, German, Dutch and Belgium coasts, which is an area of high biomass and catch. However, the distribution of areas with high biodiversity (i.e. Kempton's Q) was more dispersed with a higher concentration along the British coast and along the 50m depth contour towards the east. The extent to which the MPAs covered fishing grounds varied greatly: the IUCN scenario overlaps significantly with major fishing grounds in terms of catch, the biodiversity-based closure only partially coincides with fishing grounds in the coastal areas. Therefore, the exclusion of fishing in these highly productive coastal grounds covered by the IUCN-based scenario has a much larger impact on the catch but also on the responses of biomass indicators. The importance of coastal areas along the southern German Bight is not surprising since it is a highly productive region with high net primary production (Holt et al., 2015). Fish communities in this area are dominated by flatfish, such as the commercially important plaice and sole (Engelhard et al., 2011).

Our spatial simulations hence demonstrate that evaluating conservational areas solely on their size might therefore be deceptive and considering the location in relation to the management goals is crucial when designating MPAs or even networks of MPAs (Langton et al., 2020).

An interesting result of our study is that the spatial patterns of the Kempton's Q index do not overlap with most other indicators for biomass and catch. For Kempton's Q, the British coast and the central North Sea was found to be the most important regions, both right along the 50 m depth contour. This contour can be seen as a boundary, loosely separating epibenthic and fish communities (Callaway et al., 2002) but with highest mixing between round fish and flatfish (ICES, 2019). Furthermore, in this area species (especially elasmobranchs) that are associated with the northern part of the North Sea mix with species that mostly appear in the southern part of the North Sea. Species like haddock (*Melanogrammus aeglefinus*), Norway pout (*Trisopterus esmarkii*) or starry ray (*Amblyraja radiata*) are at the edge of their southern distribution, while the distributions of species like plaice (*Pleuronectes platessa*) or cod (*Gadus morhua*) shifted northward in the past decades (Engelhard et al., 2011; Engelhard et al., 2014; Chevolot et al., 2007; ICES, 2017).

Not surprisingly the effect of closed areas depended on their sizes. Especially in absolute numbers large reserves were significantly more effective than small ones. Therefore, large MPAs may be needed to reach the conservational goals (Halpern, 2003; Edgar et al., 2014). Yet, the small scale of the OWFs and their impact on the substrate may be underestimated by the coarse resolution of our model (Posen et al., 2020).

Even though we did not specifically test for spatial connectivity, our results showed closing on large areas (IUCN and Kempton scenarios) performed better compared to the OWF and MPA scenarios that represent many small-scale closures distributed throughout the southern part of the North Sea. This result indicates a possible lack and the importance of coherence between the single protected areas. Although connectivity is a difficult to process to model and also our work has limitation in this respect, it clearly shows that including biogeographic processes into the design and structure of an MPA network is important to improve the effectiveness of any MPA network (Fredston-Hermann et al., 2018).

4.4.4 Indicator selection

We here used ecological indicators based on a trait-based approach to evaluate ecosystem impact by the fisheries (STECF, 2010). Within the MSFD, ecological indicators are defined in association with environmental targets allowing the observation of progress towards achieving a good environmental status (EC, 2008). We found, that in a complex ecosystem like the southern part of the North Sea, these indicators are an important tool to analyze changes in the ecosystem caused by management actions as well as spatial patterns and shifts. Nevertheless, we detected a remarkable difference in the magnitude of changes among the different indicator types.

Among all tested indicators, the community-based indicator of mean trophic level showed less than 1% change in all scenarios and indicators reflecting biodiversity displayed less than 10% change. The remaining biomass-based indicators varied up to 10% among each other, while catch-based indicators decreased by up to 50% overall. Within the large ecosystem model applied for this study, some indicators like trophic community or total biomass include a large number of species and functional groups. Changes that occur within these indicators may have an impact on a small group of species or many but in opposite directions caused by trade-offs within the food web. In contrary, indicators like mammals and bird biomass (17 species) or biomass/catch of IUCN-endangered species (21 species) only include a comparably small number of species. Therefore, it is important to consider the right aggregation level (single species, functional groups, trophic levels) and the sensitivity of an indicator to be able to monitor progress towards management goals.

Our study revealed the importance to consider the impact that single species or functional groups have on the indicators. As discussed in the previous section, the reduction in surface-feeding seabirds had a great impact on some indicators, especially the more specific indicators like “mammals and seabirds” or “IUCN-endangered species”. Initially, the overall reduction in biomass for these indicators was counterintuitive, since conservational areas are also meant to primarily protect these vulnerable groups (Gormley et al., 2012). Yet, after investigating possible driver behind this reduction, it became apparent, that only one group, surface-feeding seabirds, is the main driver behind this reduction. One approach to circumvent effects like these would be to separate species that also benefit from species that are only negatively impacted by the fishery. Nevertheless, we urge to use indicators with great caution. Otherwise, progress towards certain management goals could be overlooked or management actions are based on the wrong impressions.

4.5 *Conclusion and Outlook*

The evaluation of spatial management options and their resulting trade-offs in the southern part of the North Sea revealed the impact of the placement and size of the areas closed to the fisheries in an ecosystem context. Furthermore, we were able to illustrate the potential necessity of further fisheries management measures simultaneously to closures to reach conservational goals. Moreover, our research highlights the importance of evaluating impacts of spatial management options on a larger scale. Regional effects especially in and around an area with fishing restrictions can differ severely from the overall impact. In order to increase the precision of the model output in the future one option would be to apply a nested Ecospace model to the study area, with individually modelled MPAs in order to better capture small-scale effects (Corrales et al., 2018). Especially in the benthic ecosystem, just a few key species can affect important processes (Solan et al., 2004) and a change in the few species can cause substantial change in ecosystem functioning (Cardinale et al., 2012).

Increasing the focus on the impact of fisheries on the benthic community in in addition to commercial species would improve conclusions that can be made from a spatial modelling study such as ours. Additionally, while this study mainly looked at the general lessons that can be derived from a spatially explicit model like Ecospace, more details and processes may be needed to be captured when using such a tool to evaluate specific effects of closed areas in absolute terms. Additionally, the effects of climate change could be included in the creation of possible management scenarios, since usefulness and effectiveness of MPAs varies under climate change (Hopkins et al., 2016; Wilson et al., 2020).

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5. *Publication 4*

An ecosystem facing climate change: shifts in spatial patterns of ecosystem components in the southern part of the North Sea

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Abstract

Climate change has a great impact on the structure and functioning of marine ecosystems around the world. Especially increasing temperatures affect the distributions of species resulting in shifts in entire community structures. In this study, we explored the impact of changing temperature on the ecosystem of the southern part of the North Sea via a spatial-temporal ecosystem model (Ecospace), structured with the Ecopath with Ecosim (EwE) software. Projections of sea surface temperature were based on the representative concentration pathway (RCP) emission scenarios 4.5 and 8.5 developed for the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC). Simulations under both RCP scenarios were evaluated at two endpoints, i.e. 2050 when the divergence between the two projections is quite small and at the end of the century when both predictions vary significantly. As one of the first studies, we projected the impacts of warming on a set of ecological indicators derived with the new ECOIND plug-in for the entire ecosystem in Ecospace. Furthermore, we assessed the impact on five commercially important fish species: Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), common sole (*Solea solea*), European plaice (*Pleuronectes platessa*) and Atlantic herring (*Clupea harengus*). Our results show that most ecological indicators such as fish biomass, biomass of endangered species and catch will decrease with a warming North Sea, while invertebrate biomass will increase. We found a distinct difference between the analyzed commercial species. While the biomass of the gadoids decreased by around -25% under increased temperature, the biomass of the two flatfish species as well as herring increased up to ~42%. We further highlight spatial effects of climate change especially in the most southern regions in the North Sea where severe losses in fish biomass and biological diversity are likely. Consequently, fish catches will strongly decline resulting in a redistribution of fishing effort with strong economic consequences for the fishing sector. Our study supports the notion that distributional changes due to climate change need to be accounted for in future management decisions, which is especially true for southern part of the North Sea.

5.1 *Introduction*

Climate change has already massive consequences for the marine environment and the life within the ocean which are expected to increase in the future under increasing temperatures (e.g. Ackerly et al., 2010; Baudron et al., 2014; Beaugrand & Kirby, 2010; Blanchard et al., 2012; Bryndum-Buchholz et al., 2018, 2019; Burthe et al., 2014; Cheung et al., 2011; Dahlke et al., 2020; Dulvy et al., 2008; Heneghan et al., 2021; Hiddink & ter Hofstede, 2008; Hollowed et al., 2013; Holt et al., 2016; Kim et al., 2019; Lotze et al., 2019; Núñez-Riboni et al., 2019; Perry et al., 2005; Pinsky et al., 2013; Poloczanska et al., 2013; Pörtner & Peck, 2010; Rabalais et al., 2009; Schückel et al., 2015; Woodworth-Jefcoats et al., 2015). The Intergovernmental Panel on Climate Change (IPCC) have outlined severe consequences under different carbon dioxide (CO_2) emission scenarios. Global surface temperatures in the last four decades exceeded preceding decades since 1850, induced by increasing concentrations of greenhouse gases like CO_2. Consequently, temperatures in the global upper ocean have increased with simultaneously decreasing oxygen levels and a stronger sea level rise since 1971. Furthermore, oceans serve as carbon sink, via reaction of CO_2 with the seawater to carbonic acid. This acts as a buffer reducing the CO_2 concentration in the atmosphere, but causing a drop in seawater pH – also called ocean acidification (Laffoley & Baxter, 2012). If CO_2 levels continue to increase, the proportion of emissions absorbed by the ocean will decrease as warmer waters retain less CO_2, resulting in its release into the atmosphere and accelerating the general warming (IPCC, 2021).

In order to estimate effects of global warming, Representative Concentration Pathways (RCPs) are being used to predict future changes for a range of greenhouse gas emissions (Moss et al., 2010). These encompass a low-impact scenario (RCP2.6), two intermediate scenarios (RCP4.5 and 6.0) and one high emission scenario (RCP8.5; IPCC 2014). Among these scenarios, RCP2.6 is the most ambitious scenario, including strong mitigation measures by almost all countries and negative emissions, targeting a global mean increase in temperatures of less than 2°C (van Vuuren et al., 2011). The intermediate RCP4.5 scenario is also referred to as mitigation scenario, trying to stabilize radiative forcing and applying policies regulating emissions, while RCP8.5 assumes the absence of policies regarding climate change (Riahi et al., 2011; Thomson et al., 2011).

Within the North Sea physical changes due to climate change have already taken place (Huthnance et al., 2016). Most noticeably is the increase of sea surface temperatures (SST), especially in the shallow German Bight (Holt et al., 2012) with impacts on various components of the ecosystem (i.e. Dulvy et al., 2008; Neumann and Kröncke, 2011; Hiddink et al., 2015; van der Kooij et al., 2016). Overall, a northward shift in distribution ranges can be detected for various species, resulting in changes in community structures in the North Sea (Dulvy et al., 2008; Hiddink et al., 2015; Weinert et al., 2016). A main reason for these spatial shifts is the thermal sensitivity of a species (Dahlke et al., 2020; Pörtner & Knust, 2007). Sensitivity towards increasing temperatures can be defined by the size of the thermal window, which varies in size and preferred temperatures across different domains in the marine realm (Storch et al., 2014). Two thresholds define the thermal window of an organism; the lower and upper pejus, where limitations in oxygen supply to organs and tissue sets in and the lower/upper critical temperature, where the organism switches into an anaerobic state (Pörtner et al., 2001). Temperatures exceeding the pejus into unfavorable conditions thus have direct physiological effects, i.e. reducing growth rate or the reduction of reproduction success (Pörtner and Peck, 2010; Butzin and Pörtner, 2016). Therefore, mobile species like fish tend to avoid habitats with unfavorable temperature conditions, which induces a shift in distribution and a consequent change in community structures (Freitas et al., 2021). The resulting changes in community structure can lead to match-mismatch situations between predator and prey species or alter competition dynamics between several species (Cushing, 1990; Beaugrand et al., 2008). These effects on the abundance and composition of an ecosystem need to be considered when assessing the stock status and potential management options for commercially important fish and shellfish species.

Commercially important fish stocks are considerably affected by climate change in various ways throughout their life cycle (Fincham et al., 2013; Fouzai et al., 2015; Kjesbu et al., 2010; Laurel et al., 2016; Mcqueen & Marshall, 2017; Nielsen & Munk, 2004; Teal et al., 2008; Teal, van Hal, et al., 2012). To some extent, direct negative effects of temperature can be mitigated if species change their distribution to reach their suitable thermal habitat. Northward shifts in distribution to cooler and deeper waters are already reported for boreal species such as North Sea cod (Allison et al., 2005; Engelhard et al., 2014; Núñez-Riboni et al., 2019) and plaice (Allison L. Perry et al., 2005; van Keeken et al., 2007; Engelhard et al., 2011).

Sole as a warm-water species, increased in the Southern Bight and shallower regions (Engelhard et al., 2011; Teal, Van Hal, et al., 2012), whereas for whiting no clear climate-related shift in spatial distribution within the North Sea could be found (Kerby et al., 2013). The highly migratory spring autumn spawning North Sea herring moves between spawning and feeding areas and is known to mix with other stocks (Holst et al., 2002; Dickey-Collas et al., 2010). Shifts in herring distribution have been recorded, however impacts of climate change on widely distributed stocks is hard to predict (Trenkel et al., 2014). Finally, the simultaneous range extension of warm water species and contraction of boreal species has the potential to alter biotic interactions such as competition and predator-prey relationships, especially in the juvenile stage (Kempf et al., 2013).

Subsequently, fishing acts as a cumulative anthropogenic pressure on the ecosystem, especially in combination with climate change (Engelhard et al., 2014; Halpern et al., 2015, 2019). At the same time, climate change also poses a threat to the fishing industry due to loss in fish biomass and productivity (Cheung et al., 2012; Galbraith et al., 2017, Blanchard et al., 2017). Maximum sustainable yields in relation to changes in temperatures have already decreased in the last century (Free et al., 2019). Fishers have the potential to adapt via shifting their fishing grounds, but this is only possible to a certain extend due to economic constraints (Pinsky & Fogarty, 2012) as well as limits in inter-governmental legislation (Pinsky et al., 2018). Future fisheries management needs to adapt to changes in temperature and the consequences thereof for marine resources, to reduce social, economic and ecological risks (Bryndum-Buchholz et al., 2021; Gaines et al., 2018; Holsman et al., 2019; Lindegren & Brander, 2018). Taking into account effects of climate change on the entire ecosystem by shifting the focus from single species management to Ecosystem Based Fisheries Management (EBFM) potentially reduces the impact of climate change on fisheries and the associated stocks (Holsman et al., 2020). A tool to support current management in the direction of EBFM are spatially resolved ecosystem models that allow to integrate impact of climate change on the ecosystem in the analysis of targeted stocks.

In the southern part of the North Sea, impacts of increasing temperatures are already changing the structure of the ecosystem and affecting associated fisheries. How the climate is going to change, depends on the rate of change in anthropogenic pressure and is not certain yet.

Therefore, this study aims to i) compare two possible temperature projections by evaluating the spatially disaggregated impact of further increasing temperatures on the ecosystem in its whole and assessing changes in ecological indicators and effort distribution and ii) evaluate the impact on five commercially important fish species in an ecosystem context in more detail.

For this purpose, we adapt an existing spatially resolved ecosystem model of the southern part of the North Sea by adding temperature preferences for the existing ecological groups and incorporating predictions of spatially highly resolved temperature projections for RCP4.5 and RCP8.5. As one of the first studies, we derive spatially resolved ecosystem indicators with the ECOIND plug-in to assess the effects of climate change.

5.2 *Material and methods*

5.2.1 Model set-up

The Ecospace model developed in this study is based on an existing Ecopath with Ecosim (EwE) model (Püts et al., 2020) adapting work by Stäbler et al. (2016, 2018, 2019). The model represents the southern part of the North Sea, south of Northwestern Scotland and the Kattegat down to the English Channel between 51° - 57° N. and 4° W – 9° E. The modelled food web consist of 68 functional groups, i.e. pooled biomass of individual species or a group of species inhabiting similar life forms and diet components (Christensen et al., 2008). In order to represent different life stages, important commercial species were modelled as so-called multi-stanza groups, with a juvenile and an adult life stage. Multi-stanza groups were formed for six fish species (cod (*Gadus morhua*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), sole (*Solea solea*), plaice (*Pleuronectes platessa*)) and the brown shrimp *Crangon crangon*. Fishing vessels were assigned to twelve fishing fleets, representing pelagic, demersal and static-gear fishing activities. The food web within the EwE model reflects the ecosystem state in 1991 due to the best available diet data (ICES ‘Year of the stomach’, Hislop et al., 1997). To represent dynamic changes during the recent decades, time series of biomass, catch and effort from 1991-2010 were incorporated into the temporal model component of EwE., i.e. Ecosim. The spatio-temporal module Ecospace was then used to evaluate changes in species composition and distribution (Walters et al., 1999). Biomass distribution of the functional groups were driven by a number of factors. For species with sufficient data available in the study area, single-species distribution models were applied to produce habitat preference maps based on presence/absence data (Püts et al., 2020).

In order to reflect shifts in distribution over time, these maps are updated every five years with the aid of the spatio-temporal framework included in the EwE software (Steenbeek et al., 2013). In the case of species and functional groups not well represented in the available data sets, preferences towards sediment, depth and distance to coast were implemented. For specific details of the Ecospace model and adaptations to the original model, please see Püts et al. (2020) and Appendix A.

5.2.2 Temperature forcing EwE

We evaluated the effects of changing ocean temperature on the spatial structure of the ecosystem and commercially important fish and shellfish species by linking temperature projections to thermal preference windows for various functional groups in the model. SST data for the historical periods of 1991 to 2017 was retrieved from a highly resolved (0.05° x 0.05°) re-analysis product (ODYSSEA NW+IBI Sea Surface Temperature analysis; product unit SST-IFREMER-BREST-FR; Data form E.U. Copernicus Marine Service Information was used, downloaded on 28.09.2020 (1991-2010) and 06.07.2021 (2011-2017)) and used to simulate model behavior under present-day conditions. We used SST projections based on Representative Concentration Pathways (RCP; Cubasch, 2013) RCP 4.5 and 8.5 scenarios incorporated in three ensemble runs of the regionally coupled ocean-atmosphere climate system model MPIOM/REMO (Mikolajewicz et al., 2005; Sein et al., 2015). Bias correction between MPIOM and the ODYSSEA data was conducted by removing the mean of each grid cell per month to be consistent with the historical trends 1991 – 2005. In order to match the resolution of the Ecospace model of 0.125° x 0.125° the mean per grid cell was calculated for both data sets. For some grid points in Ecospace that were close to the shore lines, there was no data available for future predictions. Therefore, mean SST of the surrounding cells was calculated for these missing values. Grid cells with multiple missing values next to each other (mainly in the estuary Firth of Forth) were excluded from the predictions. Model runs were performed until 2100 for both scenarios and model outputs were analyzed for near (2048-2052) and far (2095-2100) futures (Figure 1).

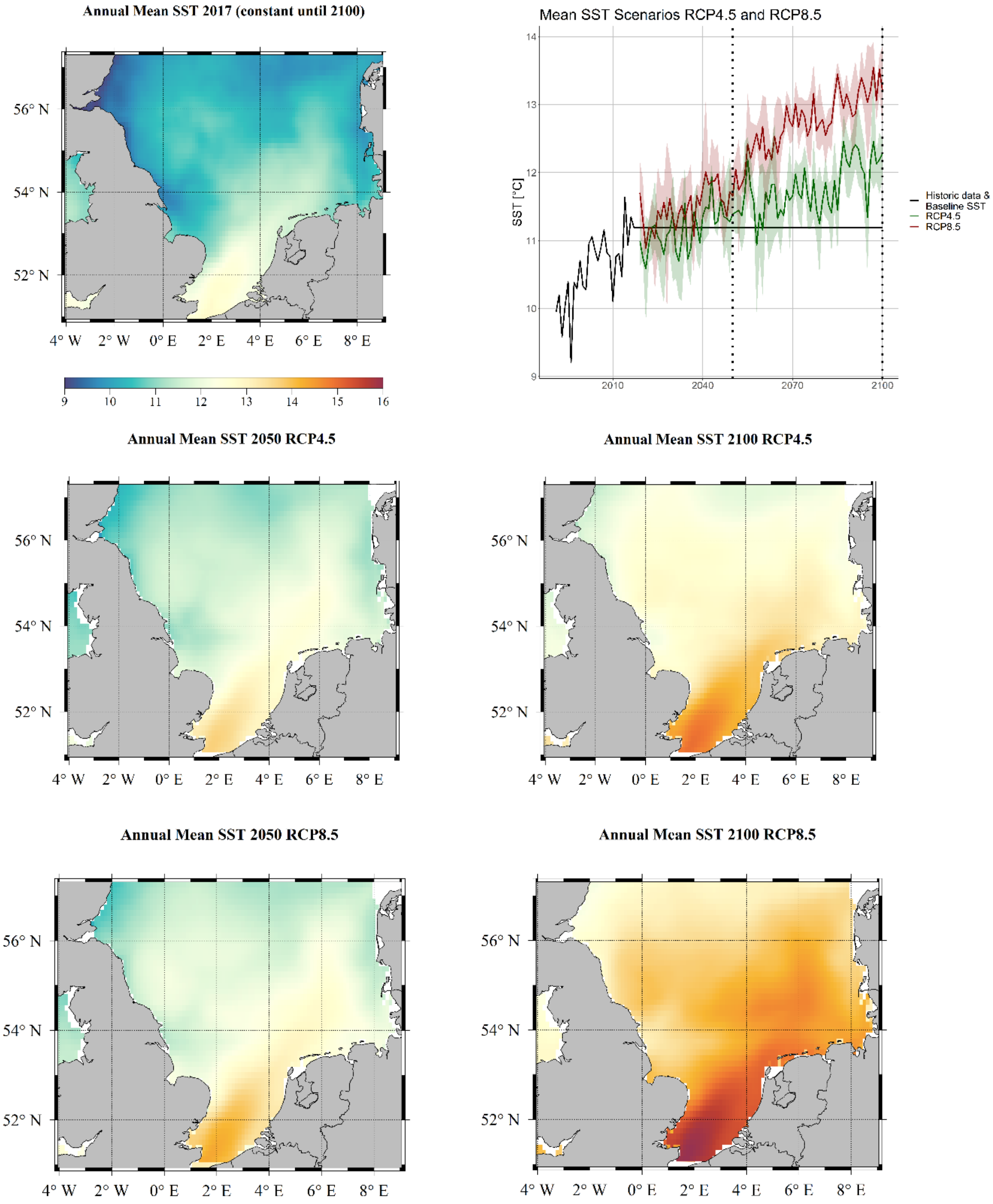


Figure 1: *Projected annual mean SST changes in the North Sea. Top left: Annual mean SST in 2017 used as baseline. Top right: Annual SST mean over study region for baseline (black), RCP4.5 (green) and RCP8.5 (red). Dotted lines depict the two points in time for which evaluation were carried out. Middle: RCP4.5 annual mean SST in 2050 (left) and 2100 (right). Bottom: RCP8.5 annual mean SST in 2050 (left) and in 2100 (right).*

EwE allows the implementation of abiotic drivers, like temperature, in the form of functional responses (Ecosim and Ecospace) and/or fractional habitat preferences (Ecospace). In Ecosim, functional responses governed by abiotic factors act as multipliers to influence consumption rates of a predator (Bentley et al., 2017, 2020; Serpetti et al., 2017). These functional responses can restrict the size of the foraging arena, which defines the vulnerability of a prey to predation. When the temperature is between the preferred minimum and maximum of a functional group, the multiplier is at its maximum of one and consumption rates are unaffected. When temperature is higher or lower than the preferred range the multiplier decreases down to a minimum of zero, restricting the size of the foraging arena and reducing consumption, leaving the species without energy uptake. This environmental response is represented by $f(Env_{function}, t)$ in the consumption (Q_{ij}) equation (1):

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times P_j \times T_i \times T_j \times M_{ij}/D_j}{v_{ij} + v_{ij} \times T_i \times M_{ij} + a_{ij} \times M_{ij} \times P_i \times T_j/D_j} \times f(Env_{function}, t) \qquad (1)$$

With the effective search rate (a_{ij}), vulnerability, i.e. the rate with which prey i move between being vulnerable and not-vulnerable (v_{ij}), prey biomass (B_i), predator abundance (P_j), relative feeding time prey (T_i), relative feeding time predator (T_j), mediation forcing effects (M_{ij}), and handling time which serves as a limit to consumption (D_j) (Ahrens et al., 2012; Christensen et al., 2005).

In Ecospace, functional responses are also linked to the foraging arena by affecting the capacity of a cell (C_{rcj}) for predators to forage on their prey (Christensen et al., 2014). This foraging capacity of a cell is a factor between 0-1 determined by the intercept between environmental drivers, in this case temperature, and the functional response function. It is implemented as a multiplier to the size of the search area in the foraging arena equation (2):

$$V_{ij} = \frac{v_{ij} * B_j}{2 * v_{ij} + a_{ij} * \frac{B_j}{C_{rcj}}} \qquad (2)$$

where v_{ij} is the prey vulnerability exchange rates, B_j representing predator biomass and a_{ij} the effective search rate.

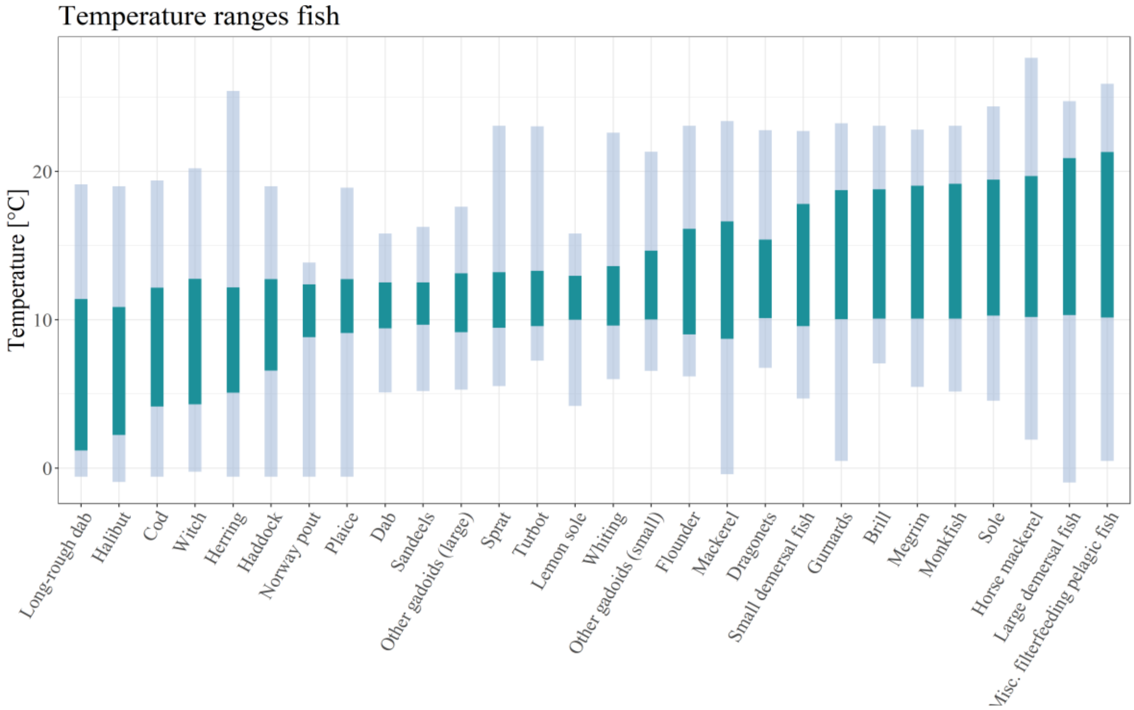


Figure 2a: *Temperature ranges retrieved for fish functional groups. Dark region represents range between the preferred minimum and maximum temperature and light colors the temperature range in which the species/group can survive.*

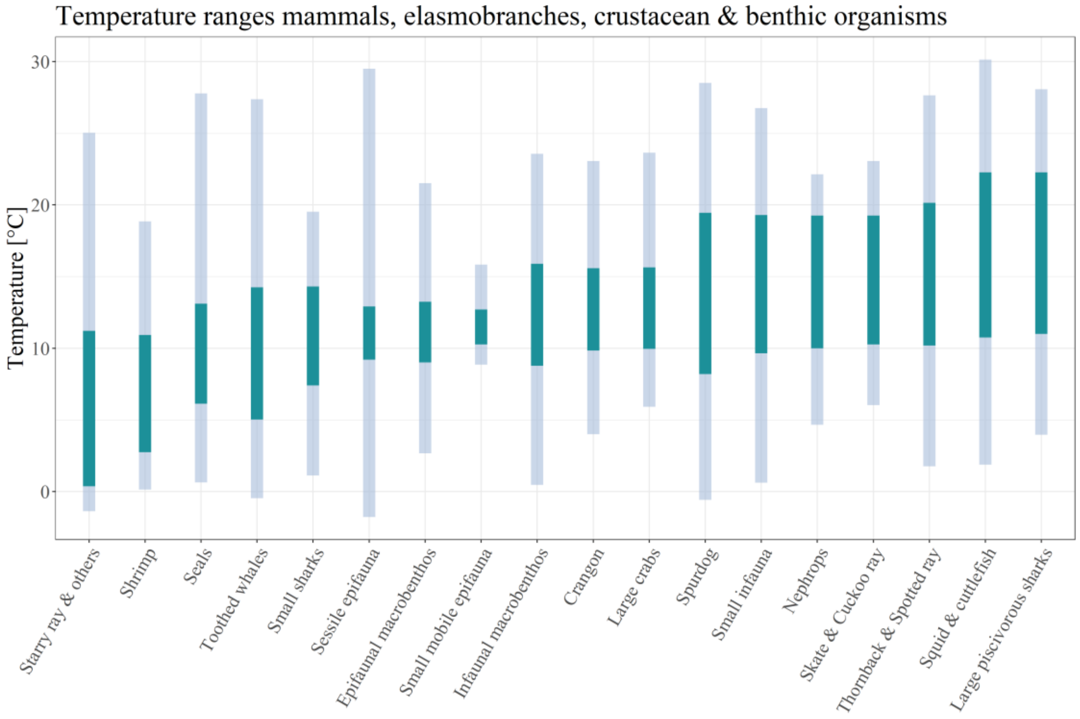


Figure 2b: *Temperature ranges retrieved for elasmobranches, mammals, cephalopods, benthic and crustacean functional groups. Dark region represents range between the preferred minimum and maximum and light colors the temperature range in which the species/group can survive.*

We implemented functional responses to temperature for 46 functional groups of our model (Figure 2a/b). These resulting temperature tolerance ranges portray the preferable temperature and temperatures in which the functional groups can survive (derived from the aquamaps.org database; Kaschner et al., 2016). A common temperature range weighted by biomass was calculated for multi-species functional groups (Serpetti, 2019). Prior to running Ecospace with SST predictions, the historic time series of SST was coupled with temperature preferences in Ecosim to fit the model. Afterwards, the same functional responses were linked to the spatially resolved SST observations and predictions in Ecospace. Therefore, the foraging capacity of a cell for each functional group was determined by external capacity based on species distribution modelling, habitat preferences and/or functional responses linked to temperature (Figure 3).

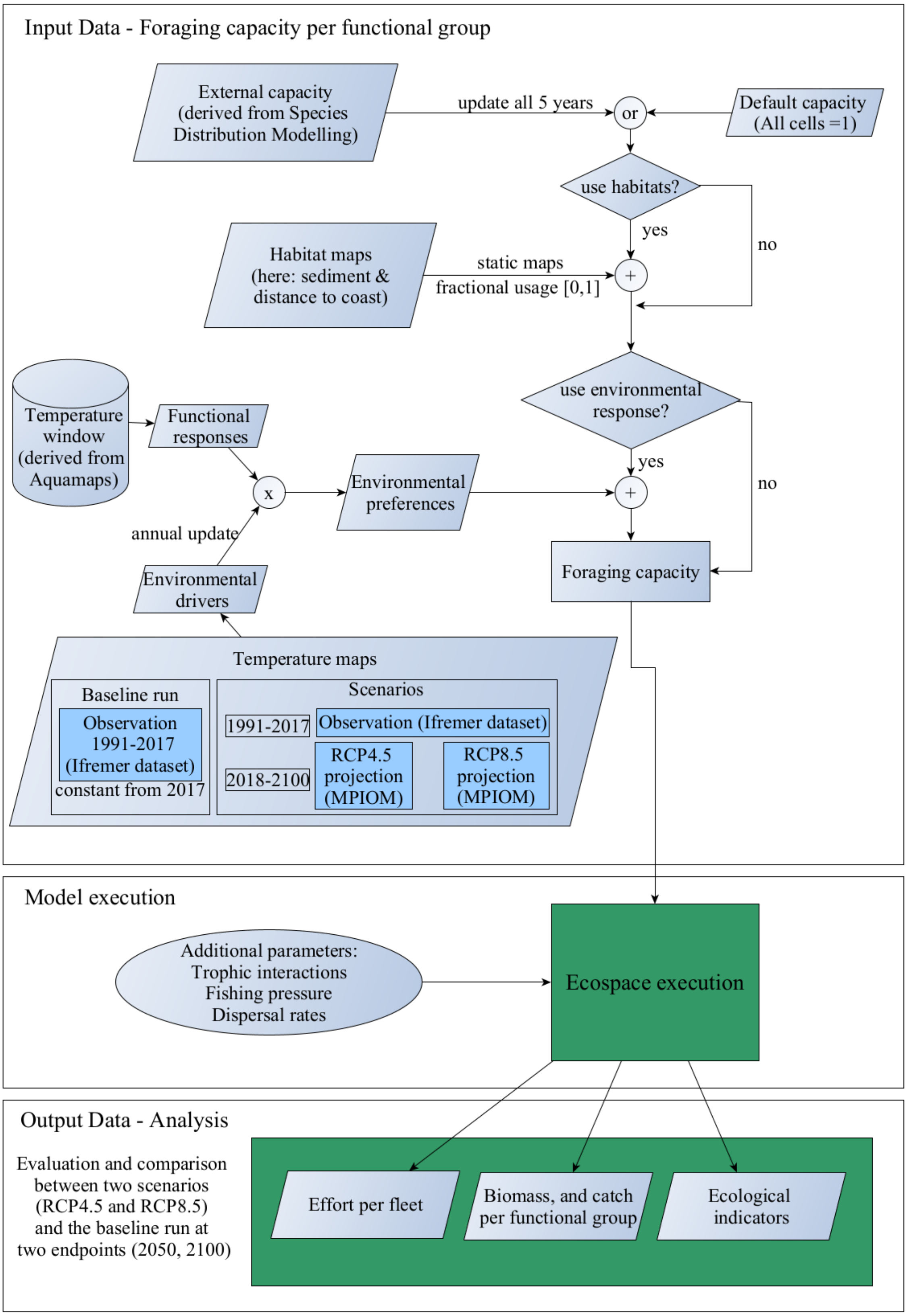


Figure 3: *Workflow describing the implementation of various drivers of foraging capacity of individual functional groups, model execution and output derived from the model*

5.2.3 Analyses of spatio-temporal projections

For scenario analysis, we extracted annual biomass and catch distribution maps for each functional group. Using the EwE plug-in ECOIND we additionally computed important ecological indicators characterizing future changes in ecosystem structure and function (Coll & Steenbeek, 2017). The calculations for these indicators consider either functional groups as an entity or information for each species included in each functional group. Traits and categories were assigned to each species in a functional group, based on type of organism (i.e. mammal, bird, fish, invertebrates), ecology (i.e. demersal, pelagic), and status on the International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015). Indicators comprised five categories: Biomass-based, 2. Catch-based, 3. Trophic-based, 4. Size-based and 5. Species-based. The first two indicator categories evaluate biomass and catch data for several groups, like fish or invertebrates, pelagic or demersal species. Additionally, Kempton's Q and Shannon are calculated as indicators to represent diversity in the ecosystem. Trophic-based indicators reflect the trophic structure of the community in the food web, while size-based indicators reflect the mean size and weight of species in the community. Species-based indicators are based on conservation status or the IUCN status and further categories. In this study, size-based indicators were not calculated, since adequate data on length or weight solely on species in the southern part of the North is not available for most functional groups. Furthermore, we extracted biomass values for five commercially important species, Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), common sole (*Solea solea*), European plaice (*Pleuronectes platessa*) and Atlantic herring (*Clupea harengus*). These five species are among the commercially most important species that are targeted by main fisheries in the southern part of the North Sea: demersal, pelagic and beam trawlers. Furthermore, they are included in the model with a juvenile and adult stanza, which allows the evaluation of impacts on different life stages.

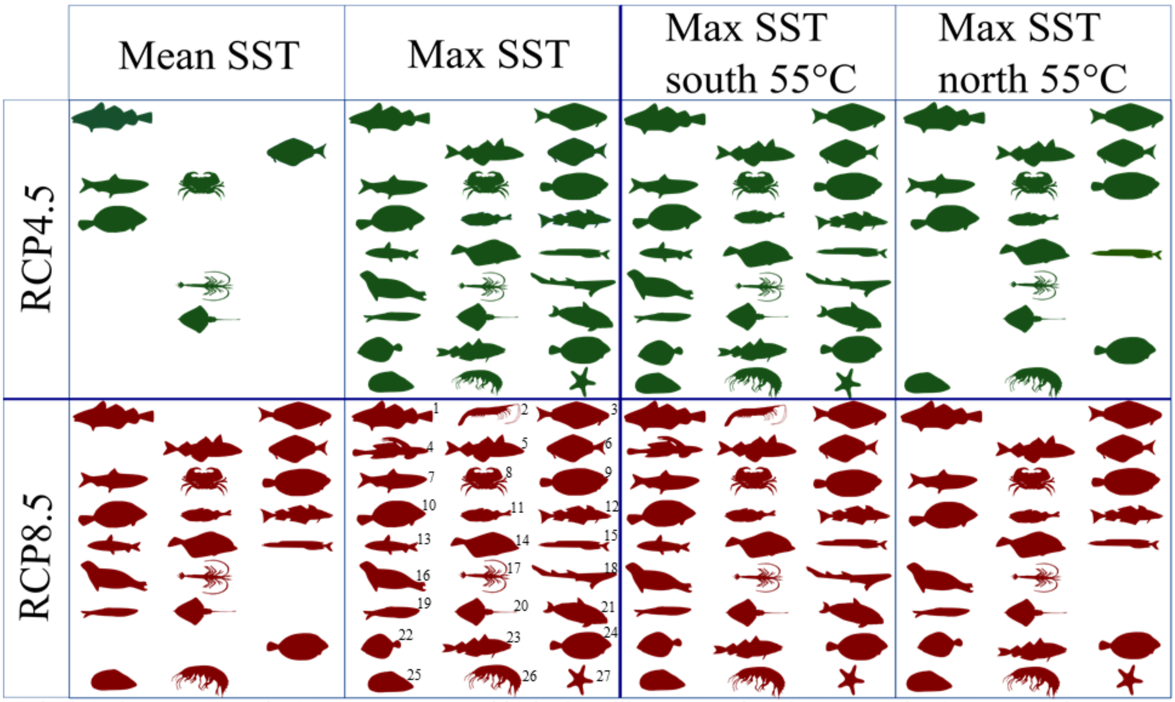
In the further analysis, impacts of the two RCP projections were evaluated at the endpoints 2050 and 2100. For both endpoints an average over 5 years (2048-2052 and 2095-2100) was calculated to reduce the impact of small model instabilities. We compared the spatial mean of each indicator to a baseline run with constant temperatures from 2017 onwards and evaluated latitudinal differences in the spatial distribution of selected indicators as well as biomass and effort distribution for the commercial species and their main fisheries between the scenarios.

5.3 Results

5.3.1 Impact of warming on ecological indicators

Annual mean mid-century SST in the southern part of the North Sea for RCP4.5 and RCP8.5 are expected to be quite similar, ~11.4°C (+0.2°C compared to the baseline of 2017) for RCP4.5 and ~11.7°C (+0.5°C) for RCP8.5 (Figure 1). However, projected annual mean SST as a result of the two emission scenarios diverge more at the end of the century, i.e. ~12.3°C (+ 1.1°C) for RCP4.5 and ~13.2°C (+2°C) for RCP8.5. Therefore, the impacts of the two RCP projections on the different components in the ecosystem only varied strongly at the end of the century. In 2050, for both RCPs the thermal optima of only four functional groups did not overlap with the predicted spatial average of the annual mean SST for the study area (see Appendix A for overlaps in 2050). By the end of the century, these numbers increased to 7 functional groups for RCP4.5 and to 19 functional groups for the RCP8.5 scenario respectively (Figure 4). Considering the maximum SST rather than the spatial average, the difference is not so salient when comparing maximum temperatures to the thermal windows in 2100; here we found 25 mismatches for RCP4.5 and 27 for RCP85. Nevertheless, there are regional differences. When dividing the study area in half, roughly around the most southern edge of the 50m depth contour at 55°N, these differences become most apparent for the RCP4.5 scenario. While south of 55°N 25 species are affected by temperature changes, only 16 are impacted north of 55°N. For RCP8.5 maximum SST exceeds the thermal optimum window north of 55°N of 22 species, which are 5 species less than below 55°N.

All climate change scenarios had a great influence on the ecosystem and the chosen ecological indicators (Figure). At the end of the century, changes in indicator values did not exceed ~10% for the RCP4.5 scenario, while changes inflicted by the RCP8.5 scenario reached up to ~30% difference compared to a constant temperature scenario. In general, the increase in temperature led to a decrease in most indicator values. The only exception was total and invertebrate biomass, both increased up to ~5% with increasing temperatures. Total biomass is composed of ~87% invertebrate biomass and therefore reflects mainly the impact the scenarios have on invertebrate biomass.



1. Cod, 2. Crangon, 3. Dab, 4. Dragonets, 5. Haddock, 6. Halibut, 7. Herring, 8. Large crabs, 9. Lemon sole, 10. Long-rough dab, 11. Norway pout, 12. Other gadoids (large), 13. Other gadoids (small), 14. Plaice, 15. Sandeels, 16. Seals, 17. Shrimp, 18. Small sharks, 19. Sprat, 20. Starry ray & others, 21. Toothed whales, 22. Turbot, 23. Whiting, 24. Witch, 25. Sessile epifauna, 26. Small mobile epifauna, 27. Epifaunal macrobenthos

Figure 4: *Temperatures exceeding functional groups optimum range. Functional groups appearing in a rectangle are affected by mean or maximum SST in RCP4.5 or RCP8.5. Rectangles on the right-hand side depict the regional differences in exceeding temperature optima. Only functional groups affected are shown.*

Overall, the least difference between scenarios was visible for total and invertebrate biomass and the two diversity indicators Shannon diversity and Kempton's Q in 2100. For these particular indicators, even the RCP8.5 scenario with the greatest impact on the ecosystem only led to a maximum change of around -3%. Somewhat stronger is the response of species included in the calculation of the biomass of IUCN-endangered species and for mammals and birds. Here the impact of the RCP8.5 scenario led to a decrease of around -8%. Fish related indicators were impacted most by both RCP scenarios with reductions in fish biomass, total catch, fish catch and discards by around -2.5% already for RCP4.5 and -2 to 4% for RCP8.5 in 2050. By the end of the century, this decrease reached a reduction of -5 to -10% for the RCP4.5 scenario and -18 to -30% under the RCP8.5 respectively.

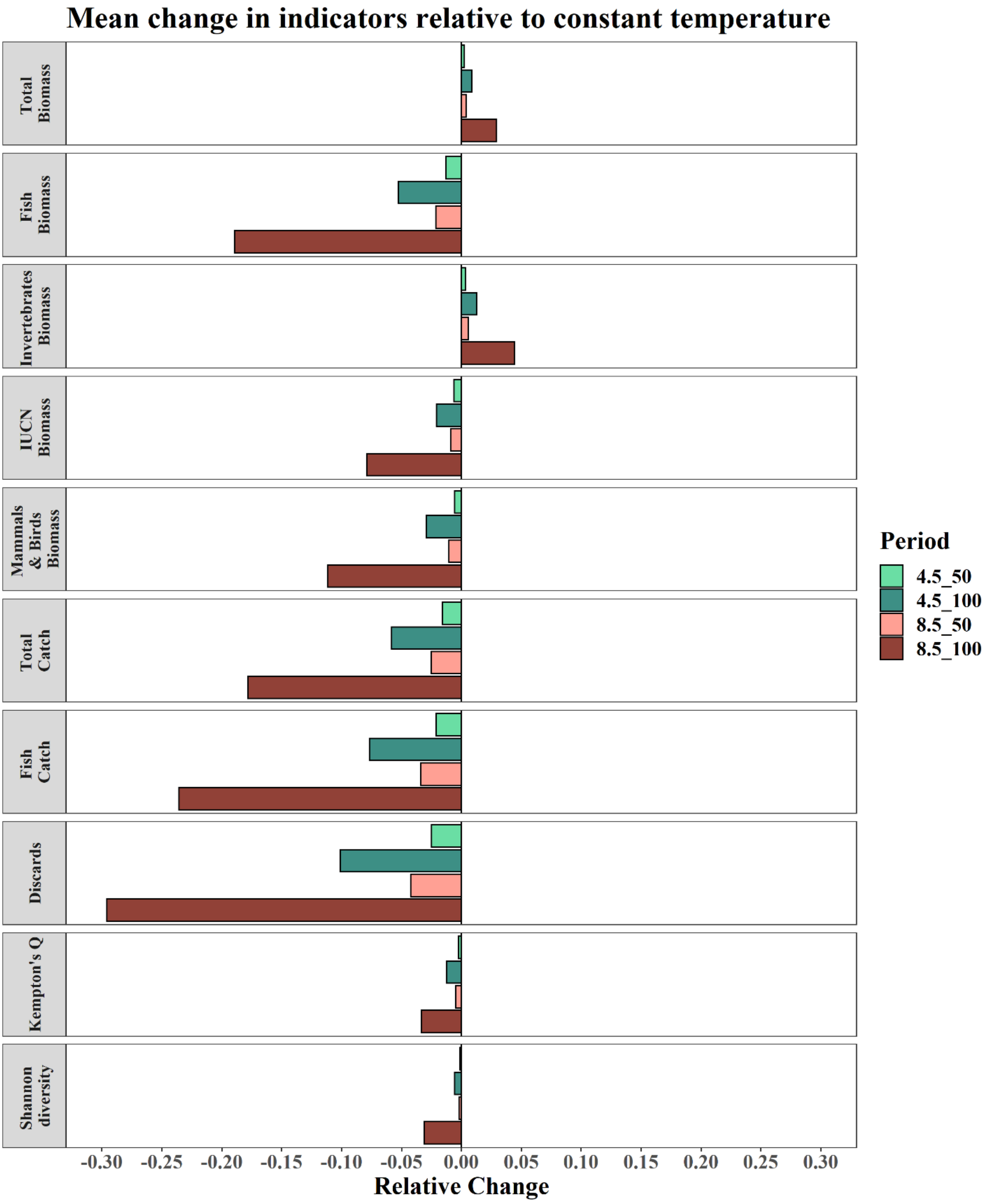


Figure 5: *Relative difference in the spatial mean per indicator between scenarios and baseline run with constant temperature fields.*

5.3.2 Impact of warming on selected species

A more diverse impact of the climate change scenarios was found for five commercially important fish species cod, whiting, plaice, sole and herring (Figure 6). While biomass of the adult gadoid species decreased with increasing temperatures, biomass of the flatfish species and herring increased. Within gadoids we observed a stronger temperature effect on adult, while in flatfish the biomass of the juveniles was stronger impacted, while for herring both juveniles and adults were impacted equally. Among the gadoid species, the impact on adult cod was the strongest with a biomass decrease under the RCP8.5 scenario by around -26% in 2100. In contrast, juvenile cod biomass stayed constant in all scenarios. We observed a similar pattern for whiting, yet the maximum decrease in adult whiting biomass was only -8%. Among the flatfish species, sole was strongly affected by warming with a maximum increase in biomass of ~45% for juvenile sole at the end of the century under RCP 8.5. Under the stronger mitigation scenario sole biomass increased by 16% and 13% for juveniles and adult, respectively, and both exceeding the maximum increase for juvenile plaice biomass (~11%). Herring juvenile and adult biomass increased by ~26% and ~27%, respectively, in 2100.

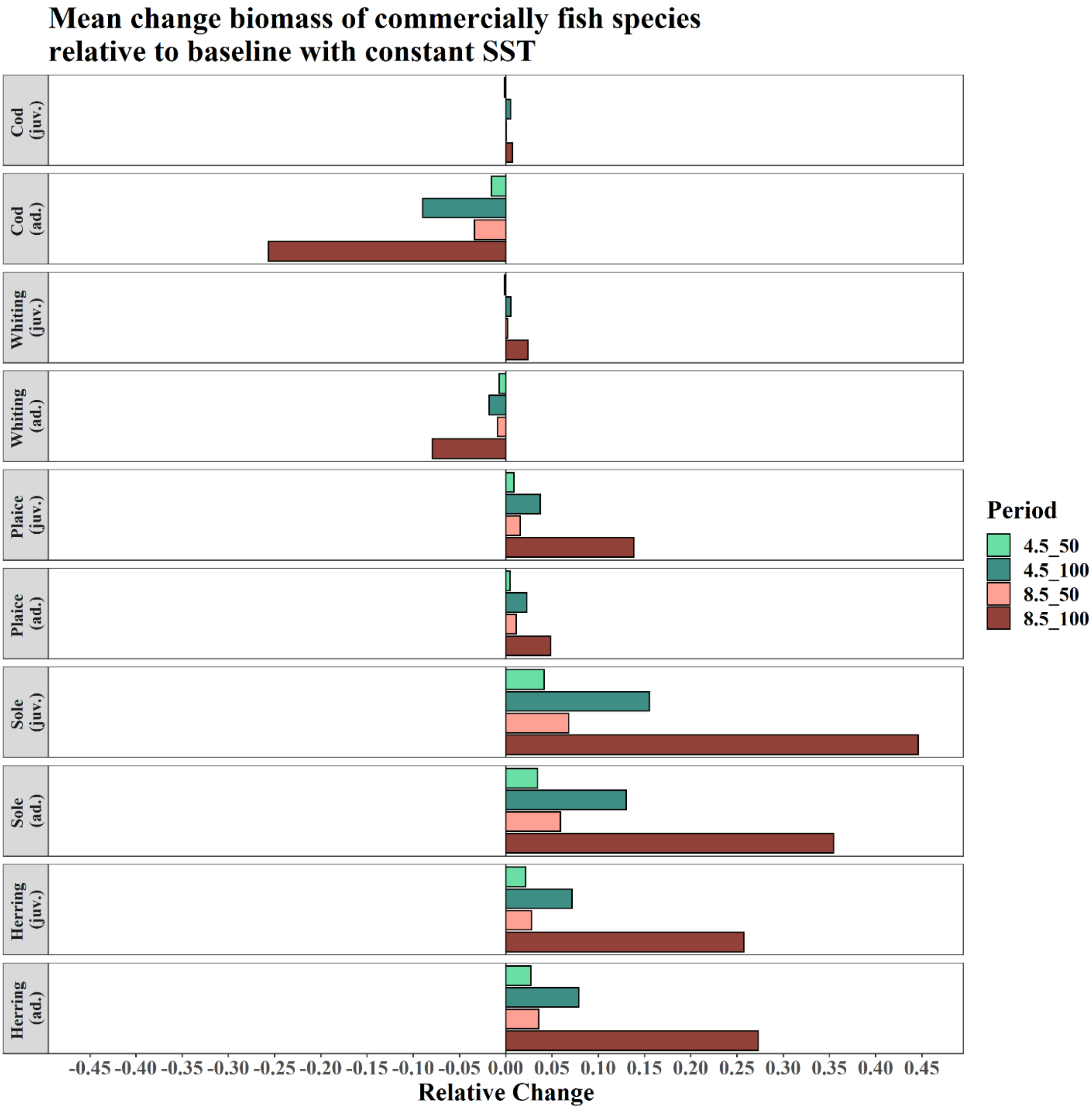


Figure 6: *Relative difference in biomass between scenarios and baseline run with constant temperature fields per stanza of four commercially important species.*

5.3.3 Shift in spatial distribution

The strength of temperature increases in the North Sea strongly varies in space. Consequently, the effect of warming on ecological indicators and the biomass of commercially important species is spatially explicit. Nevertheless, our model runs revealed shifts in spatial distribution for most of the evaluated variables with a predominance of poleward redistributions. Fish biomass generally decreased in the entire area, with a gradient from south to north of the study area, whereas fish catch decreased primarily in the south, with an increase in catches under the RCP8.5 scenario in the northern part of the modelled in 2100 (Figure). Simultaneously, total biomass increased, with a gradient from north to south. The increase of total biomass is particularly strong in the English Channel and along the Dutch, Belgian, German and Danish coast, while fish biomass and catch decreased strongest in the same regions.

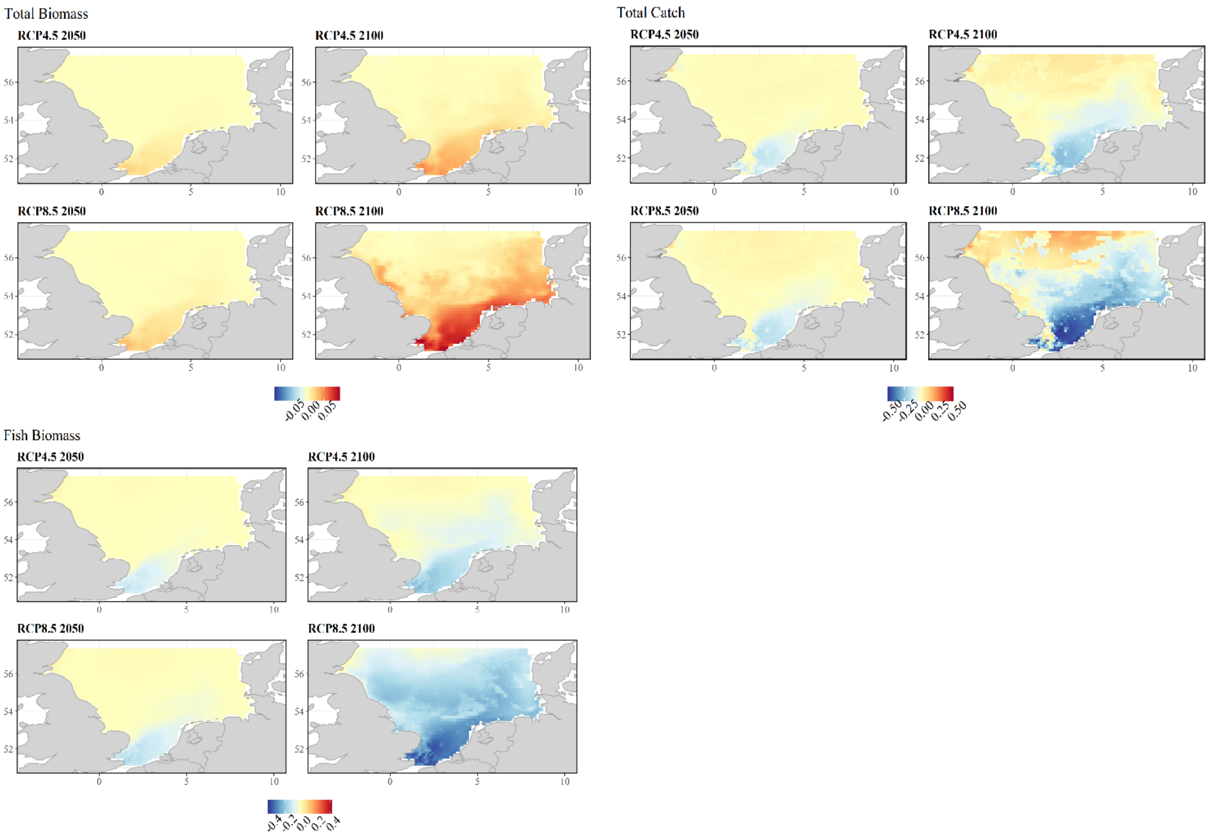
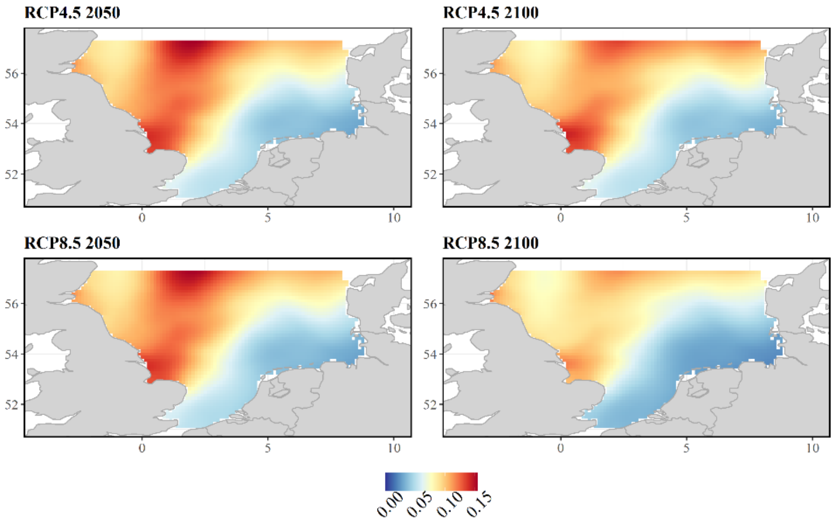


Figure 7: *Shift in spatial distribution of total and fish biomass as well as catch for four scenarios relative to baseline distribution.*

Most commercially exploited functional groups examined in our study exhibited a latitudinal shift in distribution with increasing temperatures, yet, not all in the same direction. Juvenile and adult cod increased poleward while overall biomass decreased, especially at the end of the century under RCP8.5. In contrast, juvenile and adult sole biomass increased with warming towards the south, especially along the coastlines and in the English Channel (Figure 8). Adult cod and juvenile sole showed the strongest spatial changes in biomass among the commercially important demersal species. Maps for the remaining commercial species discussed in this study can be found in Appendix B.


Adult Cod (-40cm)

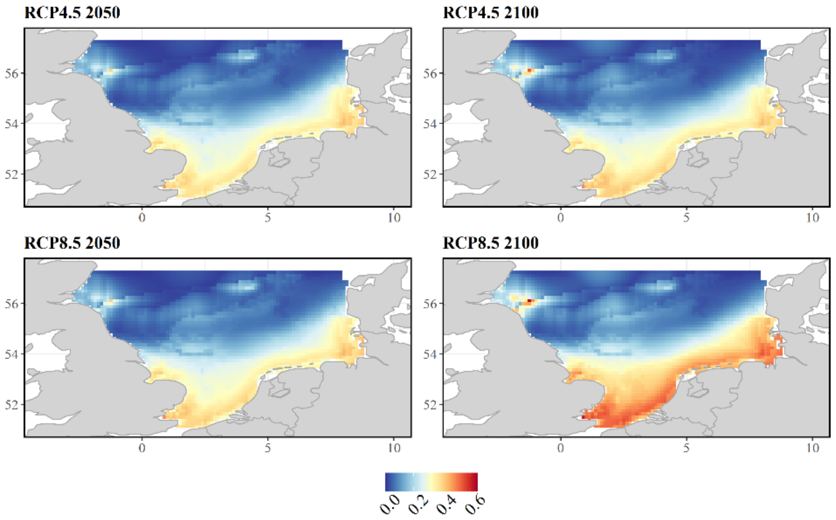

Juvenile Sole

Figure 8: *Biomass distribution for each scenario for the two most impacted stanza groups cod (adult) and sole (juvenile).*

Similar shifts were also detectable in the ecological indicators (Figure). Overall, eight indicators, three of the five single species adult stanzas and beam trawl and pelagic trawl effort showed a decreasing south to north trend. Kempton's Q, trophic level of catch and adult cod instead increased towards the north. Biomass of mammals and birds, Shannon diversity, plaice adult biomass and demersal trawl effort in contrast, did not display a specific south-north trend under all scenarios.

Not surprisingly, almost all indicators experience the strongest distribution change at the end of the century under RCP 8.5, indicators like Shannon diversity or trophic level of catch display strong differences between RCP8.5 in 2100 and the other scenarios. However, in some indicators this shift was only small, for example in total biomass, catch of IUCN- endangered species or adult whiting biomass. In most cases, this effect was strongest in the southern part of the model area, with only small changes in the north, accompanied by a shift in the center of gravity (see Appendix B Table B1 for center of gravity of the ecological indicators).

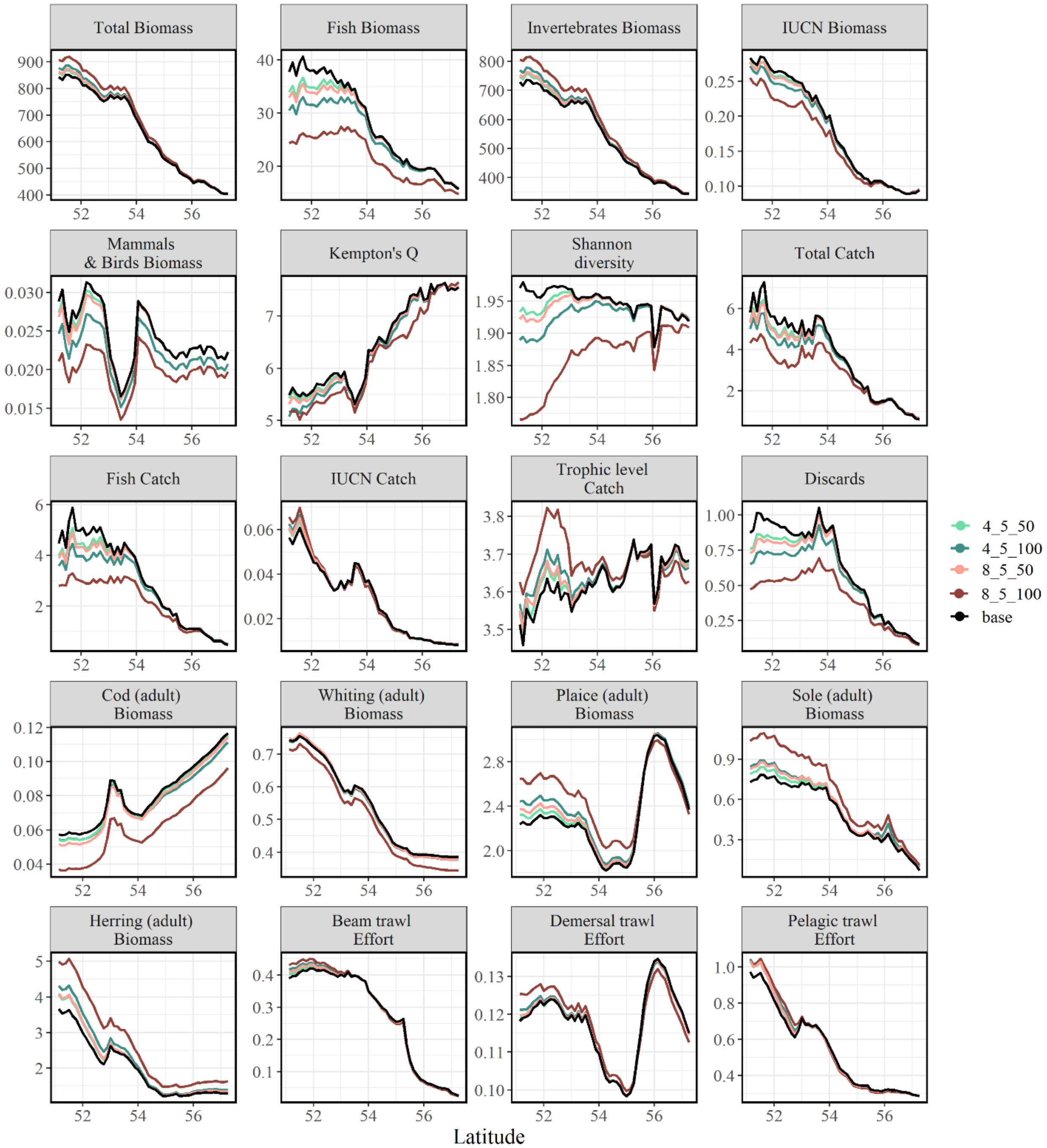


Figure 9: *Latitudinal changes from south (51°N) to north (57.25°N) in each scenario (x-axis left to right). Y-Axis refers to absolute values of the indicators, species biomass or fleets effort. Values were averaged over longitudinal degrees.*

5.4 *Discussion*

5.4.1 Impacts of climate change on the ecosystem – lessons learned and uncertainties

Our study highlights potential impacts of climate change on the ecosystem of the southern part of the North Sea. Using a spatially resolved ecosystem model like Ecospace, we were able to show the different magnitudes of change between the southern parts of the study area and the central and northern parts. In the shallowest regions, temperatures are expected to reach the highest values, which exceeded many of the optimum temperature thresholds for the different functional groups, affecting all ecosystem indicators. Both RCP scenarios induced positive and negative effects on the ecosystem and the associated fisheries. While the effects only varied slightly by 2050, the impacts of RCP8.5 projections were up to three times as strong as for RCP4.5 for some indicators, like fish biomass and catch, in 2100. Total biomass and invertebrate biomass were the only two indicators that displayed an increase with increasing temperatures. Because ~87% of the biomass in the southern part of the North Sea consists of invertebrates, the change in total biomass is highly reflective of the impact on invertebrates alone. Simultaneously, all other indicators displayed decreasing trends with increasing temperatures. Among the strongest impacts were the reduction in fish biomass, which was also reflected in the reduction in catch and discards. When focusing on a few commercially important fish species, the impact of increasing temperatures was more diverse. While the biomass of gadoid species, especially adult cod, decreased with warming, flatfish species seem to benefit from climate change, similar as herring. Yet, our study also demonstrated that trophic interactions modify the direct impacts of climate change on the different ecosystem components.

A few caveats and uncertainties have to be mentioned nonetheless. Despite the complexity of our model, not all potential impacts of climate change could be implemented, especially because of lacking information for some functional groups at low trophic levels. For most of the fish and mammal species we could base our modelling on a sufficient data availability. However, data on temperature affinities of benthic and zooplankton species is quite scarce, especially for the study region, and hence these groups are mainly regulated in the model through trophic interactions. Furthermore, emigration and immigration are not considered by the model. At the same time, no new functional groups or species were accounted for, that may enter the southern part of the North Sea due to climate change.

While boreal (cold-favoring) species disappear from the southern North Sea, lusitanian (warm-favoring) species are entering the ocean basin through the English Channel (Ter Hofstede & Rijnsdorp, 2011). Moreover, our model is forced by annual mean temperatures not considering seasonal dynamics and especially extreme temperatures often occurring in summer, including seasonality would be an important addition. While implementing species distribution maps for various functional groups ensures a good representation of their overall distribution in the study area, seasonal migration patterns are not reflected. Especially, since spawning migration patterns may be affected by climate change, due to changes in the onset of spawning migrations and duration of spawning periods (Jansen, 2011; Hufnagl, 2013).

Warming of the ocean does not only have direct effects on species. With increasing temperatures, currents may weaken which reduces and changes larval transports and impacts nutrient distribution (Holt et al., 2018). Furthermore, oxygen uptake is reduced which results in anoxic events, especially in combination with eutrophication (Rabalais et al., 2009). Additionally, ocean acidification may lead to physiological changes in calcifying species (Beare et al., 2013; Beaugrand et al., 2013; O'Dea et al., 2014), but can also have an impact on the development of fish larvae (Stiasny et al., 2019). These other factors are presently not included in our model, but would be important additions when further studying the impact of climate change on the ecosystem of the southern part of the North Sea.

5.4.2 Trophic interactions and shifts in communities

As mentioned before, the only ecological indicators that were positively affected by warming of the North Sea were total and invertebrate biomass. Primary productions is an important bottom-up regulator and regardless of the missing direct forcing of primary production our results reflect expected trends described in other studies, where the changes in primary production are expected to vary globally (Blanchard et al., 2012), with an increase along the shelf region of the North Sea. The increase is expected to occur in regions of the North Sea where the water is well mixed, while a small reduction is expected within the stratified water masses of the central and northern North Sea (Holt et al., 2012). The increase in invertebrate biomass in our model is primarily due to a reduction of predation pressure, especially in the southern part of the model region. This in part contradicts results from Hiddink et al. (2015), who found temperature to be an important driver of benthic invertebrates and that there center of gravity has already changed in the past.

However, they also found a lag between changed temperatures and changes in distribution, which might be explained by already occurring changes in predator pressure and slower dispersal rates. Furthermore, invertebrates included in our model comprise both pelagic and benthic species, with a large variety of temperature affinities. While for instance species included in the group "squid and cuttlefish" have a higher temperature tolerance and are expected to increase in the North Sea (van der Kooij et al., 2016), species in the functional group "shrimps" are more adapted to colder temperatures (Blahudka & Türkay, 2002; Ouellet et al., 2017).

All other indicators derived from our model decreased with increasing temperatures, especially those with highly predatory species, like fish biomass, biomass of IUCN-endangered species or mammals and birds. Contrary to invertebrate biomass, fish biomass shifts are primarily induced by the thermal window of the various functional groups but also by trophic interactions. Especially the strong reduction in the south reflects the expected poleward shift of many fish species (Dulvy et al., 2008; Pinsky et al., 2013; Poloczanska et al., 2016; Baudron et al., 2020). Some of the fish species are also included in the calculations for the biomass of IUCN-endangered species, which decreased with increasing temperatures as well. Twenty-one species from 14 different functional groups in this model are currently listed as near threatened, vulnerable, endangered or critically endangered (IUCN, 2021). Most of these species are higher trophic level species; rays, sharks, birds or whales. Species included in both indicators displayed a broad range of thermal optima, which implies a direct impact through shifts in their suitable thermal habitat but also secondary impacts by shifts in the suitability of thermal habitats of their prey. Seals and toothed whales have a wide temperature window, but relative to their overall temperature tolerance a small optimum temperature window that ranges from 6.13°C to 13.11°C and from 5.02°C to 14.2°C, respectively. While they would be able to withstand the increase in temperature to some extent, the shift in major food sources northwards facilitates a reduction in the south and overall decrease in biomass in the model. Loss in food availability has been recorded as a major threat to marine mammals, even-though threats of climate change can be versatile across the globe (Evans & Waggitt, 2020). Seabirds already face a decline in population numbers and biomass, caused by various, mostly anthropogenic, pressures (Mitchell et al., 2020), with climate change being one of the most sever (Furness, 2016).

Yet, the pressure induced by climate change is only partly caused by physiological changes, the bigger impact is caused by a reduction and shift in food availability (Cury et al., 2011; Sydeman et al., 2012; Furness, 2016; Mitchell et al., 2020). Therefore, seabirds were not forced by temperature in the model directly, but declined as well due to loss in prey in the ecosystem.

We used the indices of Kempton's Q and Shannon to characterize changes in biodiversity. Both indices showed only small changes except for RCP8.5 in 2100. Here the decrease in the spatial average is comparatively strong with ~3%. In latitudinal direction, Shannon diversity decreased strongly in the most southern region of the study area, while Kempton's Q shows the strongest decrease between 54°N and 56°N, along the 50m depth contour. Latitudinal distributions indicate that Shannon diversity was evenly spread in the baseline run, with a small decrease in the northern center of the study area, while Kempton's Q was highest right along the 50m depth contour. This discrepancy between the Shannon index and Kempton's Q originates in the structure of the two indicators. Whereas the Shannon index emphasizes species numbers and their abundance, Kempton's Q focuses on the average species composition via cumulative logarithmic abundance, excluding upper and lower quantiles of common and rare species. In EwE Kempton' Q is adapted to reflect species richness and evenness of functional groups rather than individual species (Ainsworth & Pitcher, 2006). Kempton's Q is highest around the 50m depth contour, where communities with a more northern distribution overlap with communities that have a more southern distribution, leading to a high species richness and evenness (Reiss et al., 2010). By excluding rare and most abundant species and including evenness, Kempton's Q not only provides inside into diversity, but also the dispersion of the species.

5.4.3 Commercial species and implications for fisheries management under climate change

We evaluate the impacts of increasing temperatures on five commercially important fish species in an ecosystem context. Gadoid species were negatively affected by increasing temperature, especially adult cod. By the end of the century, the biomass of adult cod decreased on average by about -26%. Yet, the reduction in biomass for both gadoids cod and whiting adult seemed to be uniform across the latitudinal gradient. Therefore, we could not find a clear northward movement, rather a simultaneous reduction of biomass across the study area. Under the projected change in SST, cod's distribution already shifted towards the northern boundary of the model area in 2018. Historically, the displacement of cod northwards and slightly eastward is well documented and studied (Engelhard et al., 2014; Hedger et al., 2004; Núñez-Riboni et al., 2019; Perry et al., 2005).

Especially after historically low spawning-stock biomass in 2006, the southern part of the stock failed to increase again (ICES, 2019a). Therefore, the reduction in prey and physiological impacts due to climate change may lead to a reduction of biomass in the entire study area, especially under RCP8.5 projections. This aligns with results derived by Núñez-Riboni et al. (2019), who found a decrease in thermal habitat suitability for cod south of 56°N under the RCP8.5 scenario, which covers most of the study area. As for whiting, the distribution has not substantially changed in the past, only a slide westward shift could be detected, with an even distribution across the study area (Kerby et al., 2013b; ICES, 2017). Whiting is an abundant, widespread lusitanian species that tolerates higher temperatures than for example cod (Dulvy et al., 2008). Therefore, the main reduction in biomass in our model, especially in 2100 under RCP8.5 is likely caused by a reduction in prey availability.

The effect for both gadoid species seemed to be stronger for adult stanzas than for the juveniles. Among gadoid fish species, cannibalism is quite common (Bromley et al., 1997). Regardless of the thermal windows of the juvenile stanzas, the reduction of the adult biomass and therefore the reduction in predation pressure seemed to be favorable for juvenile biomasses. Furthermore, the diet structure between juveniles and adults in the model are similar, since the transition between juvenile and adult stage is determined by the entry into the fishery rather than egg or larval stages. When adult biomass is reduced due to climate change, the juvenile stages profit from a reduction in competition. At the same time, prey species, primarily invertebrates, of juveniles increase under the scenarios. Within the structure of the model, copepods are gathered in one functional group so shifts in zooplankton communities and specific prey species were not reproduced in the model. Yet, zooplankton community composition is expected to change under climate change (McGinty et al., 2021), which may strengthen the negative impact on juvenile cod compared to current model results while such changes likely impact the more opportunistic whiting to a lesser extent (Shaw et al., 2008).

For the flatfish species our study shows that climate change seemed to have induced opposite trends compared to the gadoid species. Both sole and plaice increased with warming, but to different extents. Sole juveniles and adults were the big winner under climate change; plaice juveniles seemed to profit at the end of the century, while the changes in plaice adult were comparatively small, even slightly negative.

Sole and plaice are expected to react almost contrary to changes in temperature (Teal et al., 2012). In the last century, the distribution of plaice shifted offshore into deeper waters, especially adult plaice (van Keeken et al., 2007). At the same time, the core abundance of sole is still in the south of the North Sea, with slight northward expansions (Brunel et al., 2018). These shifts in distribution were correlated to the Hadley SST, positive for sole and negative for plaice, yet for both species the relationship between temperature and changes in distribution is not fully understood (Engelhard et al., 2011). The positive effect on sole was found in this study as well, along with the strongest increase in biomass in the southern areas of the study region, especially close to the English Channel and along the Belgium, Dutch and German Coast. However, the expected overall negative impact of temperature on plaice was not supported in our study. Here biomass of plaice did not change greatly, with the exception of juvenile plaice in 2100 under RCP8.5 projections. This implies that trophic interactions, like a reduction in competition and a reduction in predators had a stronger impact on plaice in the model than just the thermal habitat suitability.

Similar to the changes in plaice biomass, the increase in herring biomass was not expected, based on the thermal preference for this forage fish (Figure 2a). Mean and Max for both RCP scenarios exceed the optimum temperature for herring in 2100, implying a generally negative impact on herring by climate change and a reduction in habitat suitability in the entire North Sea (Figure 4). Therefore, these results in our study need to be taken with caution. One of the main impacts of climate change on herring is related to its recruitment success. Herring has experienced low recruitments in the past decades (ICES, 2019b). The dynamics leading to low recruitment are not entirely understood; with varying spawning strategies among the different herring stocks and complex life-histories complicating the analysis (Geffen, 2009; van Damme et al., 2009). However, the early larvae phase has been identified as a bottleneck, likely related to impaired feeding conditions (Payne et al. 2013, Lusseau et al. 2014) due to changes in the zooplankton composition of the North Sea (Alvarez-Fernandez et al. 2012, 2015). Especially copepods showed a community shift to warm-water species, accompanied by a decrease in cold-water and neritic species (Alvarez-Fernandez et al. 2012), the latter two consisting of important prey items for larval herring (Heath 1989, Lusseau et al. 2014).In our ecosystem model, copepods are currently included as one functional group, not allowing us to simulate this structural change in the zooplankton community and thus possibly overestimating the positive effect of a reduction in predators vs. a negative impact of temperature on food availability and composition.

Shifts in commercially important species also affect fishing effort and catches of the different fishing fleets. Since the focus in our study was placed on beam, demersal and pelagic trawls and seiners, only these fleets will be discussed here. Overall, the shift in species distribution to a strong reduction of catch for both RCP scenarios. Even in 2050, catches as well as discards were reduced by ~ -5% under RCP8.5. Overall catches decreased strongest in the south of the study area, due to losses in commercial fish biomass that are attributed to the shift in distribution of the majority of the fish species. Nevertheless, effort of all fleets increased slightly in the south. Sole and plaice are mainly targeted by beam trawl fisheries, and caught as by-catch with otter trawls (Engelhard et al., 2011; ICES, 2021). Since biomass of these species increased with increasing temperatures, fleets increased their effort especially in the south; where sole as one of the main target species is mainly distributed. Shifts in species distribution due to climate change can have an immense impact on the associated fisheries and fish production worldwide (Brander, 2007). Adaptations to these shifts could include changes in fishing grounds or changes in targeted species (Bennema, 2018; Hutton et al., 2004; Rybicki et al., 2021), which have to be accounted for in management to reduce the cumulative stress, especially in transboundary stocks targeted by multiple nations (Palacios-Abrantes et al., 2020). In conclusion, our study supports the notion that distributional changes due to climate change need to be accounted for in future management decisions, which is especially true for southern part of the North Sea.

5.5 *Conclusion and outlook*

The southern part of the North Sea will most likely undergo severe changes in ecosystem structure due to distribution shifts of several species, inducing changes in predator-prey interactions and restructures in the ecosystem composition. Until the end of the century, temperatures will exceed thermal optimum ranges for many species currently present in the southern part of the North Sea. Given this worst-case RCP projection, the species composition and ecosystem structures will profoundly change in the shallow, most southern regions in the North Sea, with a higher dominance of flatfish species and invertebrates and a decrease in all other major groups according to model our results. In order to consider these changes and to avoid adding even more pressure on the ecosystem, management measures will have to be adapted and take shifts in species distribution and composition into account (Lindegren & Brander, 2018).

Fishing quotas for species that move out of the study area might need to be adjusted and species moving in need to be taken into consideration in stock assessments and management (Link et al., 2020). Further research of species groups that are expected to benefit under climate change and may play a fundamental role in the future could improve model outcomes and our understanding of the ecosystem under changing conditions and consequential management actions. The model applied in this study is quite fish-centric and therefore a stronger partitioning of lower trophic levels, like benthos or zooplankton, into groups that can cope with rising temperatures and groups that are at the edge of their thermal optimum window would be beneficial.

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6. General Discussion and Conclusions

The four studies included in this thesis provide insights into two modelling techniques used to evaluate spatial distributions of single species as well as ecosystem structures. Guidelines on the inclusion of habitat preferences based on SDMs into a spatially resolved ecosystem model (Ecospace) are presented. Despite recent advancement in the EwE modelling software, Ecospace lacks an integrated and automated evaluation routine of the model fit. This thesis provides a valuable tool of a possible skill assessment based on a set of indices, evaluating the temporal, spatial and spatio-temporal model fit. With this information, the best fitting Ecospace model was applied to simulate and assess spatial processes of the ecosystem in the southern part of the North Sea. Two of the studies included in this thesis (Publication 3 and 4) are among the first to evaluate effects of spatial management decisions, such as spatial closures to fisheries and environmental pressures (e.g. climate change) on the ecosystem by deriving spatially resolved ecological indicators from the ECOIND plug-in. Placement and size of areas excluding fisheries were evaluated and the evoked effort re-distribution accounted for. Potential trade-offs emerging through spatial usage conflicts between MPAs, OWFs and fisheries were also addressed. Spatially highly resolved information about local climate change effects expanded existing knowledge about the impacts of a warming ocean on individual species and ecosystem compartments described through ecological indicators. Through the application of both, SDMs and Ecospace, insights on thermal suitability of the North Sea for cod could be gained and compared to climate change impacts in an ecosystem context. The findings of this thesis promote the applicability of spatially resolved ecosystem models by supplying guidelines on increasing realism of species distribution and bring these models one step closer to the integration into spatial ecosystem-based management.

The following discussion emphasizes lessons learned about the advantages and disadvantages of the individual modelling approaches (SDMs and Ecospace) but also highlights the combined usage of both techniques, especially regarding habitat preferences (Publication 1 and 2). Furthermore, model validation options and skill assessment methods applied are addressed (Publication 1 and 2). Climate change impacts on cod as targeted species are discussed (Publication 1 and 4) and lessons learned for spatial management of the southern part of the North Sea are reflected upon (Publication 3 and 4).

6.1 *SDMs and Ecospace – lessons learned*

Understanding what drives species distributions has become increasingly important, especially with growing environmental and anthropogenic pressures on the ecosystem (Van Echelpoel et al., 2015; Donelson et al., 2019; Thorson, 2019; Baudron et al., 2020). On the one hand, this can be addressed by evaluating the distribution of individual species with SDMs based on their affinities towards certain habitats or environmental drivers. On the other hand, species distribution can be modelled in an ecosystem context, addressing the trophic niche of a species (Coll et al., 2019; Melo-Merino et al., 2020). Recent developments allow the combination of both techniques by including spatially highly resolved habitat preference maps derived from SDMs into a complex process-oriented ecosystem model (Steenbeek et al., 2013; Christensen et al., 2014). However, this approach is still missing best-practice recommendations. The work presented in this dissertation allows to draw conclusions on the advantages and disadvantages of each individual modelling approach and serves as guideline for the combination of both for future modelling endeavors.

6.1.1 SDMs – advantages, disadvantages and structural differences

The biggest advantages of SDMs in ecological modelling is the applicability to a wide range of research questions, both terrestrial and marine. These topics can vary from the quantification of the environmental niche of a species (Bentlage et al., 2013; Fernandez et al., 2017; D’Amen and Azzurro, 2020), evaluating biodiversity based on the distribution of individual species (Probst et al., 2021), assessing possible invasion of species (Parravicini et al., 2015; Le Marchand et al., 2020), the support of spatial management by evaluating vulnerable habitats (Vierod et al., 2014; Anderson et al., 2016a, 2016b) or the impact of environmental changes on the distribution of species (Valle et al., 2014; Weinert et al., 2016). Furthermore, SDMs are flexible in their type of response variables (presence, presence/absence or abundance) as well as environmental predictors and allow the creation of habitat suitability maps. Due to the great number of applications, a variety of SDM methods are available (Guisan and Thuiller, 2005) and a general understanding of a good practice approach has been developed and followed (Zimmermann & Guisan, 2000; Elith and Leathwick, 2009b). Unfortunately, due to this flexibility of SDMs in regard to modelling methods and applied data types, it bears the risk to choose an unsuitable modelling technique required for data types at hand or proposed research question (Elith and Graham, 2009).

Due to the differences in research questions (Publication 1: temperature suitability of cod, Publication 2: integrating habitat preferences into an ecosystem model), SDMs in both studies had structural dissimilarities and similarities. Data on species presence/absence and abundance was modelled with a Generalized Additive Models (GAMs; Hastie & Tibshirani, 1986). GAMs are a commonly used regression-based modelling technique to predict species distributions (Guisan et al., 2002). By applying a smoothing function, they allow the description of non-linear responses to environmental or geographical parameters, adding further flexibility to the fitting process (Wood, 2003). Furthermore, both studies were modelled with two types of probability distribution and link functions. A binomial distribution with canonical link logit was applied to presence/absence data, while a gamma distribution with logarithmic link was used for abundance data (presence only). Finally, in order to account for a high number of zero abundance data, the hurdle approach was applied in both studies, expressing modelling results as the production of the presence/absence model and the presence only abundance model (Maunder and Punt, 2004).

A major difference between SDMs in Publication 1 and 2 is the choice of explanatory variables. SDMs can be applied to model habitat preferences in a geographical or environmental space. The environmental space refers to abiotic parameter, such as temperature (applied in Publication 1) while the geographical space addresses spatial patterns of a species (applied in Publication 1 and 2). In the past decades, data availability has improved significantly and thus environmental parameters have become increasingly important (Reiss et al., 2011). As the evaluation of climate change effects on the thermal habitat of cod was the aim of Publication 1, the highly resolved dataset AHOI (Adjusted Hydrography Optimal Interpolation) was used in combination with a regionally coupled ocean-atmosphere climate system model MPIOM/ REMO (Mikolajewicz et al., 2005; Sein et al., 2015). It allowed a spatially highly resolved representation of past thermal suitable habitats for three size classes of cod and possible changes to these habitats under climate change. Furthermore, annual cod abundance derived from the stock assessment was introduced as additional explaining covariate to account for density dependent effects (Planque et al., 2011; Pinsky et al., 2013).

Including geographical references, such as longitude and latitude, as explanatory variable accounts for most important processes that drive species distribution and allows a representation of habitat preferences (Planque et al., 2011). This reduces the possibility of spatial autocorrelation in the residuals, which generally indicates that an explanatory variable responsible for specific spatial patterns was not included in the model (Guélat and Kéry, 2018).

In both publications, spatial autocorrelation was addressed by including a thin plate regression spline as smoother for latitude and longitude. If data availability on environmental parameters is low, it is a valid approach to describe past distribution but forecasting is not possible (Elith & Leathwick, 2009a). Since the aim of Publication 2 was the evaluation of the best approach when integrating habitat preferences into a complex tropho-dynamic model, a simple SDM based modelling technique (GAM) also used in Publication 1 was applied. However, for Publication 2, only geographical references were included in the model as predictors in order to exclude any impacts caused by environmental parameters.

A major pitfall for SDMs in general is the inclusion of biotic parameters. Currently, there are only few methods that allow the inclusion of interactions between species in SDMs (Reiss et al., 2014). Even when modeling multiple key species in an ecosystem with SDMs, possibly allowing the evaluation of biodiversity across the modelled area, trophic interactions between the groups cannot be displayed explicitly. Furthermore, SDM accuracy might not be the same for all species when simultaneously applying it to multiple species in an ecosystem. Predictions of the distributions for species with a narrow ecological niche might have a higher accuracy than for species with a broader niche, due to the more restricted availability of such a niche (Reiss et al., 2011). Therefore, alternative approaches than single species modelling might be necessary to account for biotic interactions.

6.1.2 Including habitat preferences into Ecospace

While SDM applications struggle with the inclusion of biotic parameters, ecosystem models enable an impact analysis on ecosystem structures and the evaluation of impacts on single species in an ecosystem context (Fulton, 2010; Geary et al., 2020). Nevertheless, spatially resolved ecosystem models, such as Ecospace, were limited when representing known species distributions and habitat preferences. Currently however, the representation of variations in habitat quality and the usage of a spatio-temporal framework to dynamically include geographical information has become possible due to new adaptations of the software (Christensen et al., 2014; Steenbeek et al., 2013). Prior to these enhancements, the distribution of species within the modelled area could only be presented by presence/absence preferences in relation to static habitat maps. The flexibility to inform a model about spatial habitat preferences of a species increased with the inclusion of habitat foraging capacity (Christensen et al., 2014).

This enabled the coupling between SDMs and Ecospace in two ways. First, response functions of environmental parameters calculated with SDMs can be implemented and linked with spatially resolved environmental drivers, such as temperature (Grüss et al., 2016). Second, habitat preference maps derived from SDMs can be implemented directly. Both methods have been found to increase correlations between observations and modelling results by the complementary application of SDMs and Ecospace (Coll et al., 2019). This is why habitat preference maps were used for all functional groups, which have a good catchability within the scientific surveys included in the modelling, in order to construct the Ecospace model of the southern part of the North Sea.

Insights gained in Publication 2 can be used as guidelines to the complementary usage of both modelling techniques when combining habitat preference maps with Ecospace. An important aspect is the choice of the predictor variable and its profile. While the presence/absence GAM fitted with a logit link resulted in a sigmoidal profile, the GAM applied to presence data resulted in an exponential profile when fitted with a log link. These two profiles varied in their spatial precision. Habitat preferences based on a sigmoidal profile resulted in a wider distribution range, while the exponential profile revealed a clear distribution with high abundances. When applying an SDM solely for the intention to model the distribution of a single species without trophic interactions, as performed in Publication 1, the exponential profile allows spatially precise descriptions of habitat suitability. However, when combining these precise maps with trophic interactions, Publication 2 showed that they are too restrictive because they limit distribution possibilities and might lead to a predator-prey mismatch. Spatially explicit results from models based on abiotic parameters need to be broad enough to allow biotic parameters (like predation and competition) to influence the distribution. Especially when applying these models to spatial management questions like spatial fisheries closures (Publication 3) and climate change in an ecosystem context (Publication 4).

Implementing these maps into the Ecospace model increased the overall fit, especially when accounting for shifts in species distributions over time. By using a geographical distribution in the SDM model, based on latitude and longitude, factors that influence distributions are accounted for without explicitly including them as predictors. However, applying these maps also has limitations. Extending or reducing the SDMs by additional environmental responses is not as flexible as applying additional functional responses directly in Ecospace to an environmental driver map.

Therefore, if a range of scenarios including different drivers applied to the foraging capacity should be evaluated, new SDMs would have to be constructed and calculated rather than just adding functional responses and letting Ecosim or Ecospace calculate the spatial foraging capacity. Even when including forcing functions rather than maps demands a great mechanistic understanding of how abiotic drivers influence habitat preferences of each functional group, it might be a more suitable approach for models representing regions with low data availability. One further best practice recommendation that emerged from this thesis is the combination of habitat preferences maps and environmental preference functions as additional driver of species distribution in Ecospace. In order to assess the impact of climate change on the ecosystem of the southern part of the North Sea, this approach was used in Publication 4. Including habitat preference maps based on SDMs for the study period 1991-2010 ensured a good model fit, especially when updating these preferences every five years. At the same time, implemented functional responses towards temperature were used to predict changes in the ecosystem under two climate change scenarios. These functional responses were derived from the platform 'Aquamaps' (https://www.aquamaps.org/) that provides habitat preference maps based on SDMs and the associated environmental preferences for marine species. For studies testing a range of environmental response functions, or varying responses to temperature (for example temperature sensitivity during spawning seasons), adding and removing these functions is more applicable than creating SDMs with all these environmental parameters, individually and simultaneously. Especially for studies with low data availability or for functional groups with low catchability in existing surveys, platforms like 'Aquamaps' can support advances in spatial modelling.

6.2 *Skill assessment and model validation of spatially explicit models*

All models encompass a certain amount of uncertainties and it is pivotal to address them for further improvement of the models and to strengthen the confidence in scientific advice (Beale and Lennon, 2012). These uncertainties might stem from input data (e.g. sampling issues, missing covariates, spatial and temporal biases) or from the technical structures of the model itself (Barry and Elith, 2006). SDMs as well as the Ecospace model applied in this thesis succumb these uncertainties. Multiple issues influencing model performance as well as reducing uncertainties were addressed in this thesis with known evaluation methods and a proposal for a new routine in the case of Ecospace.

6.2.1 Uncertainties and considerations for SDMs

Data availability and structure – Compared to other oceanic regions, the North Sea is a well-studied and monitored area with a great variety in data sources (Emeis et al., 2015). Spatial data on environmental parameters, oceanographic features, effort distributions and species abundances are accessible to the scientific community. The SDMs are based on abundance data derived from the Database of Trawl Surveys (DATRAS) for two scientific surveys. The IBTS and the BTS are well established scientific surveys carried out with the objective to collect fisheries-independent data on the distribution as well as the relative abundance of fish species, but also certain invertebrates (ICES, 2020). Both surveys are liable to various quality control measures during the survey as well as prior to uploading data into the database (ICES, 2019a; 2020). However, regardless of well-structured survey designs and quality checks of the compiled data, some natural variations and uncertainties in the data cannot be controlled. Mechanisms like avoidance of the net or schooling behavior of fish can alter the perception of distribution and create false absences which can have a great impact on the predictions of the models (Gu and Swihart, 2003). To determine whether these absences are “real” absences or if species were just not detected due to variable gear catchability, is virtually impossible (Fraser et al., 2008). Using a so-called hurdle approach in the GAMs of Publications 1 and 2 addressed this issue. With the hurdle model, the probability of presence/absence of a species in the catch and the catch rate of only species presences are modelled separately and multiplied afterwards (Maunder & Punt, 2004).

Spatial scale – Spatial resolution, projection and extent of data implemented in SDMs as well as the projection grids for the resulting habitat preferences have to be taken into consideration carefully when structuring a spatially-explicit model (Lowen et al., 2016; Fernandez et al., 2017; Turner et al., 2019). Generally, survey data are available on a coarser grid with a lower resolution than geographical, physical or chemical datasets. When predicting species distribution in regards to such environmental parameters, predictor and response variables need to be brought to the same resolution (Núñez-Riboni et al., 2021). In Publication 1, similar issues occurred when pairing catch-per-unit-effort data with the training dataset AHOI. Both datasets varied in spatial as well as temporal scale. In order to match scales, CPUE data was mapped onto a 0.5 x 0.5° grid (roughly the mean distance between sampling locations) by applying a geographical GAM with a latitude and longitude smoother. At the same time, the AHOI dataset of higher resolution was downsampled by applying gaussian smoothing.

Following, the datasets were matched grid-point to grid-point. Furthermore, a Delaunay triangulation was applied containing only haul positions with robust data, in order to exclude CPUE that was estimated with a GAM in areas with low data availability and therefore low robustness. Finally, the trained data was predicted onto the original AHOI 0.2 x 0.2° grid. Lower resolution in data used to train the model and predicting to a higher resolution is known to increase the model performance compared to models that were trained with high resolution data (Núñez-Riboni et al., 2021).

Choice of model type and skill assessment of model performance – Regardless of good accuracy and predictive power, comparisons between different SDM techniques revealed great variations in predicted spatial distributions (Reiss et al., 2011). Therefore, it is important to apply an SDM technique that is most suitable for the data and the proposed research question. In Publication 1, GAM was chosen as modelling technique in an early state of the process. For Publication 2 however, two types of modelling techniques were tested on their applicability and performance. Next to the regression-based GAMs a Bayesian modelling approach was tested. For this approach, the integrated nested laplace approximation (INLA) was tested for the same response variables (presence/absence and presence-only) as the GAMs. Due to high computational time, this was executed and evaluated only for five functional groups (cod, whiting, starry ray & others, sole and plaice) and finally the predictive skill of the two modelling techniques were compared using a 4-fold cross-validation approach. The fit was evaluated with the area under the response curve (AUC; Swets, 1988) and root mean squared error (RMSE). However, the more time-consuming and structural complex Bayesian modelling technique did not outperform the simpler GAM approach and was therefore not considered further. Cross-validation was also applied in Publication 1, but rather than compare different modelling techniques, it was used to validate the final model. Calculating the deviance residuals with the cross-validation revealed a good model fit and representation of cod’s thermal habitat.

6.2.2 Uncertainties and model validation in Ecospace

Complex ecosystem models require large amounts of data, which all introduce a certain amount of uncertainty (Link et al., 2012). These uncertainties can be categorized into structural uncertainties, initialization uncertainties, parametric uncertainties and scenario uncertainties (Payne et al., 2016). In Ecopath with Ecosim, the spatial component Ecospace is based on the static and temporal modelling compartments (Christensen et al., 2008).

The Ecopath and Ecosim models structured for the southern part of the North Sea are already attributed to a range of uncertainties. They were parameterized with diet and survey data, output from multispecies models and stock assessments, all including a certain degree of uncertainty (Stäbler et al., 2016). Recently, the plug-in Ecosampler has been introduced into EwE, which enables the modeler to evaluate variations in model results due to uncertainties. However, the plug-in only allows the evaluation of variations in input data of the Ecopath module so far (Steenbeek et al., 2018). Bringing the model into a spatial dimension introduces new uncertainties. Next to habitat reference layers, based on different environmental and geographical parameters (i.e. depth, sediment and distance to coast), layers representing possible fishing grounds were introduced. These spatially resolved layers are based on observed and modelled values derived from different data platforms. Furthermore, assumptions about habitat preferences (Publication 2 and 3) as well as response functions towards depth and temperature (Publication 2 and 4) were included, which are also based on modelled data and literature review. One of the greatest uncertainties are dispersal rates, i.e. movement across the modelled area. When introducing modelled habitat preferences based on SDMs, model uncertainties are growing. Therefore, there is a great need for assessing the model fit of Ecospace.

Unfortunately, Ecospace does not have an implemented routine that allows the user to automatically assess the model fit yet, which is needed to increase the credibility of the outcome (Steenbeek et al., 2021). In the temporal component Ecosim, model fit is being evaluated by the comparison of the relative biomass predictions and observed reference time series (Mackinson et al., 2009). In order to ensure a good performance in the model prediction of Ecosim, the calibration of the model includes the fitting of the most sensitive vulnerabilities to adequately represent predator-prey dynamics in the food web (Ahrens et al., 2012). Furthermore, anomalies in primary production can be calculated. The fit between observed time series and time series produced by Ecosim is compared by calculating sum of squares (Christensen et al., 2008). With an automated fitting routine included in the software, a range of vulnerabilities and primary production splines can be tested in a stepwise process to find the best fitting model (Scott et al., 2016). These fitting and validation routines were used for the Ecosim of the southern part of the North Sea, which feeds into the Ecospace model.

To overcome the missing skill assessment in Ecospace and to prepare guidelines on such an evaluation, a set of possible metrices that can be applied outside of Ecospace was tested in Publication 2. Multiple metrices were used conjointly (Olsen et al., 2016; Stow et al., 2009) to address the temporal, the spatial and the spatio-temporal fit. The temporal fit between predictions and observed data (same reference time series as used in Ecosim) was addressed by calculating the RMSE (similar to Coll et al., 2019) and model efficiency (MEF) for biomass and catch time series. Due to the lack of spatially resolved catch observations for the entire modelled time period (1991-2010), an additional parameter, the Pearson correlation, was applied to assess the temporal fit of catch predictions. Spatial and spatio-temporal metrices were calculated between the Ecospace results and the hurdle maps created with SDMs. For the spatial fit the Schoener index was calculated and a Taylor diagram was created to assess the spatio-temporal fit. The results of this study showed, that assessing all three dimensions is crucial. In Publication 2, the inclusion of habitat preferences based on two types of response variables (presence/absence vs hurdle) derived from SDMs per functional group in different implementation frequencies were tested. Habitat preference maps were updated seasonally, annually, all five years and implemented only in the beginning of the execution of the model. When looking at the spatial fit, Ecospace runs with hurdle-based habitat preferences performed slightly better than preferences based on presence/absence. However, when evaluating the temporal fit, it became apparent, that the presence/absence models clearly outperformed the hurdle models, which was supported by the evaluation of the spatio-temporal fit. Including temporal updates of habitat preferences increased the fit in any case.

Nevertheless, this spatial fitting routine can only be performed when distribution maps of the different functional groups are available. This problem could be overcome by connecting Ecospace outputs directly to species distribution databases, like ‘Aquamaps’ or the ocean biodiversity information system (OBIS; https://obis.org). The same is true for the fit of catch predictions. While a temporal fit can be assessed, a spatial fit might be more difficult. However, catch databases have been extended including spatially resolved landing information, which could be used to compare predictions derived from the model with observational data (STECF, 2020). Overall, increasing the credibility of spatio-temporal modelling approaches such as Ecospace is necessary if results should be included into spatial EBM on a regular basis, for which a proper skill assessment, a reduction in uncertainties, an evaluation of ecological realism and an improved model calibration is necessary (Hipsey et al., 2020; Steenbeek et al., 2021).

6.3 *Climate change impacts on cod – evaluating differences and similarities from two modelling approaches*

Both modelling approaches described in the previous sections were applied to model the impact of climate change on cod, once in a single species approach with an SDM (Publication 1), focusing on the suitable thermal habitat in the past and under future predicted conditions and once in an ecosystem approach, including trophic interactions (Publication 4). Both approaches revealed, that the most southern regions of the North Sea will become less suitable for cod in every length and age class modelled. After cod biomass decreased in the past with a historical low in 2006, the stock recovered in the central and northern parts of the North Sea, but did not recover in the southern parts (ICES, 2019b). Publication 1 shows, that the southern North Sea below the 50 m depth contour has been thermally less suitable than the north in the past and this will increase under future projections (Publication 1, Figure 6). The Ecospace model supports the low suitability in the south and a further decrease in biomass under climate change predictions for adult cod (Publication 4, Figure 8). The distribution shift predicted with the Ecospace model for juvenile cod (Publication 4, Appendix B, Figure B1-F) is also in consensus with the predictions of the thermal habitat derived for the two smaller length classes with the SDM in 2100 (Publication 1, Figure 6).

For cod adult a strong decrease in biomass is predicted, which is projected to be similar across the study area. This implicates, that regardless of the better thermal suitability, a possible reduction in prey abundance led to an overall equally distributed reduction. However, as for juvenile cod, the Ecospace study suggests that the biomass of juvenile cod would hardly change at all, even slightly increase under climate change predictions, despite the decrease of adult cod and therefore the spawning stock. One reason for this somewhat counterintuitive projection could potentially be the reduction in competition and cannibalism due to the decline in adult cod. For cod, cannibalism as well as feeding competition are common and have therefore been included into the model through the diet matrix implemented in Ecopath (Folkvord and Otterå, 1993; Link et al., 2009). Juvenile and adult stanzas of cod were split depending on the size they need to reach to be targeted by modelled fisheries (i.e. 40 cm). The diet of juvenile cod therefore includes both larval prey as well as prey that is also targeted by adult cod, hence a reduction in adult biomass decreases competition and cannibalism and hence benefits the juveniles.

Furthermore, some important processes that might negatively impact juvenile cod under climate change might be missing due to the current model design. One negative impact is the direct influence of temperature on reproduction Higher temperatures impact oocyte development and spawning time. Elevated temperatures lead to an earlier onset of oocyte development and therefore earlier spawning (Kjesbu et al., 2010; Mcqueen and Marshall, 2017) which could lead to a match-mismatch between cod larvae and the onset of the phytoplankton bloom (Asch et al., 2019). Furthermore, zooplankton composition of the North Sea shifted with an increase in warm-water and decrease in cold-water zooplankton (Alvarez-Fernandez et al., 2012; Beaugrand, 2004; Reid et al., 2003) which led to the decline in cod recruitment due to a reduction in food quality and availability (Beaugrand et al., 2003; Beaugrand and Kirby, 2010; Sundby, 2000). These interactions are currently not well reflected in the way the lower trophic levels are structured and an adaptation of these groups might be necessary. Another important impact that might be missing is the effect of rising temperatures on spawning success. In the spring, spawning temperatures of 5-7° are favorable and reproduction success might be reduced under higher temperatures (Lelièvre et al., 2014; Gonzalez-Irusta and Wright, 2016; Höffle et al., 2017) Currently, changes in temperature are displayed on an annual basis. Including seasonality and a forcing function based on thermal preferences during spawning season could improve predictions for all multi-stanzas in the model, since temperature preferences are generally lower during spawning seasons (Dahlke et al., 2020).

There are other climate change considerations that were not included in the present publications but could have a major impact on the ecosystem and as a result on commercially important species. The ocean acts as a carbon sink as atmospheric carbon dioxide (CO_2) reacts with seawater to form carbonic acid, reducing the concentration of CO_2 in the atmosphere. This carbonic acid leads to a reduction in pH levels in the water, a process which is also known as ocean acidification (Laffoley and Baxter, 2012). Cod larvae growth an development was found to be negatively correlated with the expected ocean acidification simulated by the RCP8.5 scenario at the end of the century, which would further reduce recruitment success (Stiasny et al. , 2016, 2019). Yet, the ocean's capacity to act as a carbon sink is limited (Schuster and Watson, 2007), which is not only the case for CO_2, but also the case for the uptake of oxygen. This increases the probability of anoxic events, especially in combination with eutrophication (Rabalais et al., 2009). A general reduction in dissolved oxygen may reduce metabolically suitable habitats for many species, like cod, if oxygen demands exceed oxygen availability (Deutsch et al., 2015).

6.4 *Applying the ecosystem model – lessons learned and management implications*

Next to evaluating the impact of climate change on a single species in an ecosystem context, the study presented in Publication 4 evaluated the impact of climate change on the entire ecosystem, while Publication 3 assessed the impacts of area closures to fisheries as conservation measure and for OWF installations on the entire ecosystem. Both publications are among the first to evaluate spatial ecosystem structures, the effect of shifts in species distribution and spatial management options by applying the ECOIND plug-in with Ecospace (Coll and Steenbeek, 2017). The next sections describe general lessons learned and resulting implications for future spatial management.

Importance of ecological indicators – In order to move from single species assessments and management considerations to EBM, common ecosystem indicators need to be applied and used, that are able to reflect ecosystem health, resilience and productivity (Blanchard et al., 2010). They can be applied to evaluate spatial and temporal characteristics of ecosystem dynamics and the impacts of environmental changes (Tam et al., 2019; Trifonova et al., 2021). With these indicators, changes in biodiversity should be detectable, but also the impact of fishing on the ecosystem, for which multiple ecological indicators might have to be taken into consideration (Fulton et al., 2005). Finally, these indicators can be implemented into management actions by translating them into fishing decision criteria like ecosystem-based control rules (Link, 2005). By extending EwE with the ECOIND plug-in, the calculation of ecological indicators on functional groups as well as species level are now possible for all three model compartments (Coll and Steenbeek, 2017). So far, these indicators have been used for instance to evaluate food web structures prior and after establishing MPAs (Vilas et al., 2021a), evaluate changes in an Arctic deep-see ecosystem (Vilas et al., 2021b) and assess the impacts of climate change and alien species (Corrales et al., 2018).

Responses of ecological indicators might be triggered by changes of different drivers, i.e. fishing or environmental parameters, and not respond to the same extent to each driver and it is therefore crucial to carefully evaluate outputs (Shin et al., 2018). Additionally, these responses to change may vary between indicators. After applying ecosystem indicators in Publication 3 and 4, results showed that specific attention needs to be payed to (i) what functional groups/species are included in the calculation of the indicator and (ii) how many different functional groups/species are included.

The first instance that raised these issues was connected to the indicator "mammals and bird biomass" when increasing protection through MPAs in Publication 3. Intuitively, the biomass should increase, especially inside the areas closed to fishing due to increases in fish biomass and therefore prey abundance. However, biomass of mammals and birds decreased. Looking closer at the functional groups included in this parameter, it became clear, that the strongest impact was displayed by one group, surface-feeding seabirds. A large amount of seabird's diet consists of discards (Sherley et al., 2020). With the closure of fishing grounds, a reduction in discards was caused, which simultaneously led to a reduction in prey for seabirds. Furthermore, it reduced the attractiveness of MPAs for seabirds since fishing (and therefore discards) is not taking place. Modelled mammals included in the calculations feed on many prey groups and are only caught as by-catch. Therefore, the actual impact of static MPAs was small and the negative impacts on seabirds dominated. This example shows, how important a close evaluation of driving mechanisms of individual indicators can be.

Including the range of indicator response in the final evaluation turned out to be quite important. Each indicator encompasses different numbers of functional groups. Some indicators are even calculated on a species level, after listing species per functional group and allocating specific traits (Coll and Steenbeek, 2017). While total biomass or invertebrate biomass include all functional groups or the majority of biomass in the model, indicators such as biomass of IUCN-endangered species only include a couple of species. Including a large amount of species per indicator potentially reduces the impact that drivers have substantially, especially when the trend in reaction varies between groups. One additional impact that arose during the preparation of the study is the inclusion of indicators based on length. When constructing a model for a sub-region, such as the model for the southern part of the North Sea, reference values may reflect species across the entire North Sea, which can be quite dissimilar between species living in the northern North Sea to those living in the southern North Sea (Baudron et al., 2014). Therefore, a careful selection of input values and applicability of ecological indicators needs to be considered. In order to move from the evaluation of ecological indicators to the inclusion in EBM, a common framework and a suit of indicators is necessary, which can be applied to determine ecosystem reference points and be comparable across model applications and ocean regions (Otto et al., 2018). Varying sensitivity and thresholds in responses among the indicators need to be assessed to compare indicators between different stressors and understand the underlying processes (Fu et al., 2019).

Importance of predator-prey relationships – The main goal of applying a spatially resolved ecosystem model is the desire to study spatio-temporal dynamics in an ecosystem, to understand complex processes and the ecological organization (Walters et al., 1999). The core of an ecosystem model is represented by the food web with its feeding relationships and describes the flow of energy through the system (Walters et al., 1997). These predator-prey relationships in the spatio-temporal model are highly influenced by the spatial overlap of distribution niches between a predator and its prey (Grüss et al., 2016). Encapsulated in this relationship is the idea of the foraging arena (Ahrens et al., 2012). The key assumption of the foraging arena is, that prey organisms can be vulnerable or invulnerable to predators and that foraging generally takes place when prey is in a vulnerable state (Ahrens et al., 2012). In Ecosim, the foraging arena theory is the basis for the calculation of vulnerabilities for each prey species to its predator (Christensen et al., 2008). These vulnerabilities are transferred over to Ecospace in which the suitability of a habitat in a cell has an impact on the ability to predate and is thus in direct interaction with the vulnerabilities (Christensen et al., 2014). Biomass values derived from Ecosim are dynamically distributed over the modelled area based on preferred and non-preferred habitats, defined by the cell suitability (Christensen et al., 2008). Next to cell suitability, predation risk, low feeding rates in non-preferred habitats as well as fishing pressure defines the distribution of biomass on the map (Christensen et al., 2008). Therefore, every change in species distributions due to environmental drivers or displacement of fishing effort has a direct impact on the distribution of all functional groups in the ecosystem through predator-prey interactions and cell suitability.

Changing spatial dynamics due to fishing closures based on MPAs or OWFs led mostly to negative changes in the ecosystem (Publication 3). Closing areas to fisheries has two effects, (i) it reduces/excludes the fishing pressure to specific cells in the model and (ii) increases the fishing effort in the remaining fishing areas since the effort placed in the restricted areas has to be re-allocated. This increases the suitability of the closed areas, especially for highly fished species and decreases the suitability outside. In turn, predation pressure inside the closed areas is strongly increasing while it is reduced outside. Therefore, the results showed an increase in fish biomass inside the closed areas and an increase in total biomass (primarily invertebrate biomass) outside the closed areas (Publication 3, Figure 4). As for OWF, even if the size of the closed areas was not as large as when closing designated MPAs, the impact on fish biomass and total biomass was similar (Publication 3, Figure 3).

The additional artificial substrate increased the suitability for benthic species and thus increased prey biomass, which increased predatory and fish biomass. Overall, however, did the increase in fishing effort outside these areas negatively impact the calculated ecological indicators to an extent, that the increases inside the closed areas were outweighed by the reductions outside. These results show, that even if species might benefit from MPAs when evaluated individually predator-prey relationships might alter the impacts on the entire ecosystem and need to be considered when assessing the effectiveness of MPAs. Even if the impact of increasing oceanic protections is expected to be substantial (Sala et al., 2021) and have the potential to increase fishing yield when strategically placed (Cabral et al., 2020), trophic interactions between species should not be neglected, since these interactions can have strong consequences and therefore change the expected effectiveness of a protected area.

Induced changes in ecosystem structure by warming waters in Publication 4 revealed similar interactions. Independent of which scenario, many indicators decreased especially in the southern region of the modelled area. Primarily fish biomass, but also overall biodiversity measured with the Shannon index (Publication 4, Figure 8). This shift increased the suitability for lower trophic level species, due to a reduction in predator species. Despite their own thermal window, the reduced predation pressure increased invertebrate biomass, showing that predator-prey interactions might be stronger than expected influence of habitat suitability (Hiddink et al., 2015). Combining the trophic effects simulated in Publication 3 and 4 would be necessary, to test future effectiveness of spatial management measures such as MPAs under climate change conditions. An increase in biomass inside the closed areas might not be achievable, if climate change impacts induce further shifts in species. Thus, an adaptation of MPAs towards climate change might be necessary (Bruno et al., 2018)

Importance of regional differences – Across the entire model area, different regions can be distinguished. Towards the English Channel and along the Dutch, Belgian and German coastline shallow depth, mixed water masses and high productivity are characteristic. At the same time, the region towards the north is defined by depths down to 100 m and a mixing in species that are either on their most southern or most northern distribution range, causing high biodiversity (Ducrotoy et al., 2000; Emeis et al., 2015). In both publications presented in this thesis these strong regional differences were highlighted, especially in relation to the response of ecological indicators.

Results of Publication 4 show, that especially the most southern, shallow regions of the model area will succumb stronger increases in temperature. By 2100, the maximum SST south of 55° predicted for RCP8.5 exceeded the temperature optima of 27 (RCP4.5 = 25) out of 46 functional groups forced with temperature. Consequently, due to the high sensitivity of species to ocean warming, functional groups shift in their distribution, as range shifts of marine species due to warming water masses is an important mechanism (Pinsky et al., 2013, 2020). This reduction of species in the south, predominantly predatory fish species, led to an overall decrease in fish biomass, yet an increase in invertebrate biomass due to a reduction in predatory pressure.

Simultaneously, in Publication 3 the modelled spatial distribution of the ecological indicator representing biomass of IUCN-endangered species identified this southern region, especially the Dutch, Belgian and German coast, to be the regions with the highest biomass in IUCN-endangered species. Based on this spatial pattern, a hypothetical MPA was created in this location to evaluate the impact it would have on the system. This closed area for conservation purposes had the greatest overall impact on all indicators, negative and positive. This emphasizes the importance of this region further. At the same time, a hypothetical MPA based on high biodiversity illustrated by the spatial distribution of Kempton’s Q was located roughly along the 50 m depth contour, with a wider range along the British Coast. Even though this MPA had the same extent as the one based on the IUCN biomass indicator, the impact was comparably low. This MPA did not cause a strong decrease in indicators like fish biomass, catch or trophic levels, however, any caused decrease in indicators was comparably low. However, not only the location but also the size of the area closed off to fisheries was important. The spatial coverage of all currently designated MPAs is roughly the same as for the hypothetical MPAs, but due to the fragmentation into small areas, the impact was only small, and overall negative. This fragmentation is due to the structural settings of the Natura 2000 network, which builds the legal ground for most of the MPAs included in this study (Appendix Publication 3, Table 1.2A). As pillar of the conservational effort of the European Union, the Natura 2000 network currently covers approximately 11.5% of EU territorial waters, with a large number of individually designated MPAs (Mazaris et al., 2018). This coherent network was structured to support connectivity between the individual MPAs, however, regional and national efforts towards the implementation of such areas including management measures vary strongly (Fraschetti et al., 2018).

The importance of species and fishing effort distributions – With warming temperatures, spatial management measures like MPAs or the introduction of closed areas due to OWFs induce shifts in species distribution, major consequences for the ecosystem can occur (Hiddink et al., 2015; Poloczanska et al., 2016). These changes in the ecosystem can, in turn, impact the associated fisheries, which depend on a high productivity of their targeted species (Hernvann et al., 2020; Lotze et al., 2021). Publication 3 and Publication 4 both showed, that the redistribution of commercial biomass due to climate change and closed fishing grounds had a great impact on the fisheries, especially in terms of catch. Furthermore, Publication 3 revealed a strong trade-off between conservation measure and fishing.

Closing fishing grounds led to an increase in total catch (Publication 3, Figure 5). However, on the scale of the entire modelling region, this could not outweigh the losses of catch inside the closed areas, especially when closing the hypothetical area in the most southern area. Due to the high productivity in this area, a major fishing ground is cut off and this is reflected in overall losses of catch. Local biomass spill-over effects did not suffice to compensate for shifts in effort and losses of fishing grounds, Furthermore, results showed, that with the effort re-distribution the fishing pressure is too high on the remaining commercially targeted biomass in order for the MPAs to work properly, which would decrease the catch and therefore economic profit of the modelled fleets even further. Spill-over effects of MPAs vary, depending on the size of the MPA and the maturity of the ecosystem (Colléter et al., 2014) and benefits to the fisheries depends on the movement pattern of the targeted species as well as the behaviour of the fleet (Lenihan et al., 2021). Including the economic perspective into the evaluation of MPA effects in an ecosystem context and further implementation in marine spatial planning process could thus promote food security (Cabral et al., 2019), especially in a heavily utilized ecosystem like the southern part of the North Sea.

One effect that was not well captured in the Ecospace model were potentially positive effects of OWF installations on fisheries. Even though OWFs are closed for fishing, they increase the habitat suitability for many benthic species and serve as a nursery ground for many fish species. Commercially targeted species, like cod, have been spotted in increased abundance in the vicinity of OWFs (Kerckhof et al., 2018; Mavraki et al., 2021). Simultaneously, high abundances around OWFs of invertebrate species interesting for commercial fisheries, such as brown crab (*Cancer pagurus*), would serve the increasing demand of this resource (Stelzenmüller et al., 2021).

Turbines cause local spill-over effects that were measured up to a distance of 500 m from the individual turbines (Stelzenmüller et al., 2021). In the Ecospace model, fishing grounds were closed for the entire wind park, including a varying number of turbines and possibly overestimating the area that is closed for fishing. Therefore, spill-over effects might be underestimated and could be portrait in a more regional model with a higher resolution.

Climate change scenarios analyzed in Publication 4 suggest a strong reduction in fish biomass and therefore a reduction in catches, especially below 55°N. At the same time, there was no distinct change in effort distribution (Publication 4, Figure 8). This implicates a general reduction in biomass, especially under the RCP8.5 scenario at the end of the century, with a shift of the center of gravity towards the northern edge of the model area. Movements of commercially important fish stocks will become a challenge for future fisheries management. A redistribution of targeted biomass has negative and positive impacts on different fishing communities (Rogers et al., 2019). Maximum sustainable yields have already decreased from 1930 – 2010, with a loss of up to 35% in some regions (Free et al., 2019). As temperatures are increasing, this reduction in yields is becoming a global issue and a concern for food security, especially in countries without economical stability (Bryndum-Buchholz et al., 2018; Sumaila et al., 2011) These distribution changes of fish resources have great impacts on the fisheries, as access to fish stocks might be restricted by political boundaries and fishing grounds may shift further away, causing more hours at sea and therefore higher costs (Pinsky et al., 2021). Therefore, distribution changes need to be accounted for in future management considerations (Link et al., 2020).

Implications for management – The consequences of shifts in species distribution due to the various drivers discussed in the previous sections demonstrate, how important it is to account for shifts in species and therefore resources in spatial management. It also reveals, how important the evaluation of cumulative pressures is, as impacts described in separate studies, might amplify when applying them at the same time.

Future shifts in species distribution can be expected to change the structure of ecosystems in all ocean basins. Global animal biomass is expected to decrease, especially higher trophic levels, by the end of the century (Lotze et al., 2019; Tittensor et al., 2021). Marine systems of the North and South Atlantic, Pacific and the Indian Ocean are expected to suffer from a large reduction in marine animal biomass (15%-30%), especially under the RCP8.5 scenario (Bryndum-Buchholz et al., 2018).

However, the variation in results between RCP4.5 and RCP8.5 of the study included in this thesis show, that an adaptation of policies to reduce the amount of produced greenhouse gases could reduce the impact of climate change effects. Nonetheless it is ever so important to include climate change considerations in spatial as well as fisheries management. Linking fisheries management to ecosystem considerations needs to include migration and shifts in distribution patterns of species, for example by spatial fishery allocation (Link et al., 2020) or setting spatially distinct TACs (Bosley et al., 2019). Migratory fish species are not following management boundaries and an adaptive management needs to be applied, especially for species that are expected to cross management boundaries (Baudron et al., 2020). Political disputes, like current issues due to Brexit, might hinder a common management and change access rights to specific species. If no common ground can be found for a joint management of shared fish stocks, overexploitation of targeted species can likely be the result (Heath and Cook, 2020). In the light of climate change, these differences about access rights might increase. Quota allocation based on relative stability might complicate adaptations, while it is important to increase the adaptive capacity of regulations and principles (Pinsky et al., 2018; Bahri et al., 2021). Moreover, the adaptive capacity of fishers needs to be increased, by increasing awareness and working cross-sectorial between fishers, politicians and scientist (Lindegren & Brander, 2018).

In the case of conservational management, future marine spatial planning should include areas that would allow the creation of conservation areas as well as locate areas that support sustainable economic growth under climate change (Queirós et al., 2021). Furthermore, implementing MPAs that are spatially adaptable or take shifts in species due to climate change into consideration need to be discussed (Carr et al., 2017; Fredston-Hermann et al., 2018; Tittensor et al., 2019; Wilson et al., 2020). In the end, future discussions need to include questions about the desired outcome of management approaches. There will always be trade-offs within the ecosystem, as well as trade-offs between conservation and human usage of the ocean. The question remains, what managers, fishers or consumer want and what would be best for the ecosystem. Should the main goal of management be an increase in resources that can be harvest as food provision for the growing human population? Or does the concern about the protection of endangered species outweigh economic and consumer aims and should protection measures be established, potentially at the cost of yield and fisheries income? Should the goal of environmental protection measures be to protect large marine mammals and large fish species at the cost of lower trophic levels?

6.5 *Future perspective and concluding remarks*

The work presented in this thesis outlines a way to increase empirical realism in a spatio-temporal ecosystem model and provided guidelines on how to evaluate the performance of this model. Evaluations on different pressures allowed first insights into the complex management processes of such a highly utilized region like the southern part of the North Sea and its dynamic ecosystem. With the spatially highly resolved Ecospace model constructed for this thesis, future management issues can be addressed in an ecosystem context and spatial food-web interactions evaluated. A further evaluation of parameter sensitivity in the Ecospace model of the southern part of the North Sea could enhance the understanding of drivers and which ecosystem components might be most vulnerable to change.

In order to prepare this model to be used to support spatial management decisions, the model should be reviewed by preparing a key-run for the ICES working group on multispecies assessment. So far, these reviews have been carried out for a set of models, including the EwE model for the entire North Sea, the Baltic and the Irish Sea, however, so far only for Ecopath and Ecosim (ICES, 2019c). This way, the model could be used in order to enhance existing management. It would be interesting to follow a similar approach as the Workshop on an Ecosystem Based Approach to Fishery Management for the Irish Sea (WKIRISH) who used stakeholder engagement to increase the predictiveness of the Ecosim model (Bentley et al., 2019a, 2019b; ICES, 2018). Including knowledge about species hot spots, or areas that might be highly vulnerable to change could increase the predictability of the model and the acceptance among fishers and other stakeholders.

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Appendix

This appendix compiles the supplementary material prepared along the four publications (I-IV). In each section, the supplementary material is referenced as it is in the peer-reviewed and prepared manuscripts.

Publication 1 - *Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (Gadus morhua) under climate change*

Supplementary Material

Appendix S1: Model choice and additional validating criteria

A large effort has been invested to arrive to the habitat model, Equation 5. Various other models (with different covariates, terms and degrees of freedom) were tested and rejected, based not only on the cross-validation described in the paper but also on other criteria. For the definition of those models, both mechanistic and theoretical constraints were considered. The following sections describe these issues and other aspects of the analysis which, for the sake of simplicity, were not described in the main body of the paper. All equations and figures referenced here are those of the article. The references to this section are at the bottom.

Additional validating criteria

In addition to the general cross-validation described in the paper, we also considered to base our model choice on the smallest Akaike Information Criterion (AIC; Akaike, 1974) and, when two models differed in AIC in 2 or less, on the smallest number of degrees of freedom. However, these criteria lead often to more complex models (with more covariates or model terms) but without noticeably changing the main results of this study (Figure 6). Therefore, models were first pre-selected based on mechanistic feasibility and these two criteria: A)

Matching our year partial effect with the abundance time series of the ICES stock assessment (which will be described below under “Observed and modelled past changes of CPUE”) and B) Obtaining a realistic representation of temperature partial effect, described in what follows.

For this study relating climate change, the representation of the temperature partial effect was considered an important criterion for model choice. Temperature is one of the most important environmental variables for fish and, thus, it is expected that a deterministic relation between abundance and temperature exists, reflected by a realistic mathematical dependence or curve a(T). Specifically, a(T) should reflect expected or widely accepted physiological or ecological properties: it should always be positive, since negative abundances make no sense, and it should not increase to infinity (but be bounded), since growth of any population is always limited. Moreover, because the maximum of a(T) reflects the temperature preferred by fish (either physiologically or ecologically), this maximum should be reached inside a reasonable temperature range. Models presenting an a(T) lacking of any of these properties were rejected without further ado. Finally, three models making mechanistic sense and fulfilling criteria A) and B) were compared through AIC and the median deviance residual of the 10-fold cross validation (Table S1). Using these criteria, Equation 5 was finally chosen as best model equation.

Table S1. *AICs and mean deviance residual from the 10-fold cross validation (CV) for full habitat model (Equation 5) and two other models tested. Notation for the models is explained in the Section "Habitat modelling as function of environmental variables".*

	AIC			***Mean deviance residual from CV***		
	Length class			**Length class**		
Model	**0-25cm**	**25-40cm**	**40-140cm**	**0-25cm**	**25-40cm**	**40-140cm**
$\hat{y}_T = s_{R1}(lon,lat) + a(Y) \cdot s_{R2}(lon,lat) + (T + T^2)$	54200.4	52859.9	50950.1	0.511	0.403	0.154
$\hat{y}_T = a(Y) \cdot s_{R2}(lon,lat) + (T + T^2)$	56601.5	54488.1	53773.1	0.625	0.475	0.205
$\hat{y}_T = s_{R1}(lon,lat) + a(Y) + (T + T^2)$	55035.9	53173.6	52218.5	0.564	0.416	0.177

Chosen covariates

The only *observed* environmental covariates possibly (directly or indirectly) causing shifts of fish habitat at climate scale are temperature and salinity. From other possible covariates, like oxygen or pH, there are no long (various decades) observed data records. Besides temperature, we also considered the use of salinity as model covariate in Equation 5. In spite of yielding a smaller AIC, salinity neither visibly changed the pattern of habitat changes (Figure 6), nor considerably contributed to the model explained variance. In contrast, a model excluding temperature but including salinity alone did not show any significant suitability trends after removing the year effect. We considered these as clear signs of the lack of influence of salinity on the long-term habitat variations of cod and chose the simpler analysis with temperature alone.

While unvarying covariates like bathymetry and sediments cannot explain shifts of fish habitat with time, they could play a role on their geographical attachment. However, including in the model both bathymetry and spatial smoothers like $s_R(lon, lat)$ render one or the other as non-significant, indicating the spline term contains information relating to other static spatial preferences, such as bathymetry.

Observed and modelled past changes of CPUE

Spatial distribution of the historical changes 1967-2015 from the annual CPUE maps are shown in Figure S1, averaged in periods of 12 years. These maps indicate that each of the three fish length classes had largely decreased in abundance through the last 6 decades. Parallel to this decrease, each fish length class has undergone different regional fluctuations:

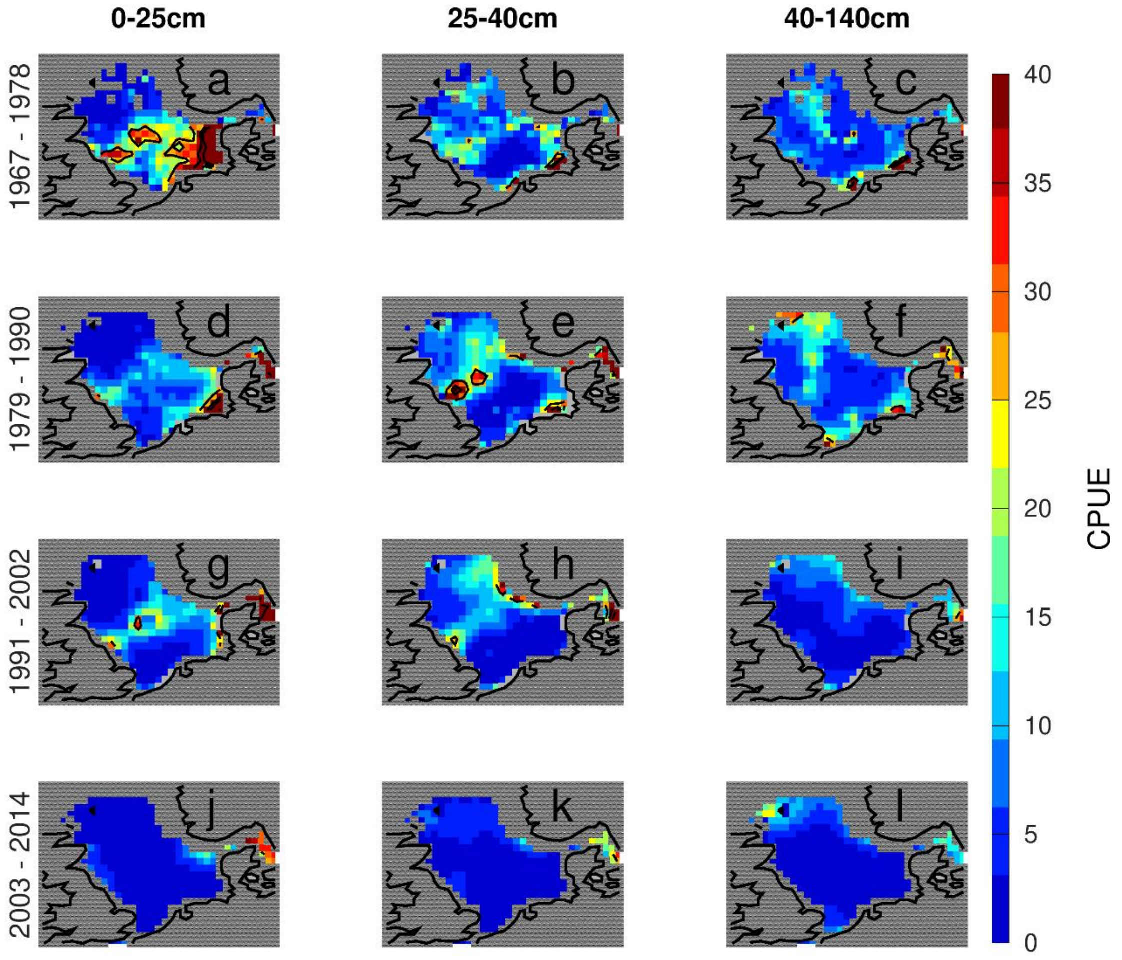

Figure S1. *Changes on Q1 distribution of cod (CPUE; Equation 2) within areas encompassed by Delaunay triangles for* $LC_{0\text{-}25}$ *(left panels),* $LC_{25\text{-}40}$ *(middle panels) and* $LC_{40\text{-}140}$ *(right panels), roughly for the decades of the 1970s (panels abc), 1980s (panels def), 1990s (panels ghi) and 2000s (panels jkl).*

The abundance of $LC_{0\text{-}25}$ in the 1970s (panel a) was particularly high in the central North Sea, as well as in the Southern and German Bights. Through the years, this abundance progressively decreased in the south, while it strongly fluctuated in the central North Sea in the 1980s (panel d) and 1990s (panel g). At present (panel j), $LC_{0\text{-}25}$ is mostly depleted from the North Sea with the exception of Skagerrak/Kattegat. $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$ undergo similar changes over time, but the decadal fluctuations are slightly different. For the 1970s, there is a large abundance of $LC_{25\text{-}40}$ (panel b) in the German and Southern Bights and the northeast coast of England. From the 1980s (panel e) to the 1990s (panel h), $LC_{25\text{-}40}$ has mainly displaced northwards to the coasts of Norway.

In the 1980s (panel c) and 1990s (panel f), $LC_{40\text{-}140}$ abundance was low at the coasts of England and large on the continental slope as well as the northern North Sea, the German and Southern Bight; in the 2000s (panel i) $LC_{40\text{-}140}$ cod concentrates along the Norwegian trench and the continental slope. At present, $LC_{25\text{-}40}$ (panel k) and $LC_{40\text{-}140}$ (panel l) are, similar to $LC_{0\text{-}25}$, abundant in Skagerrak/Kattegat. Additionally, higher CPUES of $LC_{40\text{-}140}$ can be found along the Norwegian trench and in the north western part of the North Sea.

These changes of cod abundance match well to previous studies based on fish abundance data from the IBTS from Kempf et al. (2013) (0-group cod), Hedger et al. (2004) (juveniles) and Nicolas et al (2014) (adults). These coincidences speak for a good representation of our CPUE maps s_M, which are the main input for our habitat model.

The general decrease of cod abundance in time shown in Figure S1 is reflected by the total cod abundance from the ICES stock assessments (Figure S2, black continuous curves). An additional indication of a fair performance by the model arises in the comparison of this time series with our year partial effect (grey dashed curves). Both, the habitat model and the ICES assessment model in part use the same data (i.e., the IBTS data), but rely on different assumptions. In a model of population dynamics, the present population of each fish cohort must balance estimates of natural mortality and fishery from the previous year, as well as recruitment and growth (Nielsen and Berg, 2014). In the habitat model, the choices about the number of degrees of freedom for Equation 5 divide the total CPUE variability between space ($s_{R1}(lon, lat)$ and $s_{R2}(lon, lat)$), time ($a(Y)$) and environment ($\boldsymbol{X} \cdot \boldsymbol{B}$) in different ways, yielding different partial effects in each case. Because the foundations of both models are so different, the fair comparison shown by Figure S2 is an encouraging indicator of a reasonable partitioning of variance in the habitat model and of a good match between chosen length thresholds and age classes.

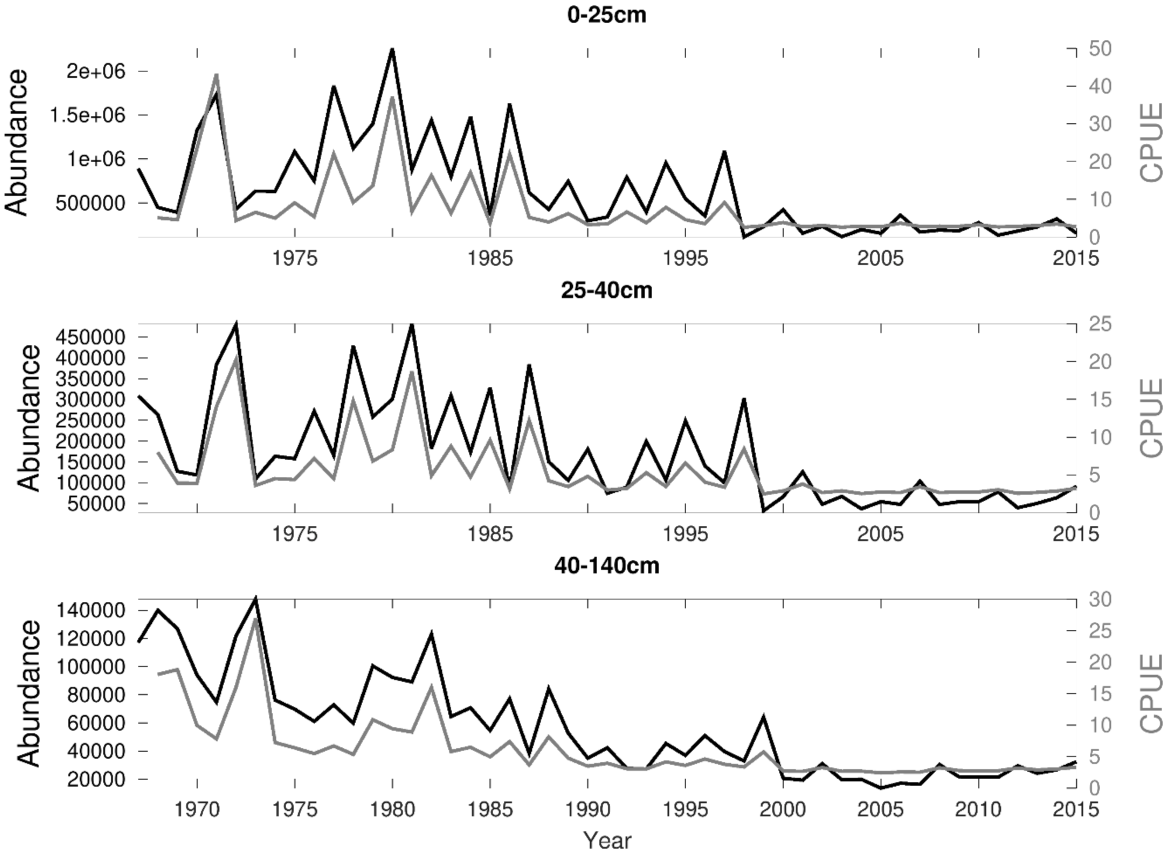

Figure S2. *Comparison between cod abundance (number of fish in thousands) from ICES stock assessment (black curves; left scale) and year partial effect from habitat model (median CPUE per grid point; no equation shown in the paper, but calculated with an equation similar to 6 and 7) in the North Sea (grey curves; right scale) for* $LC_{0\text{-}25}$ *(ages 0 and 1 year; top),* $LC_{25\text{-}40}$ *(2 years; middle) and* $LC_{40\text{-}140}$ *(3 years to 6 years; bottom panel).*

Q3 vs. Q1 temperature

We chose to model cod CPUE for the first year-quarter (Q1) because in comparison to the third quarter (Q3; July, August, September), which are only from 1991 to 2015, the time series are longer. While the natural choice for temperature would also have been Q1, we tested the performance of the model with temperatures from other year quarters and annual mean as well. In the end, we chose Q3 over Q1 temperatures based on these two criteria:

1. AIC was smaller for Q3 in comparison to the Q1 temperatures (Table S2), indicating a better performance of Q3 temperatures;

2. The spatial distribution of Q3 temperature changes (Figure 2b) is similar to those of CPUE (see for instance Figure S1 and Section "Temperature partial effect" below), with strongest changes in the southern North Sea. On the contrary, Q1 temperature changes (no figure shown) were not statistically significant in the southern North Sea, which seems a consequence of large inter-annual variability of winter temperature in this region. In agreement with this result, Dye et al 2013 also found that most of their trends of bottom winter temperature in the southern North Sea were not significant (their Figure 12).

Table S2. *AICs for full habitat model (Equation 5) fed with bottom temperature from quarters Q1 and Q3 for all three length classes.*

	Length class		
Year quarter	**0-25cm**	**25-40cm**	**40-140cm**
Q1	55189.9	53643.8	51495.5
Q3	54200.4	52859.9	50950.1

A strong seasonal migration of cod would speak against our choice of Q3 over Q1 temperatures. For instance, if cod distribution patterns in Q1 and Q3 are too different, the use of Q3 temperature to model fish Q1 distribution is not justified. To shed some light onto possible seasonal migratory patterns of cod, we have compared decadal CPUE maps of Q1 (Figure S1) with those of Q3 (Figure S3) for the overlapping period 1991-2015. Even though cod is more abundant in Q3, the geographical distribution of relative abundance each decade (the minima and maxima) are similar. This is more clearly seen when plotting the CPUE variations from grid point to grid point (Figure S4) for each year quarter, as well as from the Pearson correlation between them (numbers in the upper part of each panel). Only for LC_{25-40} in the 1990s (panel b) the correlation is poor (0.24) with all other cases showing correlations equal to 0.5 ($LC_{40-1400}$ in the 1990s, panel c; LC_{25-40} in the 2000s, panel e) or larger, reaching 0.8 for LC_{0-25} (panel d) and LC_{40-140} (panel f) in the 2000s.

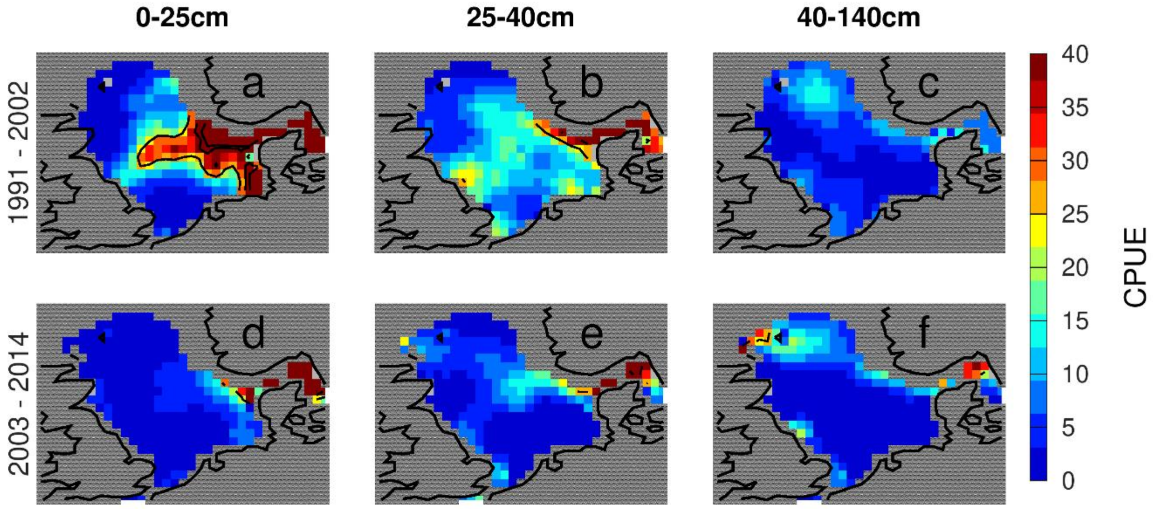

Figure S3. *As Figure S1 but for Q3 CPUE maps, 1991-2014.*

These notions speak of a moderate seasonal migration, with North Sea cod experiencing local temperatures in the North Sea all year long. This is possible in spite of the large range of temperatures observed in the North Sea throughout the year because cod tolerates a wide range of temperatures, from nearly freezing to approximately 20°C (Hedger et al., 2004; Neat and Righton, 2007). Therefore, the use of the Q3 temperature in our habitat model is justified.

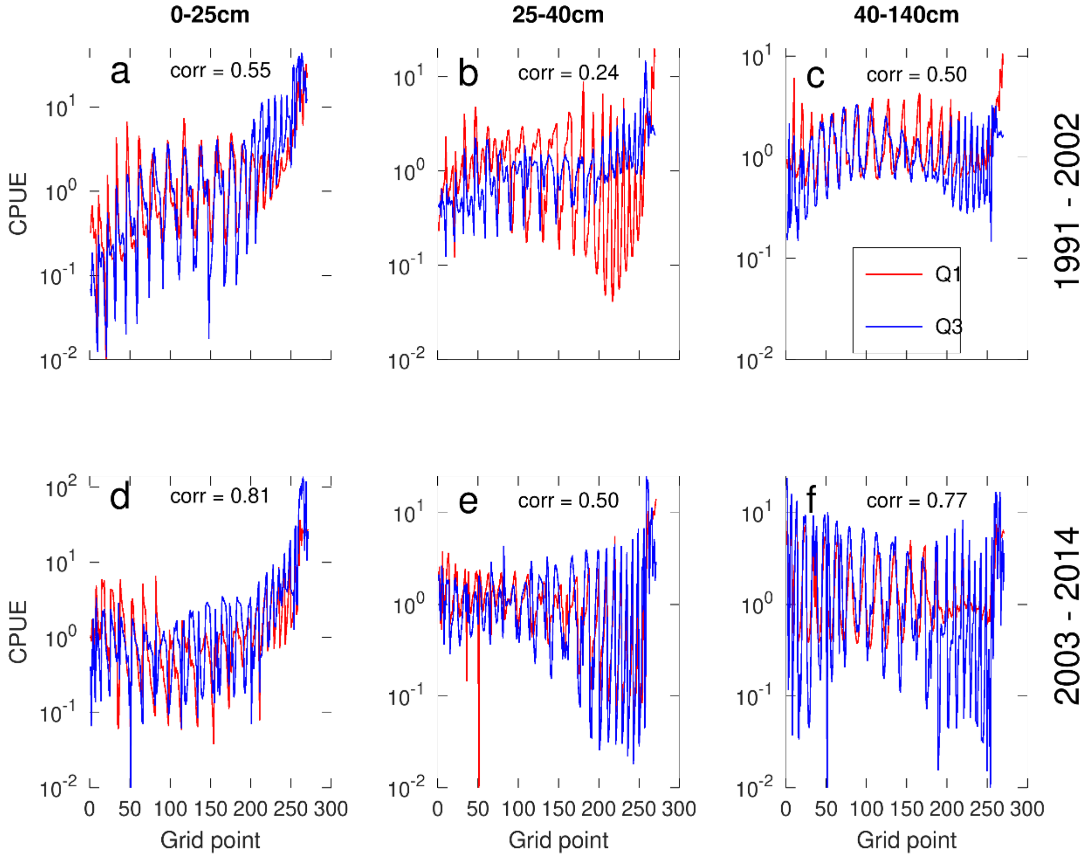

Figure S4. *Variations of abundance from grid point to grid point from the CPUE maps (Equation 2) for Q1 (red curves) and Q3 (blue curves) surveys for small (left panels), medium (middle panels) and large (right panels) cod and for the two decades (roughly the 1990s, top panels, and the 2000s, bottom panels) of overlapping data. The Pearson correlation between detrended data is shown in the upper part of each panel. The y-axis is logarithmic.*

Considering the response variable belongs to Q1, use of Q3 temperatures in the model is only possible with a lag of 6 months, either negative (i.e., previous summer) or positive (next summer). Testing the model with both lags yielded almost identical results. We opted for the negative six-month lag because the positive lag is related to temperatures not yet experienced by fish and seemed, thus, misleading. An explanation for the insensitivity of our model to one or the other six-month lag might be found on the time scales involved. While the inter-annual signal could differ in as much as 1ºC from one year to the other (for a particular position), the climate signal remains comparatively steady, changing only slowly from one year to the next one order of 0.1ºC. If our analysis effectively filters inter-annual variability and focus mostly on changes at climate scale, lags of ±6 months are insignificantly small (basically indistinguishable from zero).

The Q3 temperature yielding more reasonable results that Q1 seems to point to a specific underlying mechanism: Cod is a boreal species which, in the North Sea, is living on the southernmost boundary of its habitat. While in winter, North Sea cod would experience in average temperatures on a physiologically comfortable range, the Q3 temperatures being the maximum temperature cod is exposed during the year would play the decisive factor on limiting its spatial distribution southwards.

Degrees of freedom

The degree of smoothness of scatter plot smoothers like s_M is optimized during the model fitting by penalizing its "wiggliness" (the integral of the second derivative of s_M). Instead of solving for the full rank model matrix arising from the n observations, the fitting procedure is simplified by an appropriate eigen-decomposition. By choosing only the major k elements (with $k \leq n$) of the eigen-decomposition, the smoother is replaced by an approximation of rank k. Therefore, a large k gives the model $\hat{y}$ a large level of complexity, explaining more variance than a model with small k. A model with $k=n$ should exactly fit all n observations.

There is no objective way of choosing k (Wood, 2017), which remains part of model design. To choose k for the CPUE maps $s_M(lon, lat)$, we tested various values of k as a fraction of N, being $k=N/5$ a good balance between computational economy and parsimony of the modelled CPUE estimates. Depending on the number of data each year, such relation resulted on k values ranging from roughly 20 to 100. Because the CPUE maps are eventually used as input of the habitat model, the choice of k for s_M showed to be relatively irrelevant, contrary to the cases of s_{R1} and s_{R2}. For these, we chose $k = 150$. Larger values did not visibly change their graphics.

The temperature term in our model is given by a parametric part $\boldsymbol{B \cdot X}$ (Equation 3), associated to a Gaussian bell (Equation 5) and having implicitly a fixed number of degrees of freedom of 3. The decision to use $\boldsymbol{B \cdot X}$ over the more flexible scatterplot smoothers was based on two criteria: A) When using covariate values beyond the range used to fit the model, spline smoothers can give quite unrealistic predictions. $\boldsymbol{B \cdot X}$ seems more appropriate for future projections where possibly non-precedent temperature could be experienced. B) The smaller wiggliness of $\boldsymbol{B \cdot X}$ presenting a single maximum is more realistic than spline smoothers, which (if k is not explicitly chosen otherwise) present two or more local maxima.

Such various optimal values arising from too wiggly temperature preference curves result in unrealistic modelled changes of abundance under climatic trends, with, for instance, multiple cycles of increase and decrease of abundance for a single and constant temperature increase.

This lack of flexibility consciously chosen for our temperature preference curve $\boldsymbol{B}\cdot\boldsymbol{X}$ seems to be novel for the modelling of cod habitat in the North Sea. All previous studies modelled the relation between fish abundance and temperature based on scatterplot smoothers: Hedger et al. (2004) used the lowess suggested by Hastie and Tibshirani (1986), while all other used the penalized splines put forward by Wood (2017). They chose the degrees of freedom of their smoothers either arbitrarily (Hedger et al., 2004) or based on statistics of optimal parsimony like the AIC (Kempf et al., 2013; Engelhard et al., 2014; Nicolas et al., 2014). While such statistics are the only choice in the absence of further information, mathematical functions resembling known underlying biological or physical characteristics build more realistic models. We confirmed this notion by replacing $\boldsymbol{B}\cdot\boldsymbol{X}$ with a penalized spline of temperature with $k=10$. The larger wiggliness of the temperature spline resulted in unrealistic predictions, with CPUE growing unbound to infinity with increasing temperature instead of reaching a maximum for an optimal or preferred value.

Temperature partial effect

The cross-validation described in the main body of the paper is a useful tool to show the robustness of our complete model. However, there are two specific choices in our equation of the thermal habitat (Equation 8) which call for some additional validation: 1) the use of a Gaussian bell to model the temperature dependence, in contrast to the more popular penalized spline and 2) average of all covariates different than temperature to predict with a partial effect of temperature alone. This issue lies beyond the scope of classical model design (choice of number of degrees of freedom, covariates and functional form of the model) and is, thus, not evaluable with AIC or cross-validation.

While the choice of averaging covariates to estimate a partial effect could be intuitive for some readers, there are some other options to estimate a partial effect as well which call for a clarifying validation. Some of those options are reasonable as well (averaging all model terms not containing temperature on the scale of the linear predictor or the response) but some other are categorically wrong (ignoring all model terms not containing temperature and evaluating all model terms different than temperature on zero). However, a cross validation does not help to validate our temperature partial effect because there are no direct observations of the effect of temperature alone on cod's abundance. To estimate a proxy of such effect, CPUE maps were spatially and temporally scaled, partially removing space and time preferences of cod and isolating the influence of temperature alone as follows:

First, to obtain smooth representations of the CPUE fields stressing only the long-term climatic trends (and not short-scale spatial or inter-annual variations), a low-passed version of the CPUE maps were used by intentionally choosing a small spline basis dimension (k = 6; see Section "CPUE maps"). Second, denoting with $CPUE_{ijt}$ the CPUE value for grid point (i, j) and year t from these smooth CPUE maps, abundance was scaled with:

$$cpue_{ijt} = \frac{CPUE_{ijt}}{\overline{CPUE_{ij}} \cdot \overline{CPUE_t}}$$

where the over-line denotes the median, which was taken over all years for each grid point (i,j) in $\overline{CPUE_{ij}}$ and over all grid points for each year *t* in $\overline{CPUE_t}$. To make scaled $cpue_{ijt}$ and non-scaled CPUE comparable, the medians of both datasets were matched by:

$$cpue'_{ijt} = \frac{\overline{CPUE}}{\overline{cpue}} \cdot cpue_{ijt}, \qquad \text{(S1)}$$

where the medians were taken here over the whole data sets. This final scaling was needed to compare both data sets in a scatter plot.

These scatter plots are shown in Figure S5 (black dots) together with the non-scaled CPUE (yellow dots). The modelled temperature partial effect (red curve), with maxima at roughly 10.5°C, does not completely match the distribution of scatter plots of CPUE against temperature with maxima at ca. 8°C. The reason is that in the CPUE scatter plots not only the effect of temperature but also the temporal CPUE variations of the complete stock and the geographical attachment are present.

In other words, large CPUE values near 8°C correspond to early cold years (1970s and 1980s) and to the cold region Kattegat/Skagerrak, where cod is particularly abundant. In agreement with this notion, the scatter plot of scaled cpue' (black dots in Figure S5; Equation S1) shows smaller abundances near 8°C and larger abundances for higher temperatures than the scatter plot with non-scaled CPUEs (yellow dots). Roughly, the cpue' scatter clouds are centred at 12°C, which is in better agreement with the model temperature curves. Therefore, the habitat model seems to correctly eliminate spatial and temporal preferences, effectively isolating the effect of temperature alone.

A further assessment of the temperature partial effect is obtained by subtracting an average of cpue' in the first decade (1967-1977) from the average of the last decade (2005-2015), which results in the spatial historic changes of cod abundance (Figure S6). For $LC_{0\text{-}25}$ (panel a), there is a decrease of cpue' in the south-east (strongest in the German Bight) and an increase off the western North Sea (maximum in the eastern coast of Scotland), southern Skagerrak and Kattegat. $LC_{25\text{-}40}$ (panel b) and $LC_{40\text{-}140}$ (panel c) show both decrease of cpue' south of ca. 57°N (strongest in the Southern and German Bights) and an increase of cpue' north of 57°N (strongest in the northern North Sea).

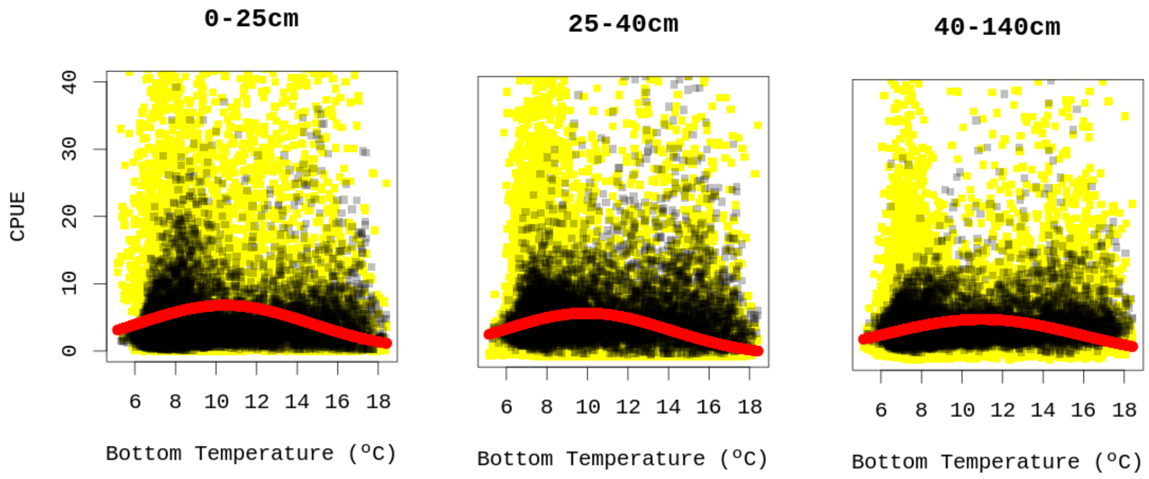

Figure S5. *Scatterplots of CPUE (yellow dots; Equation 2) and scaled abundance cpue' (black dots; Equation S1) against bottom temperature for $LC_{0\text{-}25}$ (left), $LC_{25\text{-}40}$ (middle) and $LC_{40\text{-}140}$ (right). The red curves show the partial temperature effect of the habitat model (Equation 6).*

$LC_{0\text{-}25}$ presents some differences between the observed cpue' and modelled thermal habitat changes, with cpue' showing a strong increase in the western North Sea, which was not predicted by the model. Additionally, there is some decrease in cpue' in the north-eastern North Sea, a region where the model predicts a suitability increase. A reason for these differences could be changes of juvenile cod abundance not related to temperature alone but, for instance, to prey availability and predation pressure. Additionally, the scaled cpue' might only be a rough approximation of the temperature partial effect, since signal and noise are not as effectively split as with the model, and cpue' cannot deal with spatial biases (see "Spatial biases of IBTS data" below). Albeit these differences, the general match between model (Figure 6abc) and observations (Figure S6) is fair, with $LC_{25\text{-}40}$ and $LC_{40\text{-}140}$ showing encouraging consistency: The regions of decrease and increase of thermal habitat roughly match those of observed cpue' changes, with the latter showing an isoline of zero change (black contour) only slightly farther to the north (ca. 57°N) than the former (ca. 56°N).

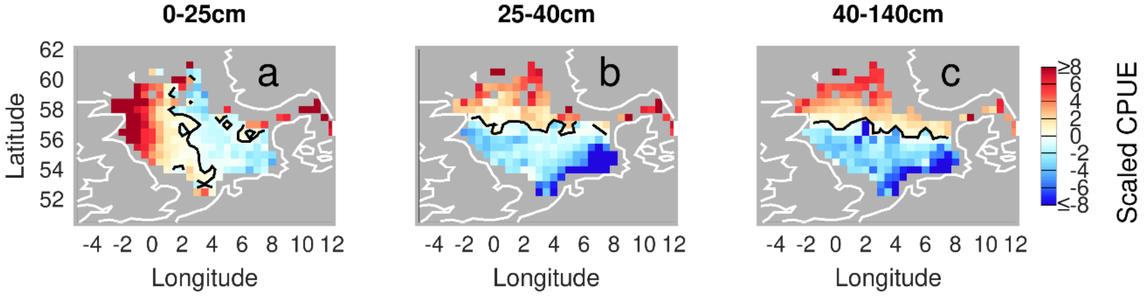

Figure S6. *Changes of observed scaled CPUE (i.e., cpue', Equation S1; CPUE per grid cell) of North Sea cod between the decade 1967-1977 and the decade 2005-2015 for $LC_{0\text{-}25}$ (a), $LC_{25\text{-}40}$ (b) and $LC_{40\text{-}140}$ (c). Red tones represent cpue' increase, blue tones a decrease. Unchanged cpue' is stressed with a thick black contour.*

Spatial biases of IBTS data

The spatial distribution of IBTS samples has changed some times since the survey started in 1965. In 1965 and 1966 (not used in the present study), the study region was only the south-central North Sea. From 1967 to 1970, the survey was extended to the whole North Sea south of 58°N and from 1971 to 1973 to 60°N (in both cases excluding the Southern Bight).

Only from 1974 on, the IBTS reached almost its present sampling distribution, spanning the complete North Sea and part of the European continental shelf, with the only exception of the Southern Bight which was included only in the 1980s. These geographical changes in the sampling area could induce regional biases in analyses of IBTS data, particularly if the complete geographical extension of the fish stock is relevant (for instance, for the calculation of a stock's center of mass). However, our separation of temperature and year effect relies little on the complete extension of the cod stock and much more on local comparisons (and their evolution with time) between abundance and temperature changes on small space scales. Moreover, GAMs should be able of optimally assessing the relative importance of all covariates involved in a model even if the input data are not homogeneously distributed in space and time. Because of this, they have become a popular method for elimination of such bias (i.e., standardization) in fishery studies in the last years, like estimates of abundance indices (Venables and Dichmont, 2004).

To verify that changes of the distribution of IBTS samples did not influence our results, we have repeated our analysis with the shorter time series 1974-2015, i.e., a period where the survey region was almost the present one. Because preferred temperature, geographical attachment, suitability changes, etc., obtained with this shorter record (no figure shown) were very similar to those obtained with the record 1967-2015, possible sampling regional bias do not seem to be an issue in our analysis. The reason why we rejected years 1965 and 1966 of IBTS data was not the risk of a regional bias, but the impossibility of fitting thin plate splines to the few data points available those years.

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Publication 2. - *Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea*

Appendix

Part A of the Appendix outlines the construction and parameterization of Ecospace. The food web of the southern North Sea and their associated fleets in Ecopath and Ecosim are introduced. Furthermore, changes to the original Ecopath and Ecosim models will be depicted. Part B focusses on the structure and comparison of the assessed single species distribution models (SDMs) and on the skill assessment following the Ecospace runs.

Appendix A

A1 Ecopath and Ecosim of the southern North Sea – structure and adaptations

The Ecospace model of the southern North Sea is based on the southern North Sea Ecopath and Ecosim constructed and published by Stäbler et al. (2016). The area of interest for this study is the southern North Sea, which encompasses areas IVb and IVc defined by the International Council for the Exploration of the Sea (ICES, Figure A1). It is bordered by France, Belgium, Netherlands, Germany, Denmark and the UK and spans the area of 51° to 56° N and 4° to 9° W. Compared to the northern part, the southern North Sea is characterized by its shallow seafloor with community defining depth contours with maximum depth just below 100 m (Neumann et al., 2012). Being enclosed by several countries, it is governed by strong land-based and anthropogenic influences (Emeis et al., 2015). The food web of the southern North Sea Ecopath model encompasses 68 functional groups (FGs) and 12 fleets (Figure A2).

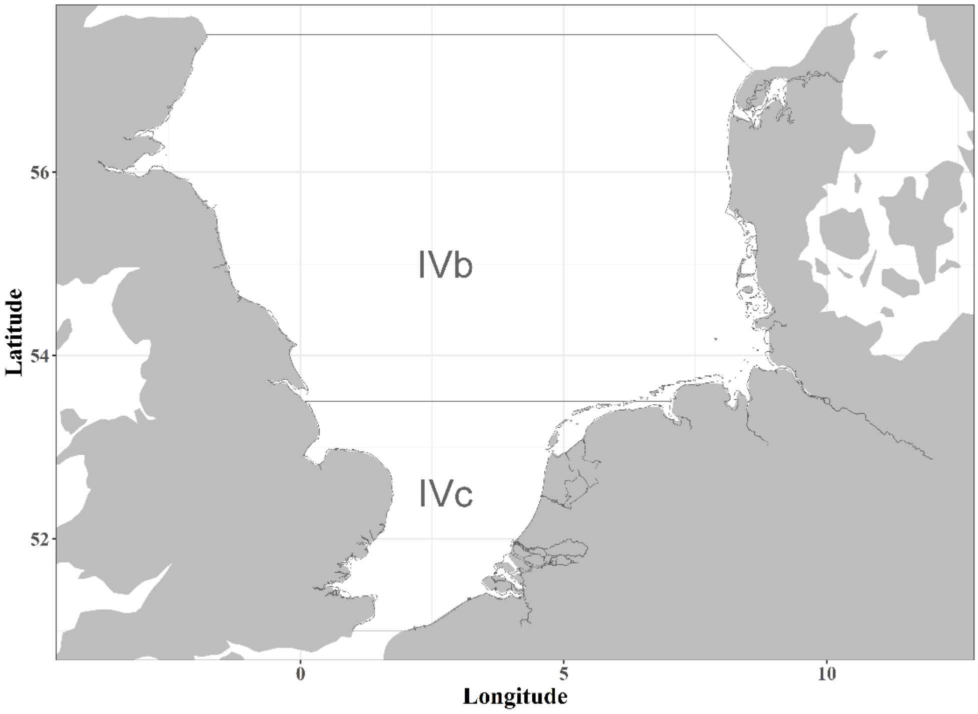


Figure A1: *ICES areas IVb and IVc in the study area southern North Sea*

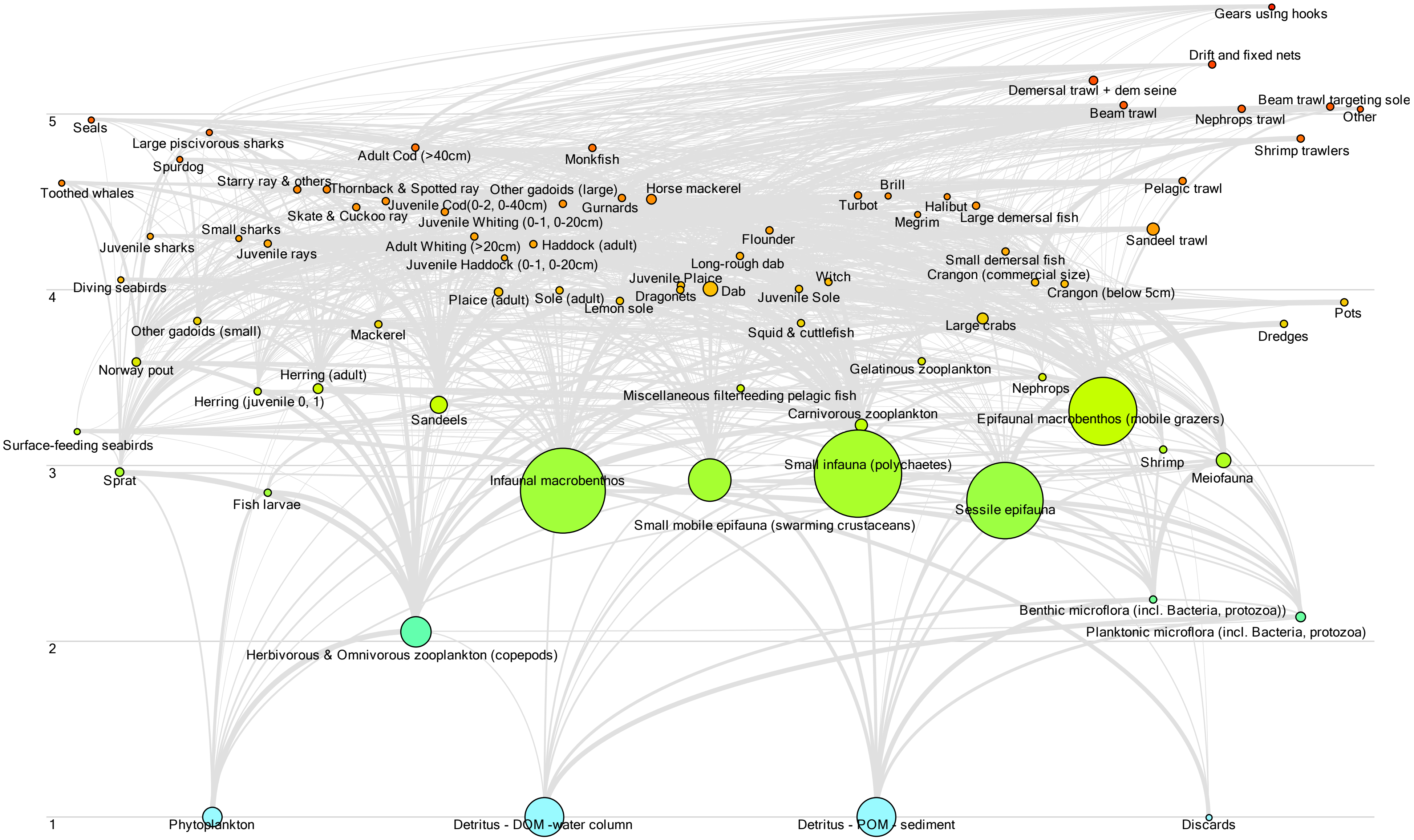


Figure A2: *Foodweb of the southern North Sea Ecopath model (modified from Stäbler et al. 2016)*

Changes in the diet matrix to the original Ecopath model

One change was made to the Ecopath diet matrix of the original model. Distributions based on the single species distribution models of flounder and lemon sole do not overlap, which led to a mismatch between these two groups. Therefore, lemon sole was removed as prey species, the remaining diet proportions were allocated among the remaining prey to the main prey of Flounder (Table A1). The removal of lemon sole as prey species was justified by information found at the Centre for Environment, Fisheries and Aquaculture Science fish stomach records (Pinnegar, 2014; data for ICES area IVb; checked predators of lemon sole as well as prey for flounder for all available years).

Table A1: *Changes in Ecopath diet matrix for flounder*

Functional groups (prey)	*Flounder diet proportions (Stäbler et al., 2016)*	*Current Flounder diet proportions*
Norway pout	0.050120	0.050120
Dab	0.069028	0.069028
Long-rough dab	0.050120	0.050120
Lemon sole	**0.050120**	**-**
Small demersal fish	0.011505	0.011505
Carnivorous zooplankton	0.058777	0.058777
Gelatinous zooplankton	0.081217	0.081217
Large crabs	0.055701	0.055701
Epifaunal macrobenthos (mobile grazers)	**0.255154**	**0.300000**
Infaunal macrobenthos	0.081217	0.081217
Crangon (commercial size)	0.000711	0.000711
Crangon (below 5cm)	0.001858	0.001858
Shrimp	0.004949	0.004949
Small mobile epifauna (swarming crustaceans)	**0.173824**	**0.179100**
Sessile epifauna	0.055701	0.055701

Off-vessel prices

Off-vessel prices of 2012 based on Fleet Landings provided by the Scientific, Technical and Economic Committee for Fisheries of the European Union were added for all commercially caught species (https://stecf.jrc.ec.europa.eu/dd/fleet, data downloaded 23 Main 2018; STECF, 2017). For those Ecospace fleets that encompass multiple gears (for more information see Stäbler et al. 2016) a mean of euro/kg was calculated. Within multi-species FGs, off-vessel values were weighted by the kg caught per fleet for each species within a group.

Table A2: *Off-vessel prices based on fleet landings for 2012 provided by the Scientific, Technical and Economic Committee for Fisheries of the European Union (STECF, 2017). Only FGs are shown, where they were applied*

Group name	*Demersal trawl + dem seine (EUR/biomass)*	*Beam trawl (EUR/biomass)*	*Sandeel trawl (EUR/biomass)*	*Pelagic trawl (EUR/biomass)*	*Drift and fixed nets (EUR/biomass)*	*Nephrops trawl (EUR/biomass)*
Spurdog	1.602093	2.231706		1.389434	1.70168	1.503244
Large piscivorous sharks	1.82784	0.6491689	1.681429		1.82723	1.404602
Small sharks	0.5702031		0.4765128		0.6599286	
Adult Cod (>40cm)	2.370303	2.40002	1.373999	2.409081	2.180955	2.056369
Adult Whiting (>20cm)	1.316794	1.120327	0.9194963	1.740831	1.762957	1.251771
Haddock (adult)	1.201036	1.476984	1.287451	1.29391	1.831697	1.199078
Norway pout			0.3269052	0.3331458		

Other gadoids (large)	2.082459	1.868755	1.876978	2.637739	3.082302	2.050151
Other gadoids (small)	0.5864441		0.54614	0.5666319	0.7950617	
Monkfish	3.968251	3.672598	3.951586	3.867873	3.965267	4.095528
Gurnards	0.5308685	0.417043		0.6748638	0.5577391	0.5200904
Herring (adult)	0.4601667	0.2634467	0.4652692	0.5424947	0.4326603	0.5058105
Sprat	1.134176		0.2759225	0.4266819	0.9242831	
Mackerel	1.366012	1.058645	1.169805	1.023193	2.036118	1.189909
Horse mackerel	0.8165568	1.238734	0.8312947	0.7144159	1.773651	0.9463005
Sandeels			0.25288		1.679788	
Plaice (adult)	1.435053	1.429623	1.318862	1.443848	1.70579	1.400857
Dab	0.7906748	0.7714989	0.5709012	0.5072053	0.772067	0.6824694
Long-rough dab	2.229035		1.344188	0.4593421	1.82	2.229035
Flounder	0.5582428	0.7144545	0.6207421	0.7419149	0.8832374	0.5169769
Sole (adult)	10.57175	9.624049	10.14384	10.63468	10.48039	10.84959
Lemon sole	3.433095	3.362326		3.27021	3.920261	3.479328
Witch	2.378651	1.693416	2.277209	4.708484	3.919184	1.803825
Turbot	9.491598	7.961926				9.517753
Brill	7.170107	5.930018				6.883293

Megrim	2.973	0	2.609	1.948	2.536	2.766
Halibut	11.51526	12.2928	8.620918	10.31255	11.01466	10.09303
Dragonets						
Large demersal fish	1.321	2.769	1.078	1.002	1.416	1.273
Miscellaneous filterfeeding pelagic fish	0.837	0.301		1.848		
Squid & cuttlefish	4.514976	2.37306		4.36817	4.338581	4.012579
Large crabs	0.000836	0	0	0	1.180712	0
Nephrops	6.910444	4.712785	5.58903	7.931822	10.92764	5.831424

Group name	*Gears using hooks (EUR/biomass)*	*Shrimp trawlers (EUR/biomass)*	*Dredges (EUR/biomass)*	*Beam trawl targeting sole (EUR/biomass)*	*Pots (EUR/biomass)*	*Other (EUR/biomass)*
Spurdog	1.095538			2.231706	0.7940434	
Large piscivorous sharks	2.203467				2.830829	
Small sharks					0.8682665	
Adult Cod (>40cm)	2.776396	2.40002	3.072098	2.40002	1.605768	2.101
Adult Whiting (>20cm)	2.824853	1.120327	0	1.120327	1.866959	
Haddock (adult)	2.448631	1.476984	1.198035	1.476984	1.064428	
Norway pout						
Other gadoids (large)	3.288357	1.868755	3.597486	1.868755	3.563817	2.636646
Monkfish	3.837	3.672598	3.631805	3.672598	4.059411	
Gurnards				0.417043	0.5196719	0.5943322
Herring (adult)	0.7370235	0.2634467	0.6163292	0.2634467	0.3446072	
Sprat	2.111515	0.2676785	0	0.2676785		
Mackerel	2.072991	1.058645	3.302226	1.058645	1.653664	0.8174385
Horse mackerel		1.238734	0.4736837	1.238734	0.5405525	
Sandeels		0.2591452	1.440999			
Plaice (adult)	2.317021	1.429623	1.297473	1.429623	1.992328	1.289657
Dab	1.093107	0.7714989	0.8107895	0.7714989	0.9131315	0.8720052

Flounder	0.5683023	0.7144545	0.3401459	0.7144545	1.133294	
Sole (adult)	14.07062	9.624049	13.14747	9.624049	11.22222	10.39131
Lemon sole	3.306719	3.362326	3.476121	3.362326	2.114121	3.351682
Witch	0		0	1.693416	1.246457	2.646735
Turbot				7.961926		
Brill				5.930018		
Megrim	5.731		4.522	1	0	
Halibut	15.04118		14.67385	12.2928	0	3.764653
Large demersal fish	1.571	2.769	1.441	2.769	0.94	1.2
Squid & cuttlefish	5.575154		4.332314	2.37306	2.761833	4.430097
Large crabs	0.7991649	0	0.908421	0	2.022612	0
Nephrops	9.6983	4.712785	4.760348	4.712785	10.43091	4.987189
Crangon (commercial size)		3.367053				

Adaptations of reference time series implemented in Ecosim

To the fitting and parameterization of the Ecosim model underlying the simulations used in Stäbler et al. 2016 and Stäbler et al. 2019, several updates to the compilation of biomass and catch time series have been undertaken. In addition to the procedures outlined in Appendix C of Stäbler et al. 2016, the following adjustments were made to the underlying Ecosim model in this study:

For stocks, whose distributions extend beyond the limits of the model domain (adult and juvenile cod, whiting and haddock), the fraction of the total assessment-derived biomass attributable to ICES divisions IVb & c was used in the model. These fractions were based on the quarterly distribution upon both areas in the IBTS. However, the sampling within all four quarters only took place for a short period of time (1991-1996) and is therefore not representative of the three species in IBTS past 1996 for the second and fourth quarter. For those years (1996 - 2010), the total assessment's biomasses were hence split into a southern North Sea and a rest portion based on IBTS data from quarters 1 and 3 only. Biomass time series have been updated for Turbot and Brill based on the recent SPiCT assessment models (ICES, 2017 and 2018; Figure A2). The estimated catch of brown shrimps in the time series underlying the above-mentioned studies was taken from data of Temming and Hufnagl (2015). These data have been replaced with catch data from the 2013 report of the ICES Working Group on Crangon Fisheries and Life History (WGCRAN, 2013; Figure A3).

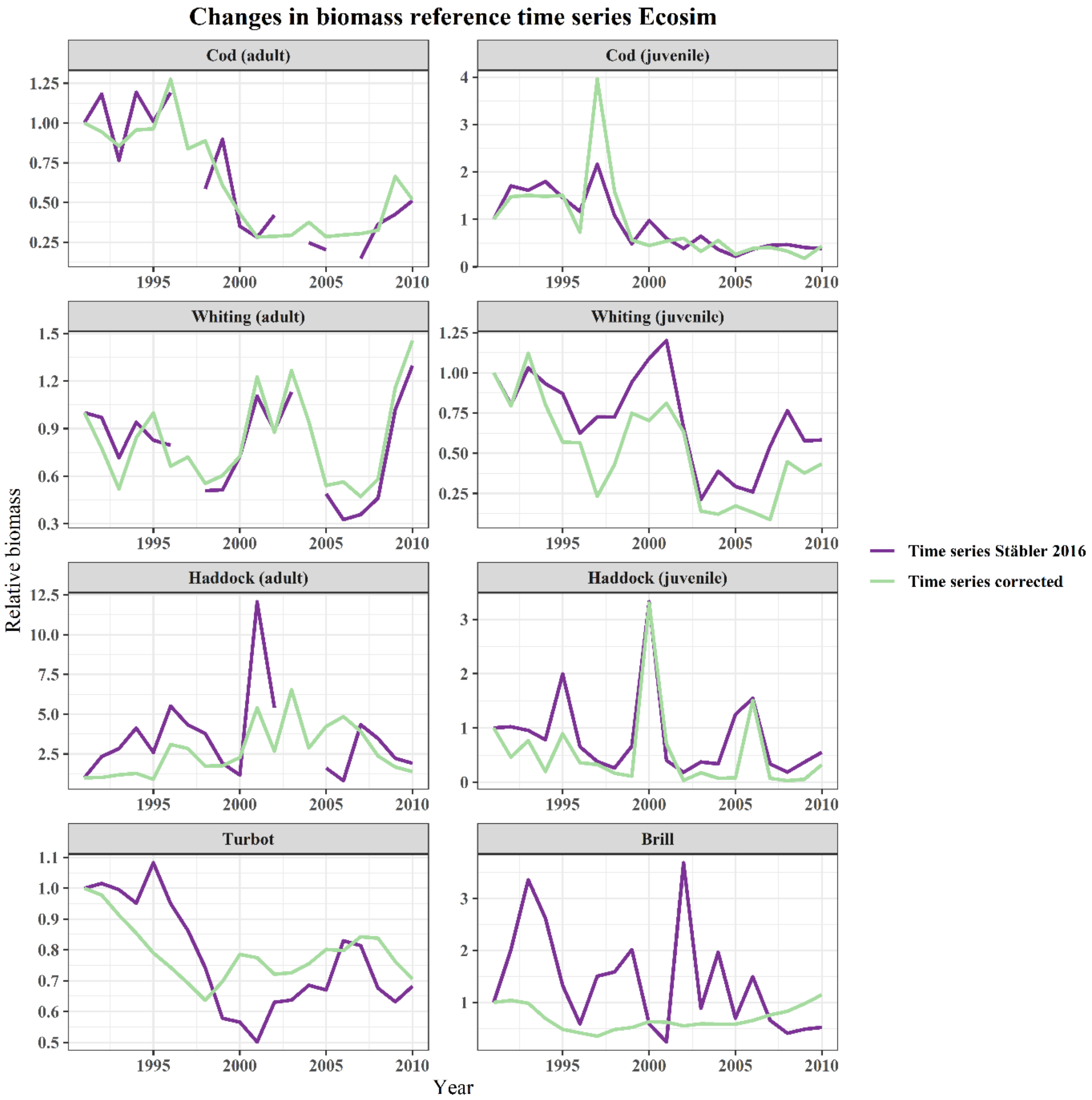


Figure A3: *Changes in reference biomass time series included in Ecosim. For cod, haddock and whiting (both stanzas) without Quarter 2 and Quarter 4 IBTS 1991-1996. For Turbot and Brill corrected after SPiCT analysis published in Turbot benchmark (ICES, 2018) and Brill advice (2017).*

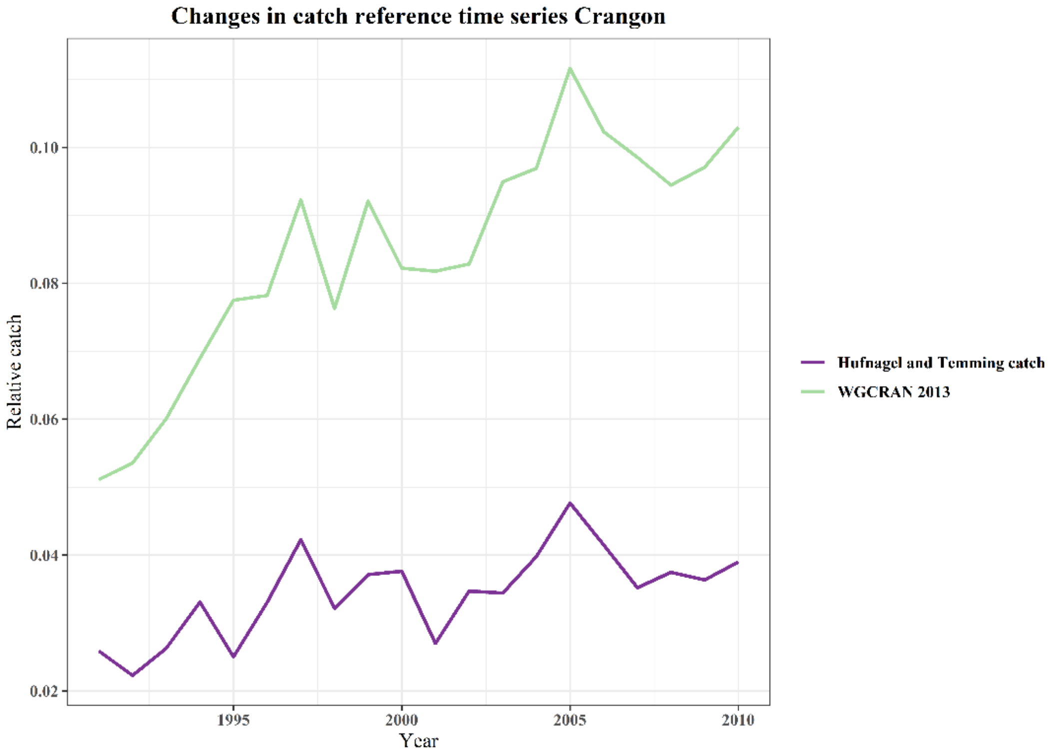


Figure A4: *Adaptations of relative catch reference for Crangon crangon based on WGCRAN 2013.*

Fitting of vulnerabilities

Vulnerabilities were adapted to the changes in the reference time series mentioned before by running the automated fitting routine. To find the settings that best describe the observed time series in Ecosim, this routine tests different parameterizations of vulnerabilities and primary production anomaly splines (Scott, 2016). The best three parameterizations with the lowest AIC (Akaike, 1974) were also compared for their sum of squares and model efficiency, as well as looking for the most parsimonious approach (Table A3). Taking all metrics into account, the parameterization with 30 fitted vulnerabilities and a primary production anomaly with four spline points was chosen and the resulting vulnerabilities applied to Ecosim and Ecospace (Table A4). High vulnerabilities were limited to a maximum value of 10 in order to decrease instabilities in the system.

Table A3: *Best results of the automated fitting routine for vulnerabilities. Settings with the lowest AICs (smallest AIC and difference to this AIC <=2) are depicted. A black box marks best results for all tested metrics.*

Name	*Sum of Squares*	*AIC*	*K*	*MEF biomass above threshold*	*Nr. biomass MEF above threshold*	*MEF catch above threshold*	*Nr. biomass MEF above threshold*
Fishing and 29v + 4pp	427.3713	-2455.29	33	0.3496	23	0.5105	21
Fishing and 30v + 2pp	428.2654	-2453.661	32	0.3282	21	0.5059	21
Fishing and 30v + 4pp	427.2775	-2453.6	34	0.3507	23	0.5116	21

Table A4: *Vulnerabilities adapted changes in the time series and diet matrix. The automated fitting routine indicated 30 fitted vulnerabilities and a four-point spline anomaly of the primary production as the best settings.*

Prey \ predator	*Toothed whales*	*Seals*	*Surface-feeding*	*Diving seabirds*	*Juvenile sharks*	*Spurdog*	*Large piscivorous*	*Small sharks*	*Juvenile rays*	*Starry ray & others*	*Thornback & Spotted*	*& Skate Cuckoo ray*	*Juvenile Cod(0-2, 0-*	*Adult Cod (>40cm)*	*Juvenile Whiting (0-*	*Adult Whiting*	*Juvenile Haddock (0-*	*Haddock (adult)*
Toothed whales																		
Seals																		
Surface-feeding seabirds																		
Diving seabirds																		
Juvenile sharks							2											
Spurdog						10	2											
Large piscivorous sharks																		
Small sharks							2											
Juvenile rays							2											
Starry ray & others														2				
Thornback & Spotted ray														2				
Skate & Cuckoo ray																		
Juvenile Cod (0-2, 0-40cm)	2	2	2	2					2	2			2	2	2	2		2
Adult Cod (>40cm)		2												2				

Juvenile Whiting (0-1, 0-20cm)	2	2	2	2	2	2		2		2	2	2	2	2	2	2		
Adult Whiting (>20cm)	2	2			2	1		2		2				2		2		
Juvenile Haddock (0-1, 0-20cm)	2	2	2	2		2					2	2	2	2	2	2		2
Haddock (adult)	2	2				2								2				
Norway pout	2		2	2	2	1	2	2	2	2	2	2	2	2	2	2		2
Other gadoids (large)	2	1	2	2														
Other gadoids (small)	2	2		2	2	1	2	2	2	2	2	2	2	2	2	2		2
Monkfish		2										2						
Gurnards				2			2	2		2		2	2	2	2	2		2
Herring (juvenile 0, 1)	2	2			2	2	2			2	2	2	2	2	2	2		2
Herring (adult)	2	2	2	2	2	1	2	2		2			2	2				
Sprat	2	2	2	2	2	2		2	2	2	2		2	2	2	2		2
Mackerel	2		2	2	2	1	2	2						2				
Horse mackerel	2	2				2							2	2	2	2		
Sandeels	2	2	2	2	2	2		2	2	2	2	2	2	2	2	2	1	1
Plaice (adult)		2					2	2			2			2				
Juvenile Plaice			2	2									2	2				2
Dab		2		2	2	2	2	2	2	2		2	2	2	2	2		
Long-rough dab	2	2						2	2	2		2	2	2	2	2	2	2

Flounder		2												2				
Sole (adult)		2						2			2	2						
Juvenile Sole			2							2			2	2	2	2	2	2
Lemon sole		2													2			
Witch		2				2				2		2		2	2			
Turbot		2																
Brill		2																
Megrim		2																
Halibut										2								
Dragonets	2	2			2	2	2	2		2		2	2	2	2	2	2	2
Large demersal fish			2	2								2	2	2		2		
Small demersal fish	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Miscellaneous filterfeeding pelagic fish			2		2			2					2	2	2	2		
Squid & cuttlefish	2		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Fish larvae																		
Carnivorous zooplankton			2	2	2			2	2	2	2	2	2	2	2	2	1	1
Herbivorous & Omnivorous zooplankton (copepods)			2	2						2			2		2	2	2	2
Gelatinous zooplankton					2								2	2	2	2	2	2

Large crabs	2	2	2	2		2	2	2	2	2	2	2	2	2	2	2
Nephrops			2	2		2				2	2	2		2	2	2
Epifaunal macrobenthos (mobile grazers)	2		2		2	2	2	2	2	2	2	2	2	2	1	10
Infaunal macrobenthos	2	2	2			2	2	2	2	2	2	2	2	2	2	2
Crangon (commercial size)			2			2	2	2	2	2	2	2	2	2		
Crangon (below 5cm)	2		2			2	2	2	2	2	2	2	2	2	2	2
Shrimp	2		2	2		2	2	2	2	2	2	2	2	2	2	2
Small mobile epifauna (swarming crustaceans)			2			2	2	2	2	2	2	2	2	2	2	2
Small infauna (polychaetes)	2	2	2			2	2	2	2	2	2	2	2	2	1	10
Sessile epifauna	2	2	2			2					2	2	2	2	2	2
Meiofauna			2			2	2						2		2	2
Benthic microflora (incl. Bacteria, protozoa))															2	2
Planktonic microflora (incl. Bacteria, protozoa)																
Phytoplankton														2		
Detritus - DOM -water column																
Detritus - POM - sediment																

Discards			2	2

Table A4 (continued): *Vulnerabilities adapted changes in the time series and diet matrix. The automated fitting routine indicated 30 fitted vulnerabilities and a four-point spline anomaly of the primary production as the best settings.*

Prey \ predator	*Norway pout*	*Other gadoids*	*Other gadoids*	*Monkfish*	*Gurnards*	*Herring (juvenile 0,*	*Herring (adult)*	*Sprat*	*Mackerel*	*Horse mackerel*	*Sandeels*	*Plaice (adult)*	*Juvenile Plaice*	*Dab*	*Long-rough dab*	*Flounder*	*Sole (adult)*	*Juvenile Sole*
Toothed whales																		
Seals																		
Surface-feeding seabirds																		
Diving seabirds																		
Juvenile sharks																		
Spurdog																		
Large piscivorous sharks																		
Small sharks																		
Juvenile rays				2														
Starry ray & others																		
Thornback & Spotted ray					2													
Skate & Cuckoo ray																		
Juvenile Cod(0-2, 0-40cm)		2		2	2				2									

Adult Cod (>40cm)			2														
Juvenile Whiting (0-1, 0-20cm)	2	2	2	2				2	2					2			
Adult Whiting (>20cm)			1														
Juvenile Haddock (0-1, 0-20cm)	2		2	2				2	2								
Haddock (adult)			2														
Norway pout	2	2	1	2				2	2					2	2		
Other gadoids (large)	2																
Other gadoids (small)	2	2		2				2	2					2			
Monkfish			2														
Gurnards				2					2								
Herring (juvenile 0, 1)	2		2	2				2	2		2						
Herring (adult)	1		1														
Sprat		2	2	2				2	2								
Mackerel			2	2				2									
Horse mackerel				2				2	2								
Sandeels	1	2	1	2				2	2		2			2			
Plaice (adult)			2														
Juvenile Plaice																	
Dab		2	2	2					2					2	2		

Long-rough dab		2		2	2					2						2		
Flounder																		
Sole (adult)																		
Juvenile Sole																		
Lemon sole				2														
Witch				2	2													
Turbot																		
Brill																		
Megrim				2														
Halibut									2									
Dragonets			2	2	2					2								
Large demersal fish					2				2									
Small demersal fish		2	2	2	2				2	2					2	2	2	
Miscellaneous filterfeeding pelagic fish				2														
Squid & cuttlefish		2	2	2	2				2	2					2			
Fish larvae																		
Carnivorous zooplankton	2	2	2		2	2	2		2	2	2					2		
Herbivorous & Omnivorous zooplankton (copepods)	2	2	2		2	2	2	2	2	2	2			2				

Gelatinous zooplankton									2	2		2				2		
Large crabs		2	2		2				2	2		2	2	2	2	2		2
Nephrops			2	2	2				2						2			
Epifaunal macrobenthos (mobile grazers)			2	2	2				2	2	2	2	2	2	2	2	2	2
Infaunal macrobenthos	2		2		2				2	2	2	2	2	2	2	2	2	2
Crangon (commercial size)		2	2		2					2		2	2	2	2	2		
Crangon (below 5cm)		2	2		2				2	2		2	2	2	2	2		
Shrimp		2	2		2				2	2		2	2	2	2	2		
Small mobile epifauna (swarming crustaceans)	2	2	2		2	2	2		2	2	2	2	2	2	2	2		
Small infauna (polychaetes)		2	2		2				2	2	2	2	2	2	2		2	2
Sessile epifauna					2				2			2		2		2		
Meiofauna									2		2	2	2	2			2	
Benthic microflora (incl. Bacteria, protozoa))									2									
Planktonic microflora (incl. Bacteria, protozoa)								2			2							
Phytoplankton								2	2		2							
Detritus - DOM -water column																		

Detritus - POM - sediment	
Discards	

Table A4 (continued): *Vulnerabilities adapted changes in the time series and diet matrix. The automated fitting routine indicated 30 fitted vulnerabilities and a four-point spline anomaly of the primary production as the best settings.*

Prey \ predator	*Lemon sole*	*Witch*	*Turbot*	*Brill*	*Megrim*	*Halibut*	*Dragonets*	*Large demersal fish*	*Small demersal fish*	*Miscellaneous filterfeeding*	*Squid & cuttlefish*	*Fish larvae*	*Carnivorous zooplankton*	*Herbivorous & Gelatinous zooplankton*	*Large crabs*	*Nephrops*
Toothed whales																
Seals																
Surface-feeding seabirds																
Diving seabirds																
Juvenile sharks																
Spurdog																
Large piscivorous sharks																
Small sharks																
Juvenile rays																
Starry ray & others																
Thornback & Spotted ray																
Skate & Cuckoo ray																

Juvenile Cod(0-2, 0-40cm)	2	2		2					2
Adult Cod (>40cm)									
Juvenile Whiting (0-1, 0-20cm)	2	2		2		2			2
Adult Whiting (>20cm)						2			
Juvenile Haddock (0-1, 0-20cm)				2		2			2
Haddock (adult)						2			
Norway pout	10	2	2	2		2			2
Other gadoids (large)									
Other gadoids (small)	2	2	2	2		2			
Monkfish									
Gurnards			2				2		
Herring (juvenile 0, 1)	2	2				1	2		2
Herring (adult)						1			
Sprat	1	2	2	2			2		2
Mackerel									
Horse mackerel									2
Sandeels	1	2	2	2		2	2		2
Plaice (adult)									2

Juvenile Plaice																	
Dab			2	2				2	2		2						
Long-rough dab											2						
Flounder											2						
Sole (adult)									2		2						
Juvenile Sole																	
Lemon sole											2						
Witch											2						
Turbot																	
Brill																	
Megrim																	
Halibut																	
Dragonets			2	2	2				2								
Large demersal fish																	
Small demersal fish	2	2	1	2	2				2		2						
Miscellaneous filterfeeding pelagic fish					2					2	10						
Squid & cuttlefish						2		2	2	2	2				2		
Fish larvae											2		2		2		
Carnivorous zooplankton								2	2	2	2		2		2		

Herbivorous & Omnivorous zooplankton (copepods)					2		2		2	10	2	2	2		2		
Gelatinous zooplankton										2							
Large crabs					2	2	2		2							2	
Nephrops																	
Epifaunal macrobenthos (mobile grazers)	2	2	2	2	2	2	2	1	2	2						2	
Infaunal macrobenthos	2	2	2	2			2		2							2	2
Crangon (commercial size)			2	2	2	2	2	2	2	2	2				2	2	
Crangon (below 5cm)			2	2	2	2	2	2	2	2	2				2	2	
Shrimp			2	2	2	2	2	2	2	2	2				2	2	
Small mobile epifauna (swarming crustaceans)					2		2	2	2	2	2		2		2	2	2
Small infauna (polychaetes)	2	2					2	2	2	2	2					2	2
Sessile epifauna	2	2														2	2
Meiofauna							2		2								
Benthic microflora (incl. Bacteria, protozoa))																2	2
Planktonic microflora (incl. Bacteria, protozoa)													2	2	2	2	2

Phytoplankton	2	2	2	2		2
Detritus - DOM -water column			2			2
Detritus - POM - sediment						2
Discards					2	

Table A4 (continued): *Vulnerabilities adapted changes in the time series and diet matrix. The automated fitting routine indicated 30 fitted vulnerabilities and a four-point spline anomaly of the primary production as the best settings.*

Prey \ predator	*Epifaunal macrobenthos (mobile*	*Infaunal macrobenthos*	*Crangon (commercial size)*	*Crangon (below 5cm)*	*Shrimp*	*Small mobile epifauna (swarming*	*Small infauna (polychaetes)*	*Sessile epifauna*	*Meiofauna*	*Benthic microflora (incl. Bacteria,*	*Planktonic microflora (incl. Bacteria,*	*Phytoplankton*	*Detritus - DOM -water column*	*Detritus - POM - sediment*	*Discards*
Toothed whales															
Seals															
Surface-feeding seabirds															
Diving seabirds															
Juvenile sharks															
Spurdog															
Large piscivorous sharks															
Small sharks															

Juvenile rays	
Starry ray & others	
Thornback & Spotted ray	
Skate & Cuckoo ray	
Juvenile Cod(0-2, 0-40cm)	
Adult Cod (>40cm)	
Juvenile Whiting (0-1, 0-20cm)	
Adult Whiting (>20cm)	
Juvenile Haddock (0-1, 0-20cm)	
Haddock (adult)	
Norway pout	
Other gadoids (large)	
Other gadoids (small)	
Monkfish	
Gurnards	
Herring (juvenile 0, 1)	
Herring (adult)	
Sprat	
Mackerel	

Horse mackerel	
Sandeels	
Plaice (adult)	
Juvenile Plaice	2
Dab	
Long-rough dab	
Flounder	2
Sole (adult)	
Juvenile Sole	
Lemon sole	
Witch	
Turbot	
Brill	
Megrim	
Halibut	
Dragonets	
Large demersal fish	
Small demersal fish	2
Miscellaneous filterfeeding pelagic fish	
Squid & cuttlefish	

Fish larvae															
Carnivorous zooplankton					2										
Herbivorous & Omnivorous zooplankton (copepods)			2		2										
Gelatinous zooplankton															
Large crabs			2												
Nephrops															
Epifaunal macrobenthos (mobile grazers)	2		2												
Infaunal macrobenthos	2		2												
Crangon (commercial size)					2										
Crangon (below 5cm)			1	2	2										
Shrimp			2		2										
Small mobile epifauna (swarming crustaceans)	2	2	2		2	2									
Small infauna (polychaetes)	2	2	2		2		2								
Sessile epifauna			2												
Meiofauna		2	2	2	2	2	2		2						
Benthic microflora (incl. Bacteria, protozoa))	2	2			2	2	2		2	2	2				
Planktonic microflora (incl. Bacteria, protozoa)	2	2			2	2	2	2		2	2				

Phytoplankton	2							2							
Detritus - DOM -water column	2	2			2	2	2			2	2				
Detritus - POM - sediment	2	2			2	2	2	2	2	2	2				
Discards					2										

A2 Settings of Ecospace for the southern North Sea

Ecospace was run with the EwE6 multi-stanza model and Ecopath base biomasses were used for initialization. The grid cell size is 0.125° per cell edge length, resulting in 5355 grid cells. Cells that were disconnected to the rest of the map (by islands) were removed (Figure A5). To account for spatially resolved primary production, a reference layer was added to the basemap. Also added to the basemap was a depth layer, which serves as environmental driver map. Furthermore, sediment and distance to coast layers were used added as habitat maps. As reference for the distance to coast habitat layer the 12 nautical miles zone representing territorial waters was applied.

To distribute FGs on the basemap, either a habitat suitability was assigned (range 0-1), an environmental response function was applied or maps based on single species distribution models (SDMs) served as capacity directly (Table A5). The assigned suitability of habitat is based on literature references. For the multi-species groups *surface-feeding seabirds*, *diving seabirds*, *sandeels* and *meiofauna*, habitat proportions were chosen that encloses preferences for all species within these FGs towards sediment or distance to coast (Table A6). Functional responses for fish FGs are based on data reported in the Fish atlas of the Celtic Sea, North Sea, and Baltic Sea (Heessen, 2015). Depth ranges for all species enclosed in the FGs were taken into account, where data was available. Minimum and maximum of all depth ranges within one FG were used to calculate the mean depth. This mean depth was the depth that was assigned full capacity, decreasing from there to minimum/maximum depth (Figure A7).

For fleets that were not distributed based on the habitat of their targeted species (e.g. shrimp, nephrops and sandeel trawl) a fishing area was created and added as habitat layer just for fleets. Spatially resolved fishing effort data (https://stecf.jrc.ec.europa.eu/dd/effort, data downloaded 27 of March 2018; STECF, 2017) of the years 2004 to 2016 were used as reference. A binomial gam was applied to effort (effort = PA_{Eff}) and then predicted to the spatial resolution of Ecospace (Figure A6):

$$logit\left(\widehat{PA_{Eff}}\right) = s(lat, lon) \qquad \text{(A1).}$$

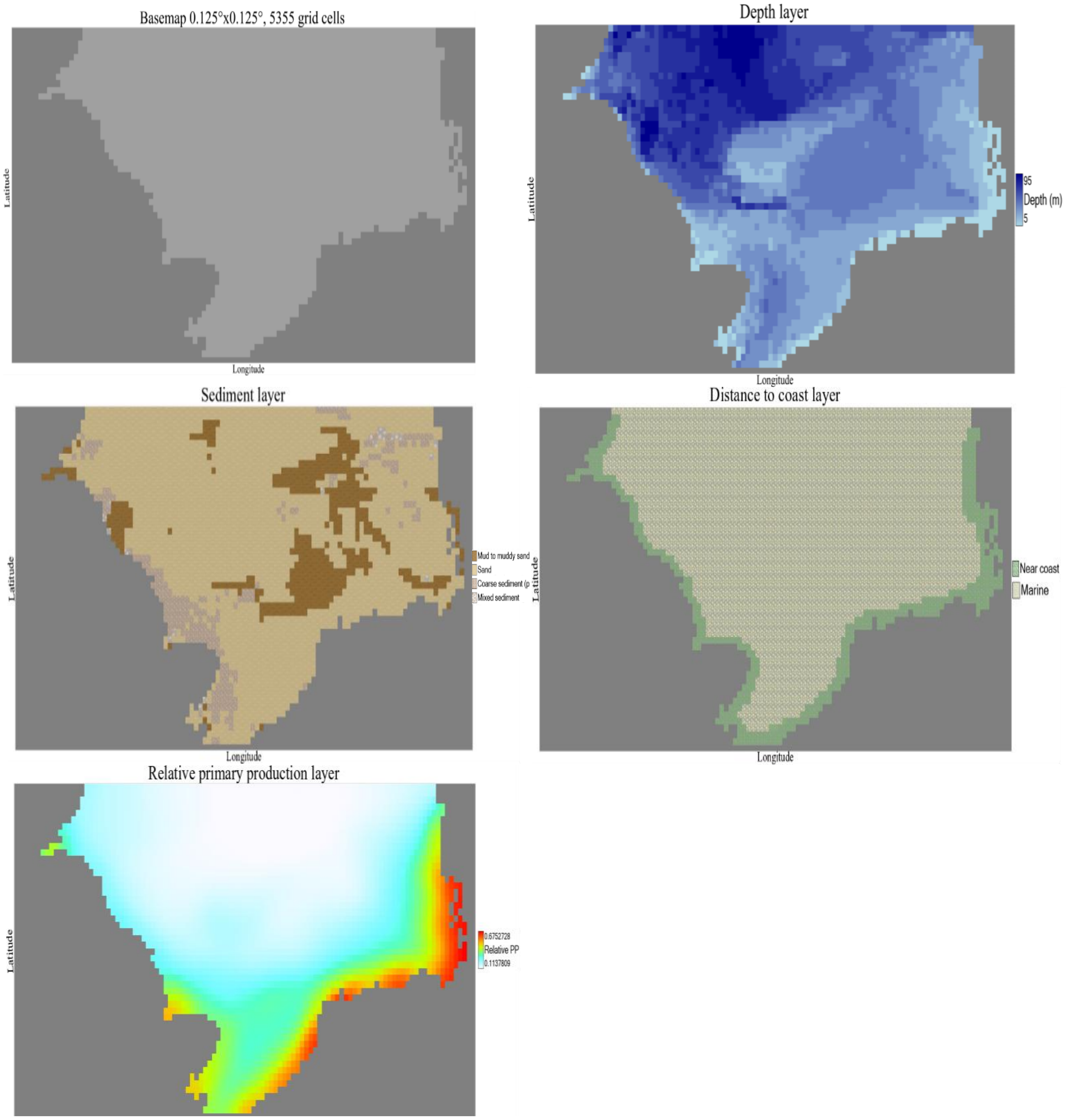
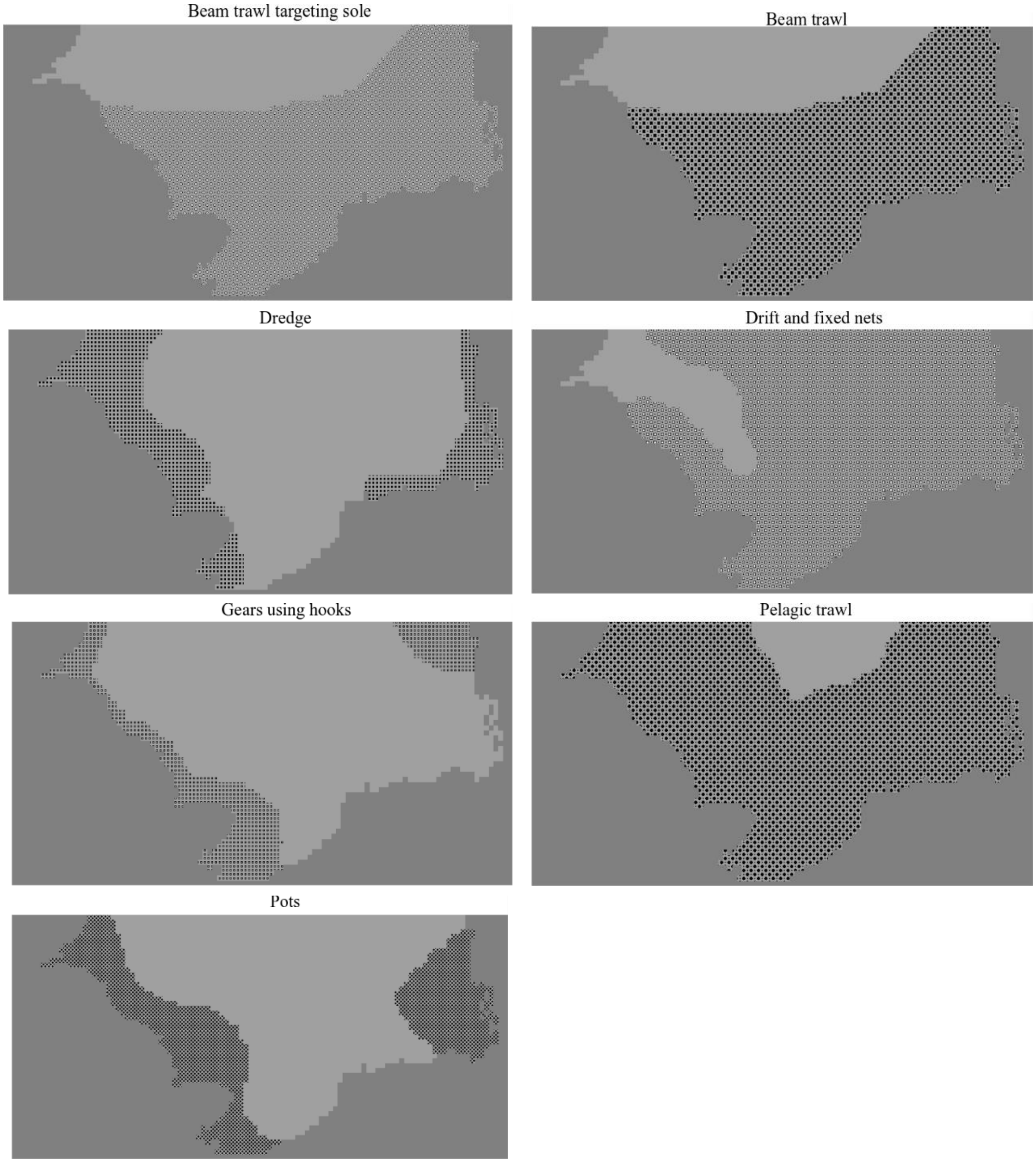


Figure A2: *Maps implemented in Ecospace. Top left: Basemap of the area. Top right: Depth map used as reference to the environmental driver functions. Middle left: Sediment layer used as habitat map. Middle right: Distance to coast based on the 12nm zone of each country as reference of distance, also used as habitat map. Bottom: Relative primary production map.*



Beam trawl targeting sole

Beam trawl

Dredge

Drift and fixed nets

Gears using hooks

Pelagic trawl

Pots

Figure A3: *Fleet effort maps. Fleets are usually assigned to the habitat maps that the FGs are assigned to, but for these fleets layers with fishing effort were created to increase realism. Shaded areas depict the zones where each fleet is allowed to fish.*

Table A5: *Habitat based foraging for each FG. Either by habitat capacity maps, created in this study with the generalized additive models, by habitat foraging which relates to the habitat layers "sediment" and "distance to coast", or by environmental response applied to the depth layer.*

Group name	*Habitat capacity map (external)*	*Habitat foraging*	*Environmental responses*
Toothed whales			x
Seals			x
Surface-feeding seabirds		x	
Diving seabirds		x	
Juvenile sharks			
Spurdog			x
Large piscivorous sharks			x
Small sharks	x		
Juvenile rays			
Starry ray & others	x		
Thornback & Spotted ray	x		
Skate & Cuckoo ray			x
Juvenile Cod(0-2, 0-40cm)	x		
Adult Cod (>40cm)	x		
Juvenile Whiting (0-1, 0-20cm)	x		
Adult Whiting (>20cm)	x		
Juvenile Haddock (0-1, 0-20cm)	x		
Haddock (adult)	x		
Norway pout	x		
Other gadoids (large)			x
Other gadoids (small)	x		
Monkfish	x		
Gurnards	x		
Herring (juvenile 0, 1)	x		
Herring (adult)	x		
Sprat	x		
Mackerel	x		

Horse mackerel			x
Sandeels		x	
Plaice (adult)	x		
Juvenile Plaice	x		
Dab	x		
Long-rough dab	x		
Flounder	x		
Sole (adult)	x		
Juvenile Sole	x		
Lemon sole	x		
Witch	x		
Turbot	x		
Brill	x		
Megrim			x
Halibut			x
Dragonets	x		
Large demersal fish	x		
Small demersal fish	x		
Miscellaneous filterfeeding pelagic fish	x		
Squid & cuttlefish			x
Fish larvae			
Carnivorous zooplankton			
Herbivorous & Omnivorous zooplankton (copepods)			
Gelatinous zooplankton			
Large crabs			x
Nephrops		x	
Epifaunal macrobenthos (mobile grazers)			
Infaunal macrobenthos			
Crangon (commercial size)		x	
Crangon (below 5cm)			
Shrimp			

Small mobile epifauna (swarming crustaceans)	
Small infauna (polychaetes)	
Sessile epifauna	
Meiofauna	x
Benthic microflora (incl. Bacteria, protozoa))	
Planktonic microflora (incl. Bacteria, protozoa)	
Phytoplankton	
Detritus - DOM -water column	
Detritus - POM - sediment	
Discards	

Table A6: *Assigned habitats. Values can range from 0= no capacity, to 1= full capacity. Only FGs where a habitat was assigned to are shown. Lower table part: Data sources.*

Group Number	*Group Name*	*All*	*Mud to muddy sand*	*Sand*	*Coarse sediment*	*Mixed sediment*	*Near coast*	*Marine*
3	*Surface-feeding seabirds*	0	0	0	0	0	1	0.75
4	*Diving seabirds*	0	0	0	0	0	1	0.75
29	*Sandeels*	0	0	1	0	0	0	0
53	*Nephrops*	0	1	0	0	0	0	0
56	*Crangon (commercial size)*	0	0	0	0	0	1	0
62	*Meiofauna*	0	0	0	0	0	1	0.5

3	*Surface-feeding seabirds*	Hatch and Nettleship (1998); BirdLife International (2018)
4	*Diving seabirds*	BirdLife International (2018)
29	*Sandeels*	Muus and Nielsen (1999)
53	*Nephrops*	Chapman and Rice (1971)
56	*Crangon (commercial size)*	Tiews (1970)
62	*Meiofauna*	Hayward et al. (1990)

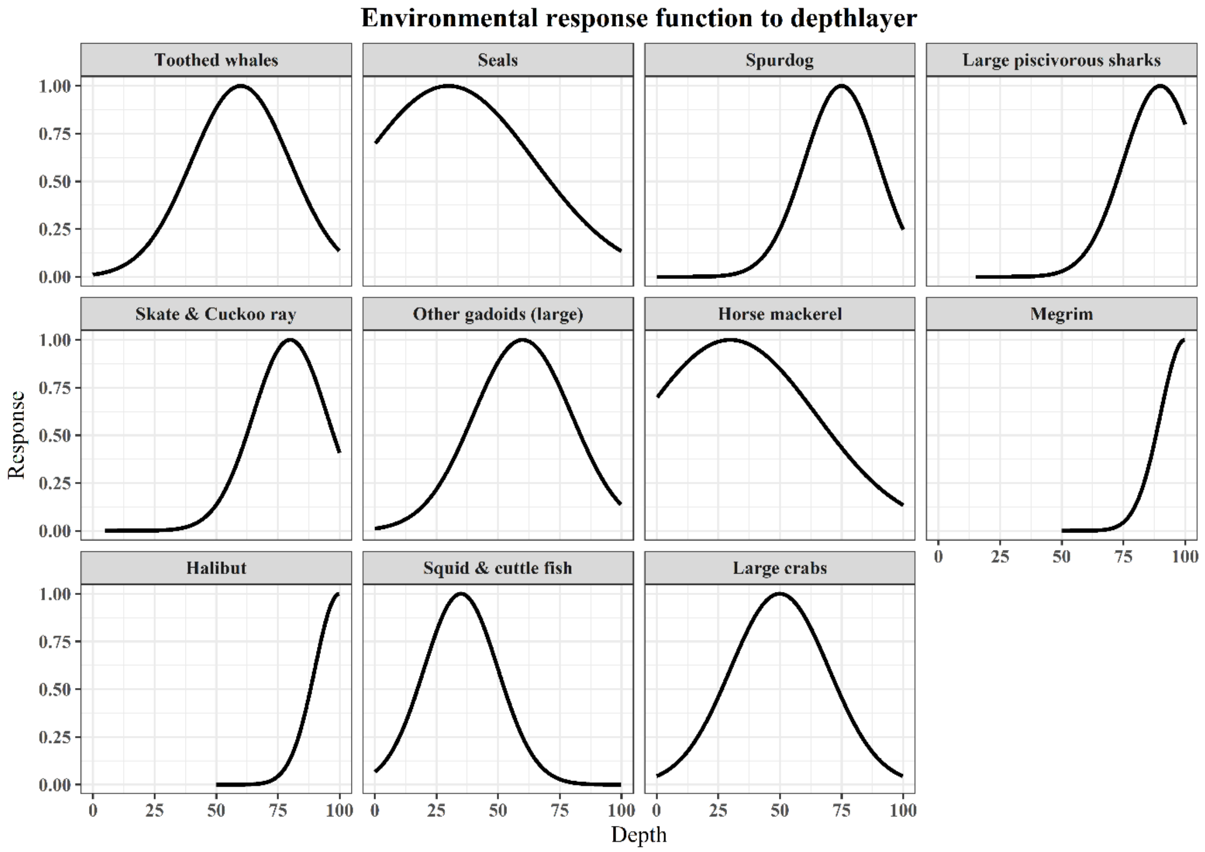


Figure A7: *Environmental response functions to depth layer applied to eleven FGs. 1 equals full capacity, therefore everything below 1 represents less capacity within certain depth.*

To account for movement, dispersal rates were chosen based on the life form of the FG. They increase from 3 for almost sessile and slow moving FGs up to 1000 for fast pelagic top-predators as well as for the bird groups.

Table A7: *Dispersal rates (km/year) per FG*

Group name	*Dispersal rate (km/year)*	*Group name*	*Dispersal rate (km/year)*
Toothed whales	1000	*Sole (adult)*	30
Seals	1000	*Juvenile Sole*	30
Surface-feeding seabirds	1000	*Lemon sole*	30
Diving seabirds	1000	*Witch*	30
Juvenile sharks	300	*Turbot*	30
Spurdog	300	*Brill*	30
Large piscivorous sharks	1000	*Megrim*	30
Small sharks	600	*Halibut*	30
Juvenile rays	300	*Dragonets*	30

Starry ray & others	600	*Large demersal fish*	300
Thornback & Spotted ray	600	*Small demersal fish*	30
Skate & Cuckoo ray	600	*Miscellaneous filterfeeding pelagic fish*	300
Juvenile Cod(0-2, 0-40cm)	300	*Squid & cuttlefish*	30
Adult Cod (>40cm)	300	*Fish larvae*	30
Juvenile Whiting (0-1, 0-20cm)	300	*Carnivorous zooplankton*	30
Adult Whiting (>20cm)	300	*Herbivorous & Omnivorous zooplankton (copepods)*	30
Juvenile Haddock (0-1, 0-20cm)	300	*Gelatinous zooplankton*	30
Haddock (adult)	300	*Large crabs*	3
Norway pout	300	*Nephrops*	3
Other gadoids (large)	300	*Epifaunal macrobenthos (mobile grazers)*	3
Other gadoids (small)	30	*Infaunal macrobenthos*	3
Monkfish	300	*Crangon (commercial size)*	3
Gurnards	300	*Crangon (below 5cm)*	3
Herring (juvenile 0, 1)	600	*Shrimp*	3
Herring (adult)	600	*Small mobile epifauna (swarming crustaceans)*	3
Sprat	600	*Small infauna (polychaetes)*	3
Mackerel	600	*Sessile epifauna*	3
Horse mackerel	600	*Meiofauna*	3
Sandeels	30	*Benthic microflora (incl. Bacteria, protozoa))*	3
Plaice (adult)	30	*Planktonic microflora (incl. Bacteria, protozoa)*	3
Juvenile Plaice	30	*Phytoplankton*	3
Dab	30	*Detritus - DOM -water column*	3
Long-rough dab	30	*Detritus - POM - sediment*	3
Flounder	30	*Discards*	10

Appendix B

B1 Species distribution models

Survey data

Before SDMs were applied, data was gathered for FGs that are represented well enough within the two different surveys ICES Beam Trawl Survey (BTS) and ICES International Bottom Trawl Survey (IBTS). The data was accessed via DATRAS (Database of trawl surveys, accessed February and July 2017, https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Small sharks, monkfish, turbot and miscellaneous filter feeding pelagic fish were represented well in most of the years for which SDMs were created. Unfortunately, in some years they were caught less than ten times. To include these groups despite those years with insufficient data, maps created for the previous year were then used during the Ecospace run. While the SDMs based on the BTS data could only be applied for quarter 3 (Q3), thornback and spotted ray as well as flounder were mainly caught in quarter 1 (Q1) by the IBTS, and therefore the SDM was only applied to Q1.

Table B1: *Functional groups and the survey the single species distribution models are based on. The quarter column displays the quarters for which maps were created. The far right column reveals years for certain functional groups with insufficient data.*

Group name	*Survey*	*Quarter*	*Excluded years with n(CPUE)<10*
Small sharks	IBTS	Q1 & Q3	Q1 = 1993, Q3 = 1995
Starry ray & others	IBTS	Q1 & Q3	
Thornback & Spotted ray	IBTS	Q1	Q3 = all years
Juvenile Cod (0-2, 0-40cm)	IBTS	Q1 & Q3	
Adult Cod (>40cm)	IBTS	Q1 & Q3	
Juvenile Whiting (0-1, 0-20cm)	IBTS	Q1 & Q3	
Adult Whiting (>20cm)	IBTS	Q1 & Q3	
Juvenile Haddock (0-1, 0-20cm)	IBTS	Q1 & Q3	
Haddock (adult)	IBTS	Q1 & Q3	

Norway pout	IBTS	Q1 & Q3	
Other gadoids (small)	IBTS	Q1 & Q3	
Monkfish	BTS	Q3	Q3 = 1991 - 1995
Gurnards	IBTS	Q1 & Q3	
Herring (juvenile 0, 1)	IBTS	Q1 & Q3	
Herring (adult)	IBTS	Q1 & Q3	
Sprat	IBTS	Q1 & Q3	
Mackerel	IBTS	Q1 & Q3	
Plaice (adult)	IBTS	Q1 & Q3	
Juvenile Plaice	IBTS	Q1 & Q3	
Dab	IBTS	Q1 & Q3	
Long-rough dab	BTS	Q3	
Flounder	IBTS	Q1	Q3 = all years
Sole (adult)	BTS	Q3	
Juvenile Sole	BTS	Q3	
Lemon sole	IBTS	Q1 & Q3	
Witch	IBTS	Q1 & Q3	
Turbot	BTS	Q3	Q3 = 1991, 1998, 1999, 2000, 2001
Brill	BTS	Q3	
Dragonets	IBTS	Q1 & Q3	
Large demersal fish	IBTS	Q1 & Q3	
Small demersal fish	IBTS	Q1 & Q3	
Miscellaneous filterfeeding pelagic fish	IBTS	Q1 & Q3	Q1 = 1992, 1993 Q3 = 1994, 2013

Comparison of two species distribution models

Next to the Generalized Additive Models (GAMs) applied in this study, the integrated nested laplace approximation (INLA) was tested as a second SDM approach for its applicability within this study. It is based on the approximation of Bayesian inference for latent Gaussian field models (Rue et al., 2009). To take spatial correlation of the samples into account, the stochastic partial differential equation approach was used (SPDE; Lindgren et al., 2011). Here, as for the GAM, the models were constructed for PA as well as presence only CPUE data and finally combined in a hurdle model. For each data set, a mesh was created using Delaunay triangulation, based on a spatial polygon of the southern North Sea and a maximum edge length of 0.5°. Both INLA models were run with the same families and link functions as the GAM.

To assess the predictive skills of the two model types, a 4 k-fold cross-validation was applied to both model types. The datasets were split into four partitions to serve as fitting and prediction sets. This was executed for each year separately. In very few cases, this splitting of data lead to an inadequate amount of data to fit the model to, so the model did not converge. These incidents were removed from further analysis. After running the cross-validation for each year and for each dependent variable (*PA* and *CPUE*), the area under the response curve (AUC; Swets, 1988) was calculated between the observations of presence/absence and the predicted presence/absence, with f representing the receiving-operating characteristic:

$$AUC = \int_0^1 f(x)dx \tag{B1}$$

To assess the fit of the full hurdle model to the sampled data, the root mean squared error (RMSE) was applied to the log-transformed CPUE ($CPUE_{obs}$) and log-transformed hurdle values (*hurd'*):

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(log\,(hurd') - log(CPUE_{obs})^2}{n}} \tag{B2}$$

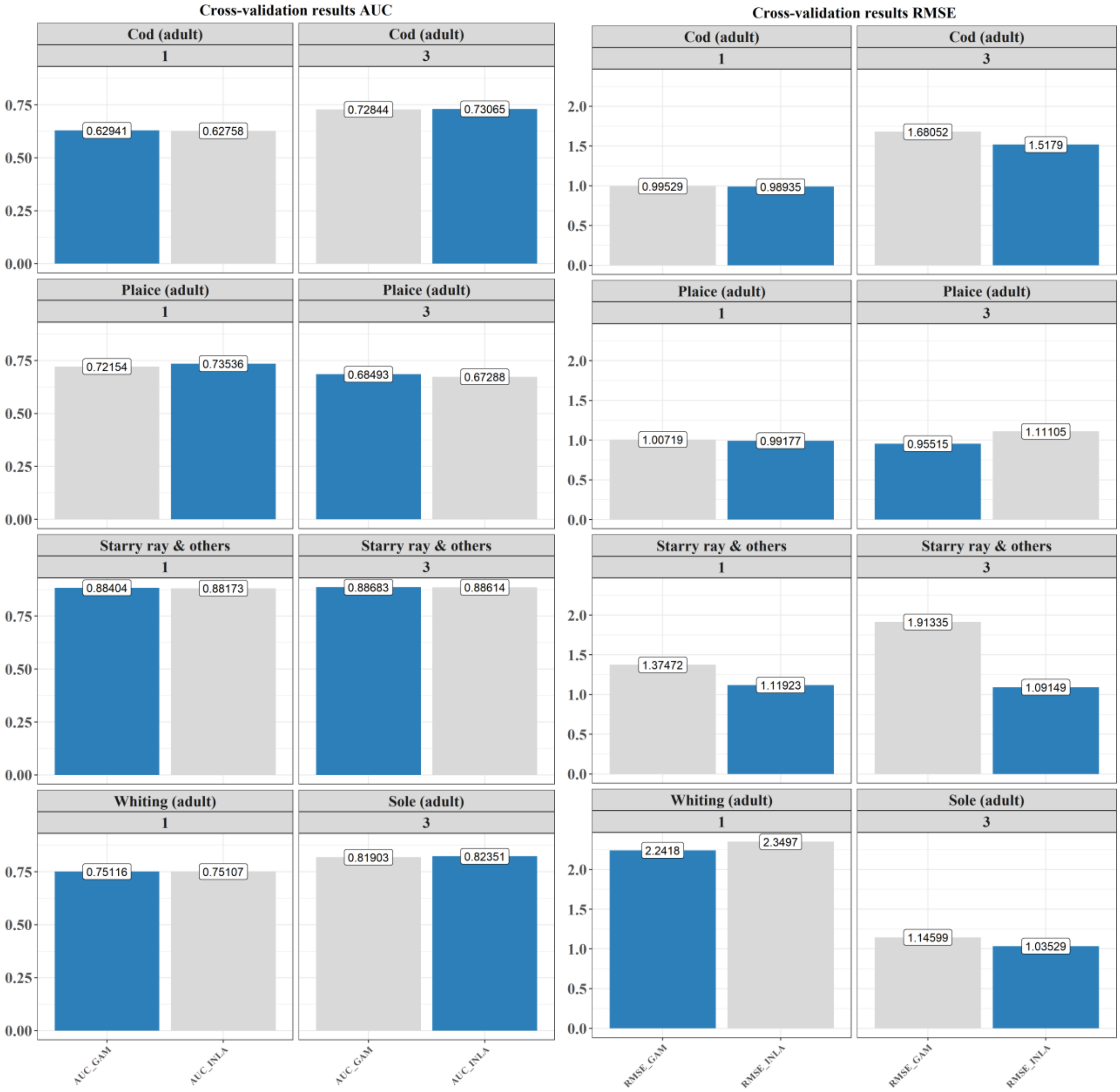


Figure B1: *Cross-validation comparison between GAM and INLA. Left: Area under the curve (AUC) based on predictive power for binomial data for individual FGs and quarter (1,3) for GAM (left column) and INLA (right column). Right :Root mean squared error (RMSE) for hurdle models for individual FGs and quarter (1,3) for GAM (left column) and INLA (right column).*

The AUC results that stem from the cross-validation for the tested FGs depicted a close match between the predictive power of GAM and INLA (Figure B1). In most cases, they only differed by the second or even the third decimal. For the metric that reflected the predictive power of the models for the present/absence dataset, the GAM showed the better result five times, while INLA was better than GAM three times. And even though the RMSE results for the only FG starry ray & others, that is less common, shows quite a better fit in Q3, other FGs (whiting, plaice) showed a better fit for the GAM. Based on the proximity of most of these results in this cost and benefit analysis, GAM was chosen over INLA. This can be justified by the higher computational costs of INLA and the simpler model design of the GAM, choosing the most parsimonious approach.

B2 Skill assessment

Time series applied in the skill assessment

The time series used within the skill assessment of this paper are the time series used as reference time series within the associated Ecosim model. For most FGs both time series were available, while for some FGs only one of the two could be applied (Table B2). Furthermore, some FGs have no reference time series. These FGs were excluded from the skill assessment.

Table B2: *Functional groups used in the skill assessment, based on the reference time series included in the associated Ecosim. For some groups only a biomass or a catch time series was available (x = time series available, - no time series). For further information on the individual time series see Stäbler et al. (2016).*

Group name	*Biomass skill assessment*	*Catch skill assessment*
Seals	x	-
Surface-feeding seabirds	x	-
Diving seabirds	x	-
Spurdog	x	x
Large piscivorous sharks	x	x
Small sharks	x	x
Starry ray & others	x	x
Thornback & Spotted ray	x	x
Skate & Cuckoo ray	x	-
Juvenile Cod(0-2, 0-40cm)	x	x
Adult Cod (>40cm)	x	x
Juvenile Whiting (0-1, 0-20cm)	x	-
Adult Whiting (>20cm)	x	x
Juvenile Haddock (0-1, 0-20cm)	x	-
Haddock (adult)	x	x
Norway pout	x	x
Other gadoids (large)	x	x
Other gadoids (small)	x	x
Monkfish	x	x
Gurnards	x	x

Herring (juvenile 0, 1)	x	-
Herring (adult)	x	x
Sprat	x	x
Mackerel	x	x
Horse mackerel	-	x
Sandeels	x	x
Plaice (adult)	x	x
Juvenile Plaice	x	-
Dab	x	x
Long-rough dab	x	x
Flounder	x	x
Sole (adult)	x	x
Juvenile Sole	x	-
Lemon sole	x	x
Witch	x	x
Turbot	x	x
Brill	x	x
Megrim	x	x
Halibut	x	x
Dragonets	x	
Large demersal fish	x	x
Small demersal fish	x	x
Miscellaneous filterfeeding pelagic fish	x	x
Squid & cuttlefish	-	x
Carnivorous zooplankton	x	-
Herbivorous & Omnivorous zooplankton (copepods)	x	-
Gelatinous zooplankton	-	-
Large crabs	-	x
Nephrops	x	x
Epifaunal macrobenthos (mobile grazers)	x	x
Infaunal macrobenthos	x	x

Crangon (commercial size)	x	x
Small mobile epifauna (swarming crustaceans)	x	-
Small infauna (polychaetes)	x	-
Sessile epifauna	x	x

Scaling factor q

Biomass time series available from single species stock assessments can be used to get a goodness of fit measure for Ecosim. EwE determines this measure every time Ecosim runs. Calculated is the weighted sum of squared deviations (SS) of log biomasses from log predicted biomasses. If the reference time series implemented are relative abundance data, they are being scaled by the factor q by the maximum likelihood estimate:

$$y = qB \tag{B3}$$

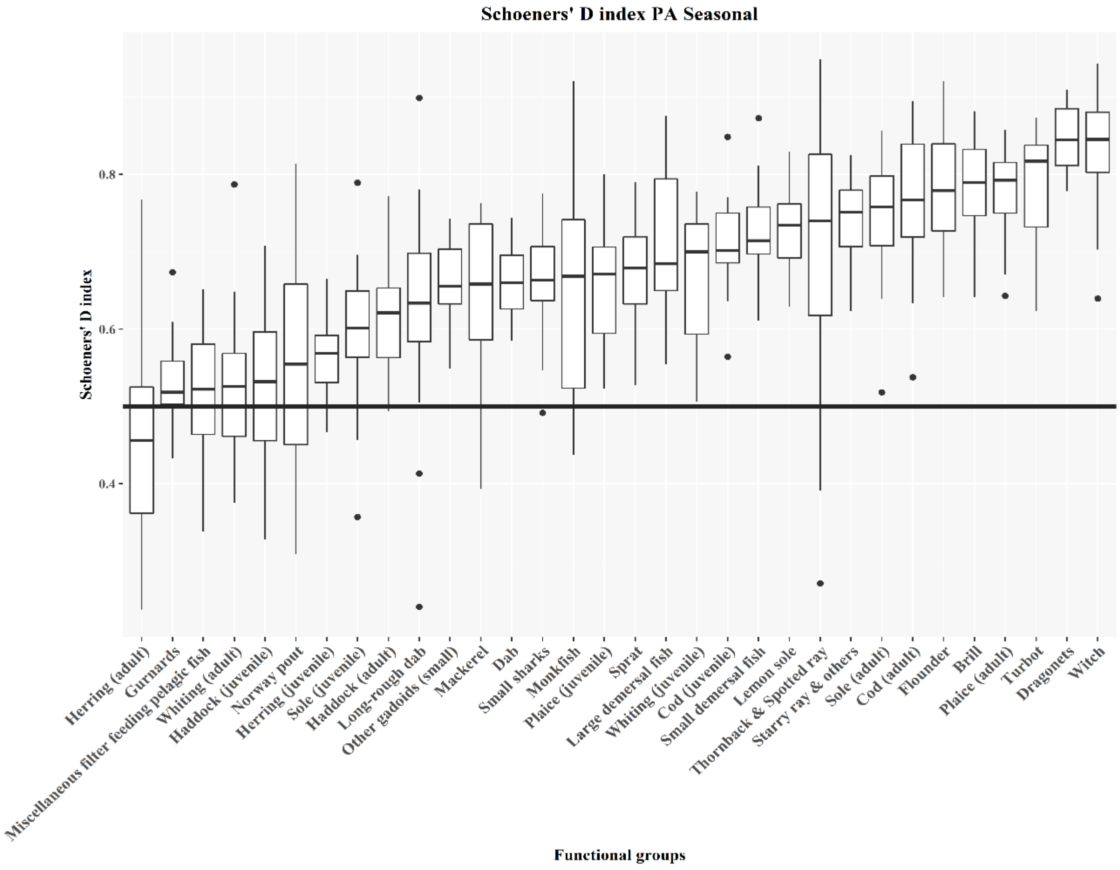
With y for relative abundance, B for absolute abundance and q as the scaling factor (Christensen et al., 2008). We applied the method of scaling relative biomass and catch time series in the skill assessment of Ecospace as well, to keep it methodologically consistent. Before applying any measure of fit, the time series were smoothed to get a better picture of the general time trend, and afterwards an individual scaling factor of q was determined on a log scale and applied to the relative time series.

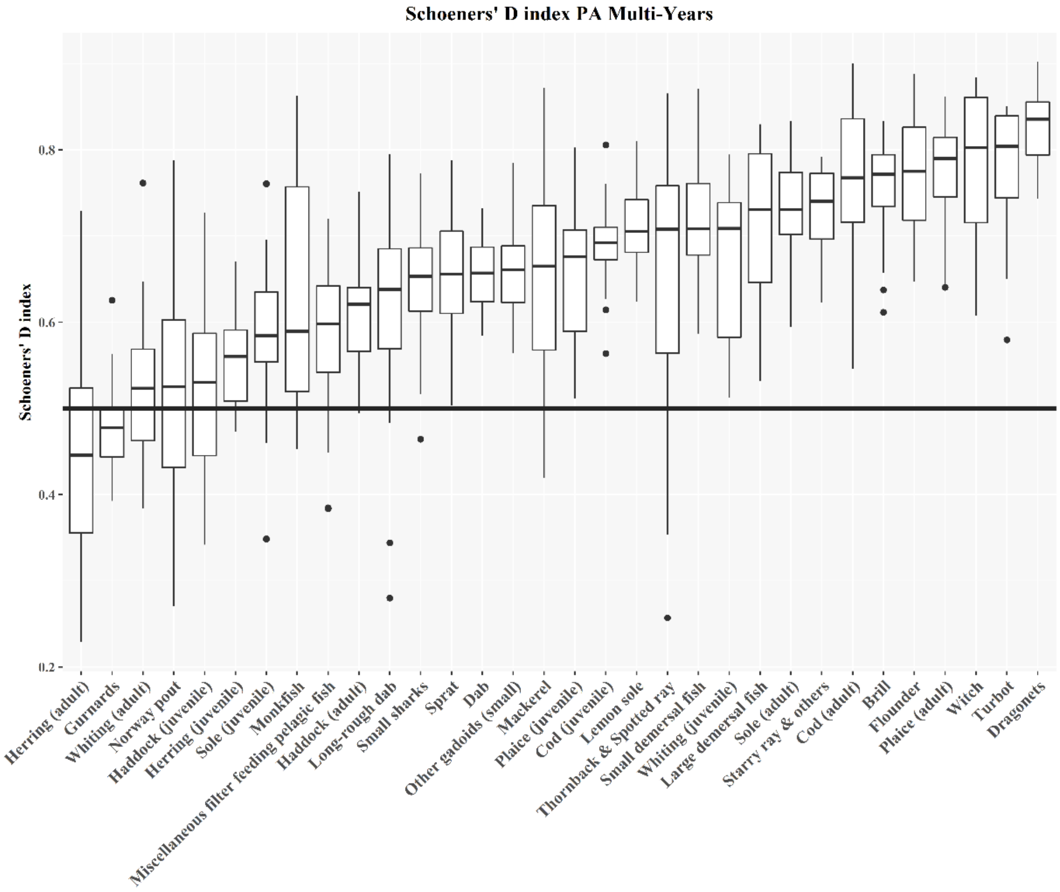
A similar approach was applied to the maps used for the Taylor diagram. Here we evaluate the fit of biomass maps created during the Ecospace run to abundance maps based on the hurdle model. These two measures cannot be compared directly for their trend over time and the changes in distribution. Therefore, both were standardized by their maximum abundance (biomass, respectively) of all years in each grid cell. Subsequently, the abundance maps were treated as relative and scaled by q as well.

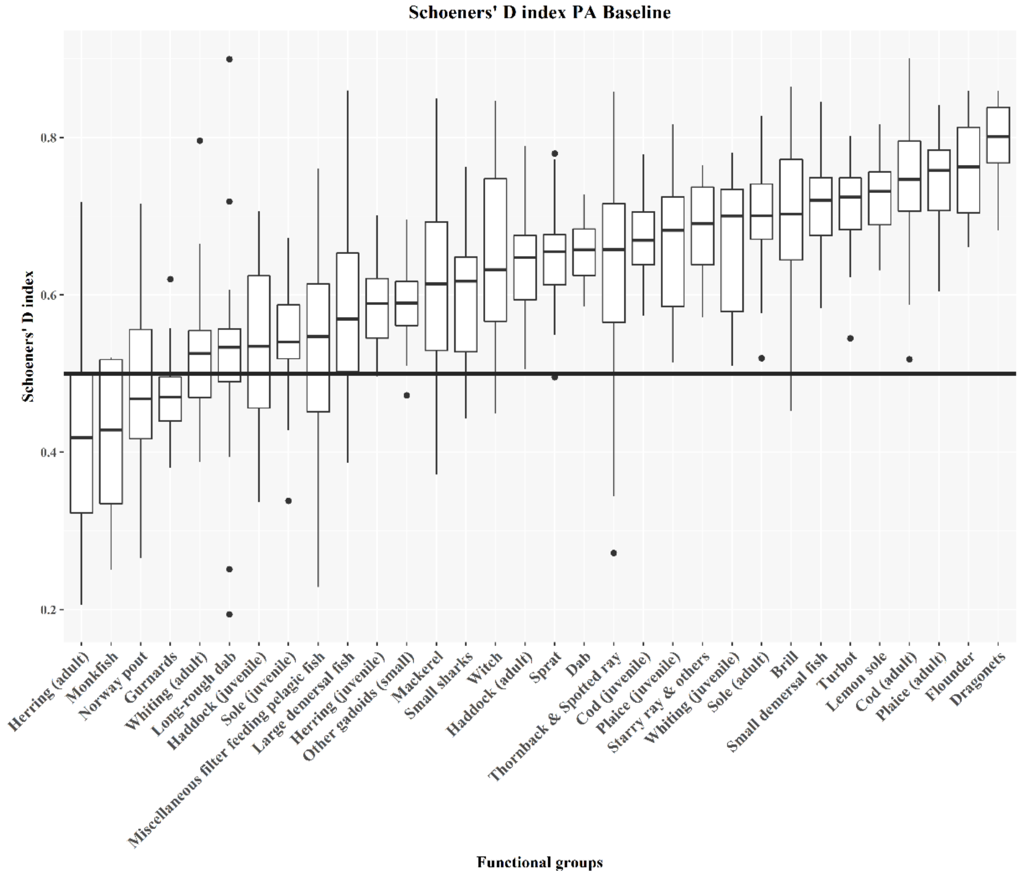
Skill assessment – additional results

For the individual Schoener’s D index, only the results for the annual PA scenario were presented in the paper. Within the scenarios that are based the same variable (on either PA or hurdle), the individual results do not differ noticeable. However, there are apparent differences when comparing scenarios driven with different variables (Figure B2).

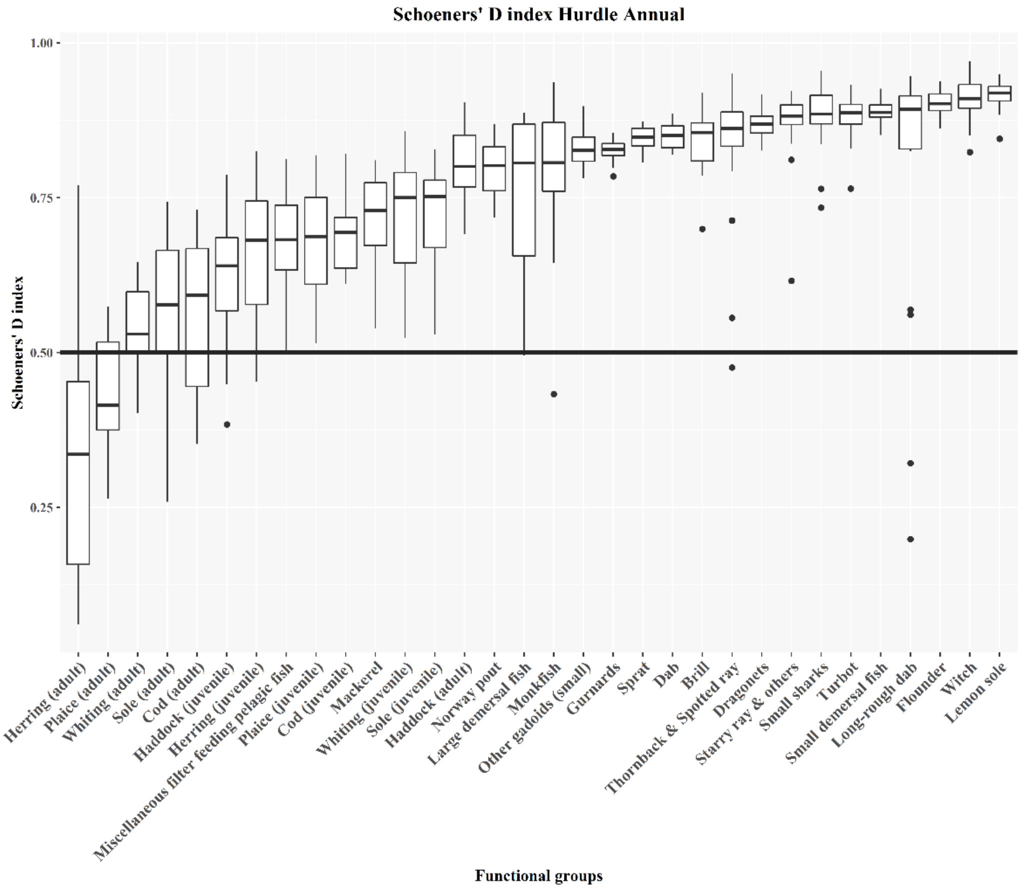
PA

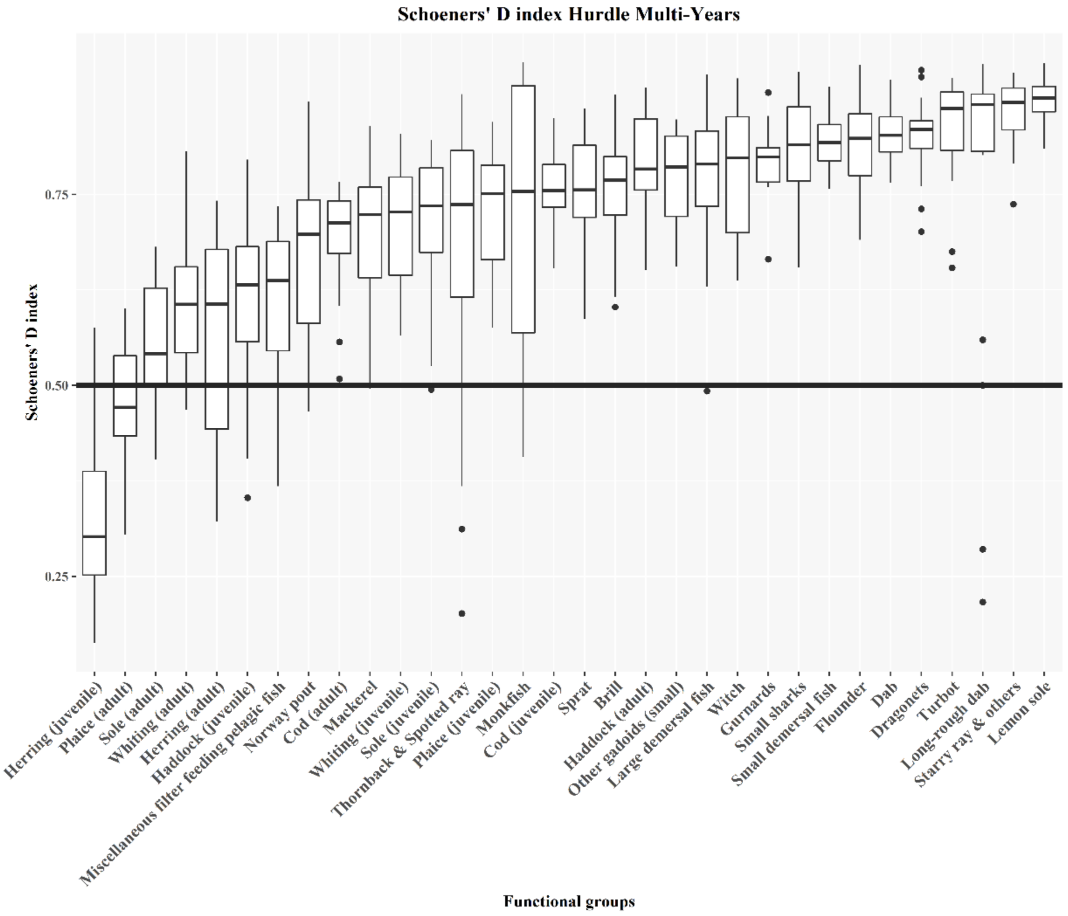

Schoeners' D index PA Seasonal
Schoeners' D index
0.8
0.6
0.4
Functional groups
Herring (adult)
Gurnards
Miscellaneous filter feeding pelagic fish
Whiting (adult)
Haddock (juvenile)
Norway pout
Herring (juvenile)
Sole (juvenile)
Haddock (adult)
Long-rough dab
Other gadoids (small)
Mackerel
Dab
Small sharks
Monkfish
Plaice (juvenile)
Sprat
Large demersal fish
Whiting (juvenile)
Cod (juvenile)
Small demersal fish
Lemon sole
Thornback & Spotted ray
Starry ray & others
Sole (adult)
Cod (adult)
Flounder
Brill
Plaice (adult)
Turbot
Dragonets
Witch


Schoeners' D index PA Multi-Years
Schoeners' D index
0.2
0.4
0.6
0.8
Functional groups
Herring (adult)
Gurnards
Whiting (adult)
Norway pout
Haddock (juvenile)
Herring (juvenile)
Sole (juvenile)
Monkfish
Miscellaneous filter feeding pelagic fish
Haddock (adult)
Long-rough dab
Small sharks
Sprat
Dab
Other gadoids (small)
Mackerel
Plaice (juvenile)
Cod (juvenile)
Lemon sole
Thornback & Spotted ray
Small demersal fish
Whiting (juvenile)
Large demersal fish
Sole (adult)
Starry ray & others
Cod (adult)
Brill
Flounder
Plaice (adult)
Witch
Turbot
Dragonets


Schoeners' D index PA Baseline
Schoeners' D index
0.2
0.4
0.6
0.8
Functional groups
Herring (adult)
Monkfish
Norway pout
Gurnards
Whiting (adult)
Long-rough dab
Haddock (juvenile)
Sole (juvenile)
Miscellaneous filter feeding pelagic fish
Large demersal fish
Herring (juvenile)
Other gadoids (small)
Mackerel
Small sharks
Witch
Haddock (adult)
Sprat
Dab
Thornback & Spotted ray
Cod (juvenile)
Plaice (juvenile)
Starry ray & others
Whiting (juvenile)
Sole (adult)
Brill
Small demersal fish
Turbot
Lemon sole
Cod (adult)
Plaice (adult)
Flounder
Dragonets

Hurdle


Schoeners' D index Hurdle Annual
Schoeners' D index
1.00
0.75
0.50
0.25
Herring (adult)
Plaice (adult)
Whiting (adult)
Sole (adult)
Cod (adult)
Haddock (juvenile)
Herring (juvenile)
Miscellaneous filter feeding pelagic fish
Plaice (juvenile)
Cod (juvenile)
Mackerel
Whiting (juvenile)
Sole (juvenile)
Haddock (adult)
Norway pout
Large demersal fish
Monkfish
Other gadoids (small)
Gurnards
Sprat
Dab
Brill
Thornback & Spotted ray
Dragonets
Starry ray & others
Small sharks
Turbot
Small demersal fish
Long-rough dab
Flounder
Witch
Lemon sole
Functional groups


Schoeners' D index Hurdle Multi-Years
Schoeners' D index
0.75
0.50
0.25
Herring (juvenile)
Plaice (adult)
Sole (adult)
Whiting (adult)
Herring (adult)
Haddock (juvenile)
Miscellaneous filter feeding pelagic fish
Norway pout
Cod (adult)
Mackerel
Whiting (juvenile)
Sole (juvenile)
Thornback & Spotted ray
Plaice (juvenile)
Monkfish
Cod (juvenile)
Sprat
Brill
Haddock (adult)
Other gadoids (small)
Large demersal fish
Witch
Gurnards
Small sharks
Small demersal fish
Flounder
Dab
Dragonets
Turbot
Long-rough dab
Starry ray & others
Lemon sole
Functional groups

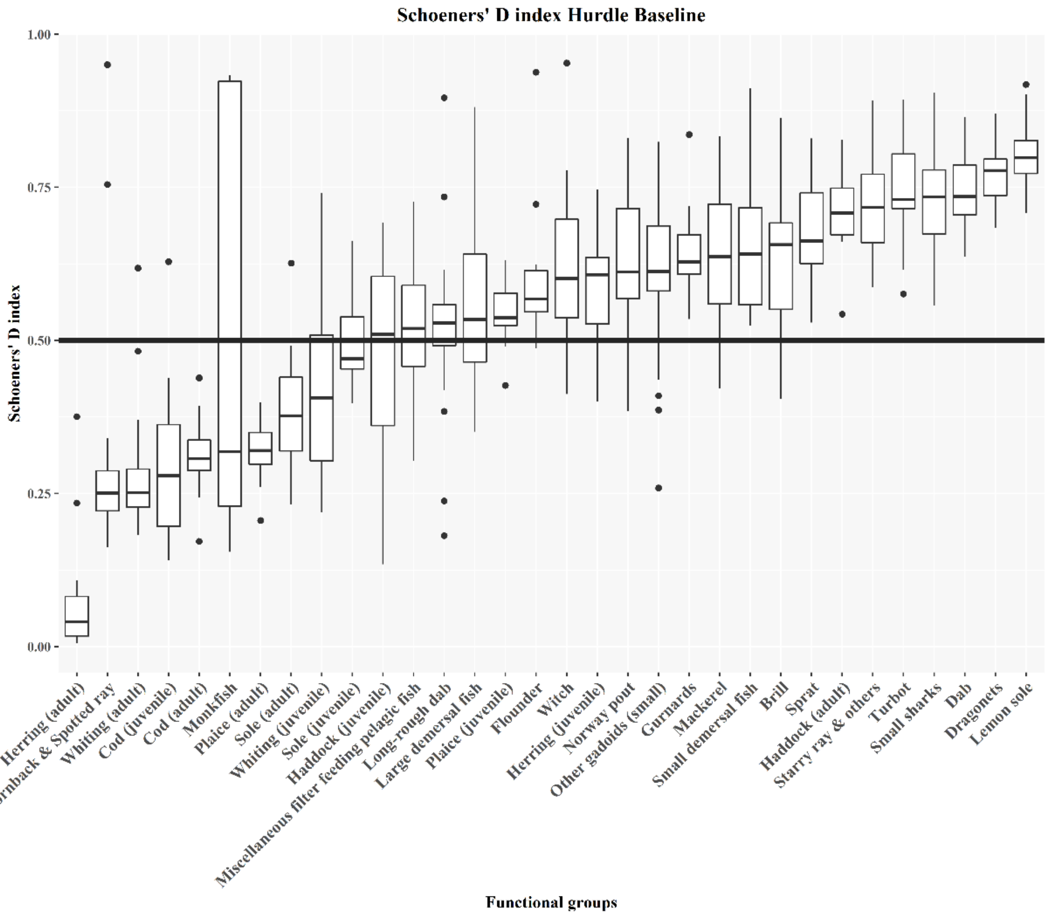


Figure B2: *Boxplots representing variations in Schoener's D index over 20 years for each FG. Top graphs show the results retrieved from the PA scenarios (Seasonal, multi-years and baseline). Bottom three graphs show the results from the hurdle scenarios (annual, multi-years and baseline).*

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Publication 3. - *Tradeoffs between fisheries, offshore wind farms and marine protected areas in the southern North Sea – winners, losers and effective spatial management*

Appendix

Additional information on marine protected areas (MPAs) and the parameterisation of the model to reflect the impact of Offshore Wind Farms (OWFs) included in the model is given in Appendix A. Furthermore, species are listed that are included in the International Union for Conservation of Nature's Red List of Threatened Species (IUCN) as well as the additional sediment preferences of specific benthic species and the impact for each functional group on each indicator is listed. Changes applied to the model compared to prior versions are described. Appendix B focusses on the remaining results not included in the publication. Ecopath and Ecosim results derived with the ECOIND plug-in are displayed as well as remaining spatial patterns of the indicators compiled during the baseline run.

Appendix A

A1 Additional information MPAs and OWFs

MPAs in the southern part of the North Sea are created and designated based on different legal grounds, national and international legislation (Table 1.1A). Most of the MPAs are part of the Natura 2000 network, a complex of protected areas created based on the Birds Directive (2009/147/EC) and the Habitats Directive (92/43/EEC). Other MPAs are designated based on national jurisdiction, like the Marine and Coastal Access Act (2009) in the United Kingdom (Table 1.2A).

Table 1.1A: *Different legal agreements that serve as cornerstones for the implementation of MPAs*

Regulation	**Legal body & Date of Adoption**	**Legal agreement**
Birds Directive (Originally: Directive 79/409/EEC; Amended: Directive 2009/147/EC)	European Union; Originally: April 1979, Amended: 30 November 2009	Protection of wild bird species in Europe
Habitats Directive (Council Directive 92/43/EEC)	European Union; 21 May 1992	Protection of rare, threatened and endangered species. Together with the Birds Directive poses legal grounds for the Natura 2000 ecological network of protected areas
Convention for the Protection of the Marine Environment of the	16 contracting parties; signed: 22 September 1992,	Marine ecosystem conservation in the north-east Atlantic

North-East Atlantic (The "OSPAR" convention) (Decision 98/249/EC, 1998)	enforced: 25 March 1998	
OSPAR Recommendation 2003/3 on a Network of Marine Protected Areas (OSPAR Recommendation 2003/3)	OSPAR commission; Adopted in 2003	Established ecologically coherent MPA network to secure species, habitats and ecological processes from damage
Marine Strategy Framework Directive (Directive 2008/56/EC, 2008)	European Union; 17 Juni 2008	Achieve "Good Environmental Status" (GES) in marine waters by 2020, definition of GES Article 3: "'good environmental status' means the environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are clean, healthy and productive within their intrinsic conditions, and the use of the marine environment is at a level that is sustainable, thus safeguarding the potential for uses and activities by current and future generations
2030 Agenda for Sustainable Development (A/RES/70/1)	United Nations; Resolution adopted by the General Assembly on 25 September 2015	Goal 14 target 2 addresses urge to keep and restore healthy marine ecosystems, demanding sustainable management and protection to ensure their productivity
Green Deal with Biodiversity Strategy 2030 (COM/2020/380)	European Union; Communication Document 20 May 2020	Reverse degradation and support recovery of ecosystems with the aid of larger EU-wide networks of protected areas, i.e. enlarge existing MPAs

Table 1.2A: *Names of the thirty-three MPAs integrated into Ecospace and their associated management objectives. Last two rows contain closure information about the two Offshore Wind Farms (OWFs). Inlets, lagoons and dunes are not listed, because the study area of the Ecospace model does not cover areas that close to the coast.*

Closed area	*Protected good*	*Ecospace fleets closed*	*Legal framework*	*Date and source*
Bancs des Flandres	Sandbanks, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/FR3102002#tab-habitats
Berwickshire and North Northumberland Coast	Mud flats and sand flats, reefs, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl,	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://sac.jncc.gov.uk/site/UK0017072

		nephrops trawl, dredges); drift and fixed nets, gears using hooks		
Borkum Riffground	Sandbanks, reefs, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://www.bfn.de/en/activities/marine-nature-conservation/national-marine-protected-areas/north-sea-eez/borkum-reef-ground-sac.html
Doggerbank [GB]	Sandbanks	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/dogger-bank-mpa/
Doggerbank [NL]	Sandbanks, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/NL2008001
Doggerbank [GER]	Sandbanks, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://www.bfn.de/en/activities/marine-nature-conservation/national-marine-protected-areas/north-sea-eez/dogger-

		and fixed nets, gears using hooks		bank-sac.html
Eastern German Bight	Sandbanks, reefs, birds	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC, Birds Directive 2009/147/EC	18.09.2020, https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=DE1011401
Farnes East	Benthos	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Marine and Coastal Access Act (2009)	18.09.2020, https://jncc.gov.uk/our-work/farnes-east-mpa/
Firth of forth bank complex	Sandbanks, benthos	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Marine and Coastal Access Act (2009)	18.09.2020, https://jncc.gov.uk/our-work/firth-of-forth-banks-complex-mpa/
Friese front	Birds	Drift and fixed nets, gears using hooks	Natura 2000 network, Birds Directive 2009/147/EC	18.09.2020, https://eunis.eea.europa.eu/sites/NL2016166
Fulmar	Sandbank, mud, mixed sediments, benthos	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Marine and Coastal Access Act (2009)	18.09.2020, https://jncc.gov.uk/our-work/fulmar/

Haisborough, Hammond and Winterton	Sandbanks, reefs	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/haisborough-hammond-and-winterton-mpa/
Inner Dowsing, Race bank and North Ridge	Sandbanks, reefs	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/inner-dowsing-race-bank-and-north-ridge/
Jyske Rev, Lillefiskerbanke	Reefs, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/DK00VA257
Klaverbank	Reefs, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/NL2008002
Lower Saxony Wadden Sea	Birds	drift and fixed nets, gears using hooks	Natura 2000 network, Birds Directive 2009/147/EC	18.09.2020, https://www.nlwkn.niedersachsen.de/natura2000/eu_vogelschutzrichtlinie_

				und_eu_vogelschutzgebiete/eu_vogelschutzgebiete_in_niedersachsen/eu-vogelschutzgebiet-v01-niedersaechsisches-wattenmeer-und-angrenzendes-kuestenmeer-132472.html
North Sea Coast [NL]	Sandbanks, mud flats, sea meadows, birds	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC, Birds Directive 2009/147/EC	18.09.2020, https://eunis.eea.europa.eu/sites/NL9802001
North Norfolk Sandbanks and Saturn Reef	Sandbanks, reefs	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/north-norfolk-sandbanks-and-saturn-reef-mpa/
North East of Farnes Deep	Sandbanks, mud flats, mixed sediment, coarse sediment	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Marine and Coastal Access Act (2009)	18.09.2020, https://jncc.gov.uk/our-work/north-east-of-farnes-deep-mpa/
Outer Thames Estuary	Birds	Drift and fixed nets, gears using hooks	Natura 2000 network, Birds Directive 2009/147/EC	18.09.2020, https://jncc.gov.uk/our-work/outer-thames-estuary-spa/
Shallow Sand	Sandbanks, glacial tunnel	Bottom contacting gear (demersal trawl,	Marine and Coastal Access Act (2009)	18.09.2020, https://jncc.gov.uk/our-work/

	valley (geological feature)	beam trawl, shrimp trawl, nephrops trawl, dredges)		swallow-sand-mpa/
Seabird protection area	Birds	Drift and fixed nets, gears using hooks	Natura 2000 network, Birds Directive 2009/147/EC	18.09.2020, https://natura2000.eea.europa.eu/natura2000/SDF.aspx?site=DE1813491
Southern North Sea	Cetacean	Drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/southern-north-sea-mpa/
SPZ1/2/3	Birds	Drift and fixed nets, gears using hooks	Natura 2000 network, Birds Directive 2009/147/EC	18.09.2020, https://eunis.eea.europa.eu/sites/BEMNZ0002; https://eunis.eea.europa.eu/sites/BEMNZ0003; https://eunis.eea.europa.eu/sites/BEMNZ0004
Sylt outer reef	Sandbanks, reefs, cetacean, mammals, lamprey	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/DE1209301
The Wash and North Norfolk Coast	Sandbanks, reefs	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://jncc.gov.uk/our-work/north-norfolk-sandbanks-and-saturn-reef-mpa/

Voordelta	Sandbanks, mud flats, sea meadows, birds, fish, lamprey, mammals, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC, Birds Directive 2009/147/EC	18.09.2020, https://eunis.eea.europa.eu/sites/NL4000017
Vadehavet med Ribe	Sandbanks, mud flats, reefs, lamprey, fish, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=DK00AY176
Wadden Sea National Park	Sandbanks, estuaries, mudflats and sand flats, benthos	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/NL1000001
Vlaamsen Banken	Sandbanks, reefs, birds, fishes, mammals, lamprey, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/BEMNZ0001
Vlakte van de Raan	Sandbanks, fish, lamprey, mammals, cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	18.09.2020, https://eunis.eea.europa.eu/sites/NL2008003

Margate and Long Sands	Sandbanks	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges)	Natura 2000 network, Habitats Directive 92/43/EEC	1.03.2021, https://sac.jncc.gov.uk/site/UK0030371
Sandbanker ud for Thyborøn	Sandbanks, Cetacean	Bottom contacting gear (demersal trawl, beam trawl, shrimp trawl, nephrops trawl, dredges); drift and fixed nets, gears using hooks	Natura 2000 network, Habitats Directive 92/43/EEC	1.03.2021, https://eunis.eea.europa.eu/sites/DK00VA340#tab-species
OWF_{op}	-	Closed for all fisheries, all year round		
OWFpla	-	Closed for all fisheries, all year round		

Implementing OWFs in the model was achieved not only by closing the areas to fisheries, but also by adding affinities of benthic functional groups towards hard substrate (Table 1.3A). Here we used affinities listed by Lynam et al. (2017), who used an Ecospace model for the entire North Sea to evaluate the impact of removal of man-made structures. Furthermore, the specification of habitat preferences towards sediment for benthic functional groups was refined based on the study conducted by Lynam et al. (2017). The Ecopath model for the southern part of the North Sea was constructed based on the Ecopath model for the entire North Sea, therefore including quite similar functional groups, which is why these affinities can be transferred directly into the model (Mackinson et al., 2007; Stäbler et al., 2016; Stäbler et al. 2018, Püts et al., 2020).

Table 1.3A: *Benthic functional groups in Ecospace and their habitat preferences towards sediment structures as well as hard substrate introduced by the structures of the individual turbines in an OWF.*

Functional group	*Mud to muddy sand*	*Sand*	*Coarse sediment*	*Mixed sediment*	*Rocks and boulders*	*OWFs*
Large crabs	0.8	0.7	0.8	0.9	1	1
Epifaunal macrobenthos (mobile grazers)	0.9	0.8	1	1	1	1
Shrimp	0.3	0.2	0.4	0.2	1	1
Small mobile epifauna (swarming crustaceans)	0.8	0.8	0.8	0.7	1	1
Sessile epifauna	0.6	0.5	0.7	0.7	0.5	1

A2 Trait and indicator information

The IUCN Red List was established in 1964 (IUCN, 2021). It holds global information on species extinction risk. The different categories are “Not Evaluated”, “Data Deficient”, “Least Concern”, “Near Threatened”, “Vulnerable”, “Endangered”, “Critically Endangered” and “Extinct in the Wild and Extinct”. Within the ECOIND plug-in, only the categories “Near threatened” to “Extinct in the Wild and Extinct” are included in the calculations (Steenbeek, pers. communication; Coll et al., 2017). In the case of the model of the southern part of the North Sea, 21 species are listed in four of these categories and thus included in the calculations of the indicators “IUCN-endangered species biomass” and “IUCN-endangered species catch” (Table 2.1A).

Table 2.1A: *Species and their associated functional group included in the model listed on the IUCN Red list. Four categories: near threatened, vulnerable, endangered and critically endangered*

Functional group	*Species included*	*IUCN status*	*Reference*
Toothed whales	Phocoena phocoena	Vulnerable	Species account by IUCN SSC Cetacean Specialist Group; regional assessment by European Mammal Assessment team. 2007. *Phocoena phocoena*. *The IUCN Red List of Threatened Species* 2007: e.T17027A6734714. Downloaded on 28.02.2020
Surface-feeding seabirds	Fulmarus glacialis	Endangered	BirdLife International. 2015. *Fulmarus glacialis*. *The IUCN Red List of Threatened Species* 2015: e.T22697866A60171190. Downloaded on 28.02.2020
Surface-feeding seabirds	Larus argentatus	Near threatened	BirdLife International. 2015. *Larus argentatus*. *The IUCN Red List of Threatened Species* 2015: e.T62030608A66711400. Downloaded on 28.02.2020
Diving seabirds	Uria aalge	Near threatened	BirdLife International. 2015. *Uria aalge*. *The IUCN Red List of Threatened Species* 2015: e.T22694841A60108623. Downloaded on 28.02.2020
Diving seabirds	Alca torda	Near threatened	BirdLife International. 2015. *Alca torda*. *The IUCN Red List of Threatened Species* 2015: e.T22694852A60109628. Downloaded on 28.02.2020
Diving seabirds	Fratercula arctica	Endangered	BirdLife International. 2015. *Fratercula arctica*. *The IUCN Red List of Threatened Species* 2015: e.T22694927A60110592. Downloaded on 28.02.2020
Spurdog	Squalus acanthias	Endangered	Ellis, J., Soldo, A., Dureuil, M. & Fordham, S. 2015. *Squalus acanthias*. *The IUCN Red List of Threatened Species* 2015: e.T91209505A48910866. Downloaded on 16.04.2020
Large piscivorous shark	Galeorhinus galeus	Vulnerable	McCully, S., Dureuil, M. & Farrell, E. 2015. *Galeorhinus galeus*. *The IUCN Red List of Threatened Species* 2015: e.T39352A48938136. Downloaded on 16.04.2020

Small sharks	Etmopterus spinax	Near threatened	Guallart, J., Coelho, R.P., Blasdale, T., Mancusi, C., Serena, F., Ungaro, N., Litvinov, F., Crozier, P. & Stenberg, C. 2015. *Etmopterus spinax*. *The IUCN Red List of Threatened Species* 2015: e.T161388A48913532. Downloaded on 16.04.2020
Small sharks	Mustelus asterias	Near threatened	Farrell, E., McCully, S., Dulvy, N., Mancusi, C. & Ellis, J. 2015. *Mustelus asterias*. *The IUCN Red List of Threatened Species* 2015: e.T39357A48940630. Downloaded on 16.04.2020
Small sharks	Mustelus mustelus	Vulnerable	Farrell, E.D., Dulvy, N.K. & Walls, R.H.L. 2015. *Mustelus mustelus*. *The IUCN Red List of Threatened Species* 2015: e.T39358A48940145. Downloaded on 16.04.2020
Starry ray & others	Dasyatis pastinaca	Vulnerable	Serena, F., Mancusi, C., Morey, G. & Ellis, J.R. 2015. *Dasyatis pastinaca*. *The IUCN Red List of Threatened Species* 2015: e.T161453A48933979. Downloaded on 24.04.2020
Starry ray & others	Leucoraja fullonica	Vulnerable	McCully, S. & Walls, R. 2015. Leucoraja fullonica. The IUCN Red List of Threatened Species 2015: e.T161461A48938639. https://dx.doi.org/10.2305/IUCN.UK.2015-1.RLTS.T161461A48938639.en. Downloaded on 24.04.2020
Thornback & Spotted ray	Raja clavata	Near threatened	Ellis, J., Dulvy, N., Walls, R. & Serena, F. 2016. *Raja clavata*. *The IUCN Red List of Threatened Species* 2016: e.T39399A103111648. Downloaded on 24.04.2020
Skate & Cuckoo ray	Dipturus batis	Critically endangered	Dulvy, N., Notarbartolo di Sciara, G., Serena, F., Tinti, F., Ungaro, N., Mancusi, C. & Ellis, J. 2015. *Dipturus batis*. *The IUCN Red List of Threatened Species* 2015: e.T39397A72122442. Downloaded on 24.04.2020
Turbot	Scophthalmus maximus	Vulnerable	Munroe, T., Costa, M., Nielsen, J., Herrera, J., de Sola, L., Rijnsdorp, A.D. & Keskin, Ç. 2015. Scophthalmus maximus. The IUCN Red List of Threatened Species 2015:

			e.T198731A45790581. Downloaded on 25 June 2020.
Halibut	Hippoglossus hippoglossus	Vulnerable	Munroe, T., Costa, M., Nielsen, J., Herrera, J., de Sola, L., Rijnsdorp, A.D. & Keskin, Ç. 2015. Hippoglossus hippoglossus. The IUCN Red List of Threatened Species 2015: e.T10097A45790126. Downloaded on 25 June 2020.
Large demersal fish	Anguilla anguilla	Critically endangered	Freyhof, J. & Kottelat, M. 2010. Anguilla anguilla. The IUCN Red List of Threatened Species 2010: e.T60344A12353683. Downloaded on 26 June 2020.
Large demersal fish	Chimaera monstrosa	Near threatened	Dagit, D.D. & Hareide, N.-R. 2015. Chimaera monstrosa. The IUCN Red List of Threatened Species 2015: e.T63114A48912471. Downloaded on 26 June 2020.
Small demersal fish	Cyclopterus lumpus	Near threatened	Lorance, P., Cook, R., Herrera, J., de Sola, L., Florin, A. & Papaconstantinou, C. 2015. Cyclopterus lumpus. The IUCN Red List of Threatened Species 2015: e.T18237406A45078284. Downloaded on 29 June 2020.
Miscellaneous filterfeeding pelagic fish	Sardina pilchardus	Near threatened	Cook, R., Fernandes, P., Florin, A., Lorance, P. & Nedreaas, K. 2015. Sardina pilchardus. The IUCN Red List of Threatened Species 2015: e.T198580A45075369. Downloaded on 30 June 2020.

The ecological indicators that are being calculated with the ECOIND plug-in include different sets of functional groups or even individual species. While values for some indicators like trophic level or Kempton’s Q are included for the entire functional group, biomass and catch IUCN-endangered species for example are calculated on a species level. Therefore, each functional group contributes to several indicators, based on the trait information entered and further information gathered from the general model (like trophic levels). Table 2.2A - 2.4A give an overview whether a functional is included in the indicator calculation or not.

Table 2.2A: *Impact of functional groups on biomass-based indicators. X displays the inclusion of a functional group in the calculation of the individual indicator.*

Functional group	*Total Biomass*	*Fish Biomass*	*Invertebrate Biomass*	*Demersal Biomass*	*Pelagic Biomass*	*Predatory Biomass*	*Kempton's Q*	*Shannon diversity*
Toothed whales	x			x	x	x	x	x
Seals	x			x	x	x	x	x
Surface-feeding seabirds	x						x	x
Diving seabirds	x					x	x	x
Juvenile sharks	x					x	x	x
Spurdog	x			x		x	x	x
Large piscivorous sharks	x			x		x	x	x
Small sharks	x		x			x	x	x
Juvenile rays	x					x	x	x
Starry ray & others	x		x			x	x	x
Thornback & Spotted ray	x		x			x	x	x
Skate & Cuckoo ray	x		x			x	x	x
Juvenile Cod(0-2, 0-40cm)	x	x		x		x	x	x

Adult Cod (-40cm)	x	x		x		x	x	x
Juvenile Whiting (0-1, 0-20cm)	x	x		x		x	x	x
Adult Whiting (-20cm)	x	x		x		x	x	x
Juvenile Haddock (0-1, 0-20cm)	x	x	x			x	x	x
Haddock (adult)	x	x	x			x	x	x
Norway pout	x	x		x			x	x
Other gadoids (large)	x	x	x	x		x	x	x
Other gadoids (small)	x	x	x	x			x	x
Monkfish	x	x	x			x	x	x
Gurnards	x	x	x			x	x	x
Herring (juvenile 0, 1)	x	x		x	x		x	x
Herring (adult)	x	x		x	x		x	x
Sprat	x	x		x	x		x	x
Mackerel	x	x		x	x		x	x
Horse mackerel	x	x		x	x	x	x	x

Sandeels	x	x	x	x			x	x
Plaice (adult)	x	x	x				x	x
Juvenile Plaice	x	x	x			x	x	x
Dab	x	x	x			x	x	x
Long-rough dab	x	x	x			x	x	x
Flounder	x	x	x			x	x	x
Sole (adult)	x	x	x				x	x
Juvenile Sole	x	x	x			x	x	x
Lemon sole	x	x	x				x	x
Witch	x	x	x			x	x	x
Turbot	x	x	x			x	x	x
Brill	x	x	x			x	x	x
Megrim	x	x	x			x	x	x
Halibut	x	x	x			x	x	x
Dragonets	x	x	x				x	x
Large demersal fish	x	x	x	x		x	x	x
Small demersal fish	x	x	x	x		x	x	x

Miscellaneous filterfeeding pelagic fish	x	x		x	x		x	x
Squid & cuttlefish	x		x	x			x	x
Fish larvae	x						x	x
Carnivorous zooplankton	x			x	x		x	x
Herbivorous & Omnivorous zooplankton (copepods)	x			x	x		x	x
Gelatinous zooplankton	x			x	x		x	x
Large crabs	x		x				x	x
Nephrops	x		x				x	x
Epifaunal macrobenthos (mobile grazers)	x		x				x	x
Infaunal macrobenthos	x		x				x	x
Crangon (commercial size)	x		x			x	x	x
Crangon (below 5cm)	x		x			x	x	x

Shrimp	x		x	x			x	x
Small mobile epifauna (swarming crustaceans)	x		x	x			x	x
Small infauna (polychaetes)	x		x				x	x
Sessile epifauna	x		x				x	x
Meiofauna	x		x				x	x
Benthic microflora (incl. Bacteria, protozoa))	x		x				x	x
Planktonic microflora (incl. Bacteria, protozoa)	x						x	x
Phytoplankton	x						x	x

Table 2.3A: *Impact of functional groups on catch-based indicators. X displays the inclusion of a functional group in the calculation of the individual indicator. Only functional groups are shown, that are subject to fisheries in the model*

Functional group	*Total catch*	*Fish catch*	*Invertebrates catch*	*Demersal catch*	*Pelagic Catch*	*Predatory catch*	*Discards*
Spurdog	x				x	x	x
Large piscivorous sharks	x				x	x	
Small sharks	x			x		x	
Starry ray & others	x			x		x	
Thornback & Spotted ray	x			x		x	
Juvenile Cod(0-2, 0-40cm)	x	x			x	x	
Adult Cod (-40cm)	x	x			x	x	x
Juvenile Whiting (0-1, 0-20cm)	x	x			x	x	x
Adult Whiting (-20cm)	x	x			x	x	x
Juvenile Haddock (0-1, 0-20cm)	x	x		x		x	x
Haddock (adult)	x	x		x		x	x
Norway pout	x	x			x		
Other gadoids (large)	x	x		x	x	x	

Other gadoids (small)	x	x		x	x		
Monkfish	x	x		x		x	x
Gurnards	x	x		x			x
Herring (juvenile 0, 1)	x	x			x		
Herring (adult)	x	x			x		x
Sprat	x	x			x		
Mackerel	x	x			x		x
Horse mackerel	x	x			x	x	
Sandeels	x	x		x	x		
Plaice (adult)	x	x		x			x
Juvenile Plaice	x	x		x		x	x
Dab	x	x		x		x	x
Flounder	x	x		x		x	x
Sole (adult)	x	x		x			
Juvenile Sole	x	x		x		x	x
Lemon sole	x	x		x			
Witch	x	x		x		x	

Turbot	x	x		x		x	x
Brill	x	x		x		x	x
Megrim	x	x		x		x	
Halibut	x	x		x		x	
Large demersal fish	x	x		x	x	x	
Small demersal fish	x	x		x	x	x	
Miscellaneous filterfeeding pelagic fish	x	x			x		
Squid & cuttlefish	x		x	x	x		
Large crabs	x		x	x			
Nephrops	x		x	x			x
Epifaunal macrobenthos (mobile grazers)	x		x	x			
Infaunal macrobenthos	x		x	x			
Crangon (commercial size)	x		x	x		x	
Crangon (below 5cm)				x			x
Sessile epifauna	x		x		x		

Table 2.4A: *Impact of functional groups on trophic-level based indicators as well as species-based indicators. X displays the inclusion of a functional group in the calculation of the individual indicator.*

Functional group	*TL catch*	*Marine trophic index*	*Trophic level community*	*Trophic level community 2*	*Trophic level community 3.25*	*Trophic level community 4*	*IUCN biomass*	*IUCN catch*	*Mammals & Birds biomass*
Toothed whales			x	x	x	x	x		x
Seals			x	x	x	x			x
Surface-feeding seabirds			x	x			x		x
Diving seabirds			x	x	x	x	x		x
Juvenile sharks			x	x	x	x			
Spurdog	x	x	x	x	x	x	x	x	
Large piscivorous sharks	x	x	x	x	x	x	x	x	
Small sharks	x	x	x	x	x	x	x	x	
Juvenile rays			x	x	x	x			
Starry ray & others	x	x	x	x	x	x	x	x	
Thornback & Spotted ray	x	x	x	x	x	x	x	x	
Skate & Cuckoo ray			x	x	x	x	x		

Juvenile Cod(0-2, 0-40cm)	x	x	x	x	x	x
Adult Cod (-40cm)	x	x	x	x	x	x
Juvenile Whiting (0-1, 0-20cm)	x	x	x	x	x	x
Adult Whiting (-20cm)	x	x	x	x	x	x
Juvenile Haddock (0-1, 0-20cm)	x	x	x	x	x	x
Haddock (adult)	x	x	x	x	x	x
Norway pout	x	x	x	x	x	
Other gadoids (large)	x	x	x	x	x	x
Other gadoids (small)	x	x	x	x	x	
Monkfish	x	x	x	x	x	x
Gurnards	x	x	x			x
Herring (juvenile 0, 1)	x	x	x	x	x	
Herring (adult)	x	x	x	x	x	
Sprat	x		x	x		
Mackerel	x	x	x	x	x	
Horse mackerel	x	x	x	x	x	x

Sandeels	x	x	x	x	x				
Plaice (adult)	x	x	x	x	x				
Juvenile Plaice	x	x	x	x	x	x			
Dab	x	x	x	x	x	x			
Long-rough dab			x	x	x	x			
Flounder	x	x	x	x	x	x			
Sole (adult)	x	x	x	x	x				
Juvenile Sole	x	x	x	x	x	x			
Lemon sole	x	x	x	x	x				
Witch	x	x	x	x	x	x			
Turbot	x	x	x	x	x	x	x	x	
Brill	x	x	x	x	x	x			
Megrim	x	x	x	x	x	x			
Halibut	x	x	x	x	x	x	x	x	
Dragonets			x	x	x				
Large demersal fish	x	x	x	x	x	x	x	x	
Small demersal fish	x	x	x	x	x	x	x	x	
Miscellaneous filterfeeding pelagic fish	x	x	x	x	x		x	x	
Squid & cuttlefish	x	x	x	x	x				
Fish larvae			x	x					

Carnivorous zooplankton			x	x					
Herbivorous & Omnivorous zooplankton (copepods)			x	x					
Gelatinous zooplankton			x	x	x				
Large crabs	x	x	x	x	x				
Nephrops	x	x	x	x	x				
Epifaunal macrobenthos (mobile grazers)	x	x	x	x	x				
Infaunal macrobenthos	x		x	x					
Crangon (commercial size)	x	x	x	x	x	x			
Crangon (below 5cm)			x	x	x	x			
Shrimp			x	x					
Small mobile epifauna (swarming crustaceans)			x	x					
Small infauna (polychaetes)			x	x					

Sessile epifauna	x	x	x
Meiofauna		x	x
Benthic microflora (incl. Bacteria, protozoa))		x	x
Planktonic microflora (incl. Bacteria, protozoa)		x	x
Phytoplankton		x	

A3 Effort reduction

Scenarios that cover at least 30% of the modelled area were executed twice, with the original effort and with a fleet-specific reduction in fishing effort due to the implementation of MPAs. For this, the extent of overlap between fishing grounds and closures was calculated. To derive the percentage of fishing ground lost due to closures, we divided the overlapping cells by the total number of fishing ground cells. Subsequently, the effort of 2010 was reduced by the percentage and implemented as effort for 2011 in Ecosim (Table 3.1A).

Table 3.1A: *Percentage of lost fishing grounds and resulting effort in 2011 implemented in Ecosim for scenarios executed again with a reduction in effort*

Fleets in EwE	*OWF_MPA Scenario Effort in 2011*	*OWF_MPA Scenario % lost fishing ground*	*IUCN Scenario Effort in 2011*	*IUCN Scenario % lost fishing ground*	*Kempton Scenario Effort in 2011*	*Kempton Scenario % lost fishing ground*
Beam trawl	0.1867	0.2555	0.1550	0.3819	0.1992	0.2053
Beam trawl targeting sole	0.2707	0.2555	0.2247	0.3819	0.2984	0.2053
Demersal trawl and demersal seiner	0.0921	0.2155	0.0875	0.2549	0.0795	0.3229
Dredges	0.7730	0.2270	0.6293	0.3707	0.6034	0.3966
Drift and fixed nets	0.6801	0.1285	0.5499	0.2953	0.5888	0.2455
Gears using hooks	0.8337	0.1663	0.5449	0.4551	0.8317	0.1683
Nephrops trawl	0.3124	0.0975	0.2904	0.1610	0.2331	0.3267
Others	0.9369	0.0631	0.9822	0.0178	0.9822	0.0178
Pelagic trawl	0.4135	0.0705	0.4361	0.0196	0.4361	0.0196
Pots	0.9128	0.0872	0.9645	0.0355	0.9645	0.0355
Sandeel trawl	0.2408	0.0662	0.2533	0.0177	0.2533	0.0177

Shrimp trawlers	0.8709	0.2259	0.7791	0.3075	0.7591	0.3253

A4 Changes to the original model

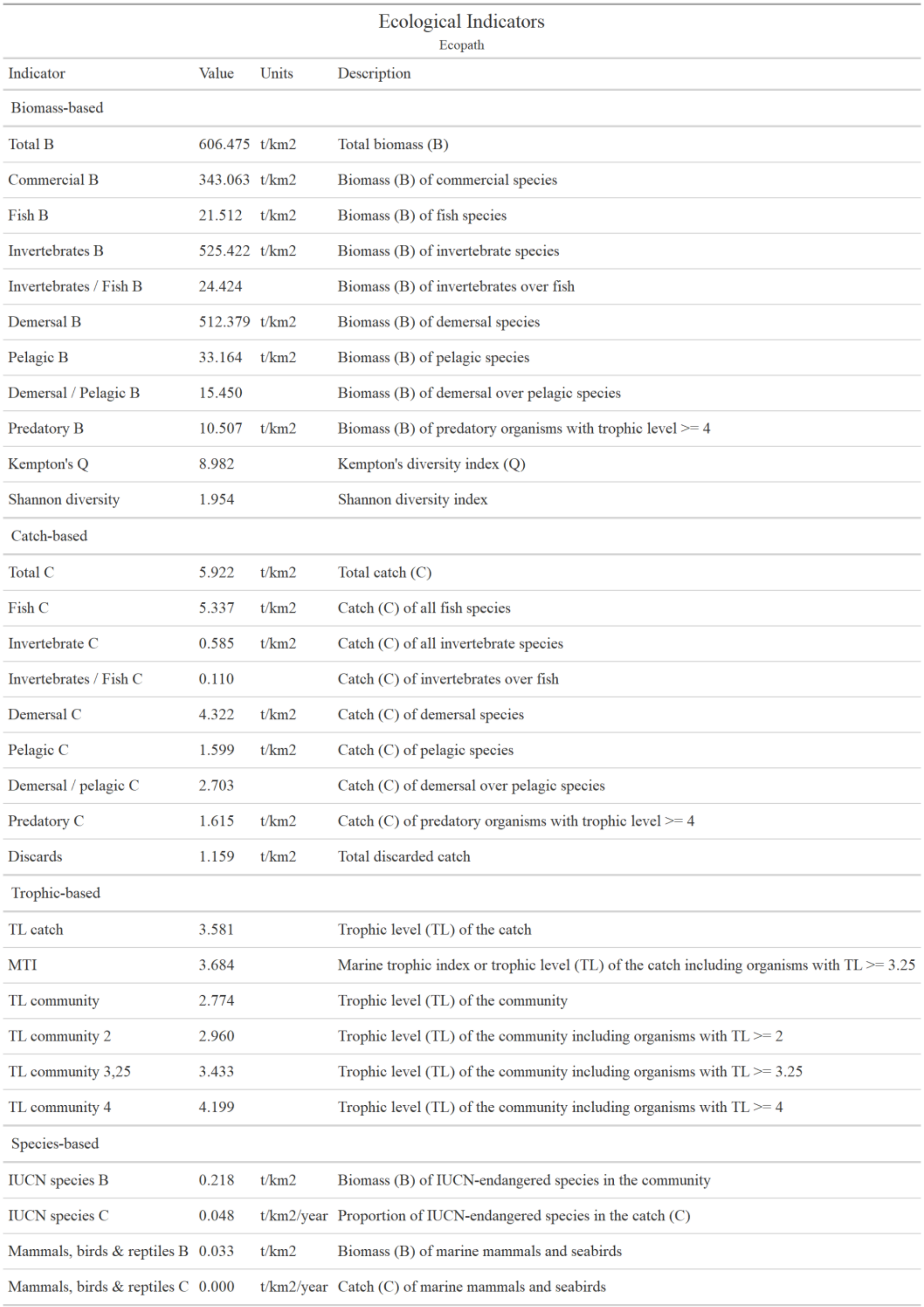
Compared to the model published in Püts et al. 2020, several small changes have been implemented. The depth preference function of halibut was adapted, since biomass in Ecospace dropped too low, due to a too restrictive preference function. Crangon (juvenile) discards were added equal to landings (50% of the catch is being discarded), with a discard mortality rate of 0.2 based on Lancaster and Frid (2002) was added. The diet of toothed whales was adapted in regards to norway pout as the proportion in the diet was too large. A comparison between biomass of Norway pout in entire North Sea to southern North Sea. Southern North Sea is 66% of stock. Therefore 66% taken (~0.147) and the rest of diet was equally distributed among all other prey groups of toothed whales. The sediment habitat layer was also adapted. Prior to the changes, each cell contained the sediment, which covered the largest area of a cell. After the adaption each cell contains proportional amounts of sediment types, data based on EMODNET sediment data retrieved for publication of Püts et al., 2020. Biomass reference time series for sole (juvenile) and sole (adult) were adapted based on the values released with the latest benchmark in 2020 (ICES, 2020). Furthermore, a temperature preference function based on cod (juvenile) preferred temperature ranges and reference temperature layers based on SST data for 1991 to 2010 retrieved from a highly resolved (0.05° x 0.05°) re-analysis product (ODYSSEA NW+IBI Sea Surface Temperature analysis; product unit SST-IFREMER-BREST-FR; Data form E.U. Copernicus Marine Service Information was used, downloaded on 28.09.2020).

Appendix B

B1 ECOIND results for Ecopath and Ecosim

Before executing the different scenarios in Ecospace, ecological indicators in Ecopath and Ecosim were compiled to get a general picture of the ecosystem (Table 1.1B, Figure 1.1B and Figure 1.2B).

Table 1.1B: *Sub-set of ecological indicators representing the Ecopath model for the southern part of the North Sea*



Ecological Indicators

Ecopath

Indicator	Value	Units	Description
Biomass-based			
Total B	606.475	t/km2	Total biomass (B)
Commercial B	343.063	t/km2	Biomass (B) of commercial species
Fish B	21.512	t/km2	Biomass (B) of fish species
Invertebrates B	525.422	t/km2	Biomass (B) of invertebrate species
Invertebrates / Fish B	24.424		Biomass (B) of invertebrates over fish
Demersal B	512.379	t/km2	Biomass (B) of demersal species
Pelagic B	33.164	t/km2	Biomass (B) of pelagic species
Demersal / Pelagic B	15.450		Biomass (B) of demersal over pelagic species
Predatory B	10.507	t/km2	Biomass (B) of predatory organisms with trophic level >= 4
Kempton's Q	8.982		Kempton's diversity index (Q)
Shannon diversity	1.954		Shannon diversity index
Catch-based			
Total C	5.922	t/km2	Total catch (C)
Fish C	5.337	t/km2	Catch (C) of all fish species
Invertebrate C	0.585	t/km2	Catch (C) of all invertebrate species
Invertebrates / Fish C	0.110		Catch (C) of invertebrates over fish
Demersal C	4.322	t/km2	Catch (C) of demersal species
Pelagic C	1.599	t/km2	Catch (C) of pelagic species
Demersal / pelagic C	2.703		Catch (C) of demersal over pelagic species
Predatory C	1.615	t/km2	Catch (C) of predatory organisms with trophic level >= 4
Discards	1.159	t/km2	Total discarded catch
Trophic-based			
TL catch	3.581		Trophic level (TL) of the catch
MTI	3.684		Marine trophic index or trophic level (TL) of the catch including organisms with TL >= 3.25
TL community	2.774		Trophic level (TL) of the community
TL community 2	2.960		Trophic level (TL) of the community including organisms with TL >= 2
TL community 3,25	3.433		Trophic level (TL) of the community including organisms with TL >= 3.25
TL community 4	4.199		Trophic level (TL) of the community including organisms with TL >= 4
Species-based			
IUCN species B	0.218	t/km2	Biomass (B) of IUCN-endangered species in the community
IUCN species C	0.048	t/km2/year	Proportion of IUCN-endangered species in the catch (C)
Mammals, birds & reptiles B	0.033	t/km2	Biomass (B) of marine mammals and seabirds
Mammals, birds & reptiles C	0.000	t/km2/year	Catch (C) of marine mammals and seabirds

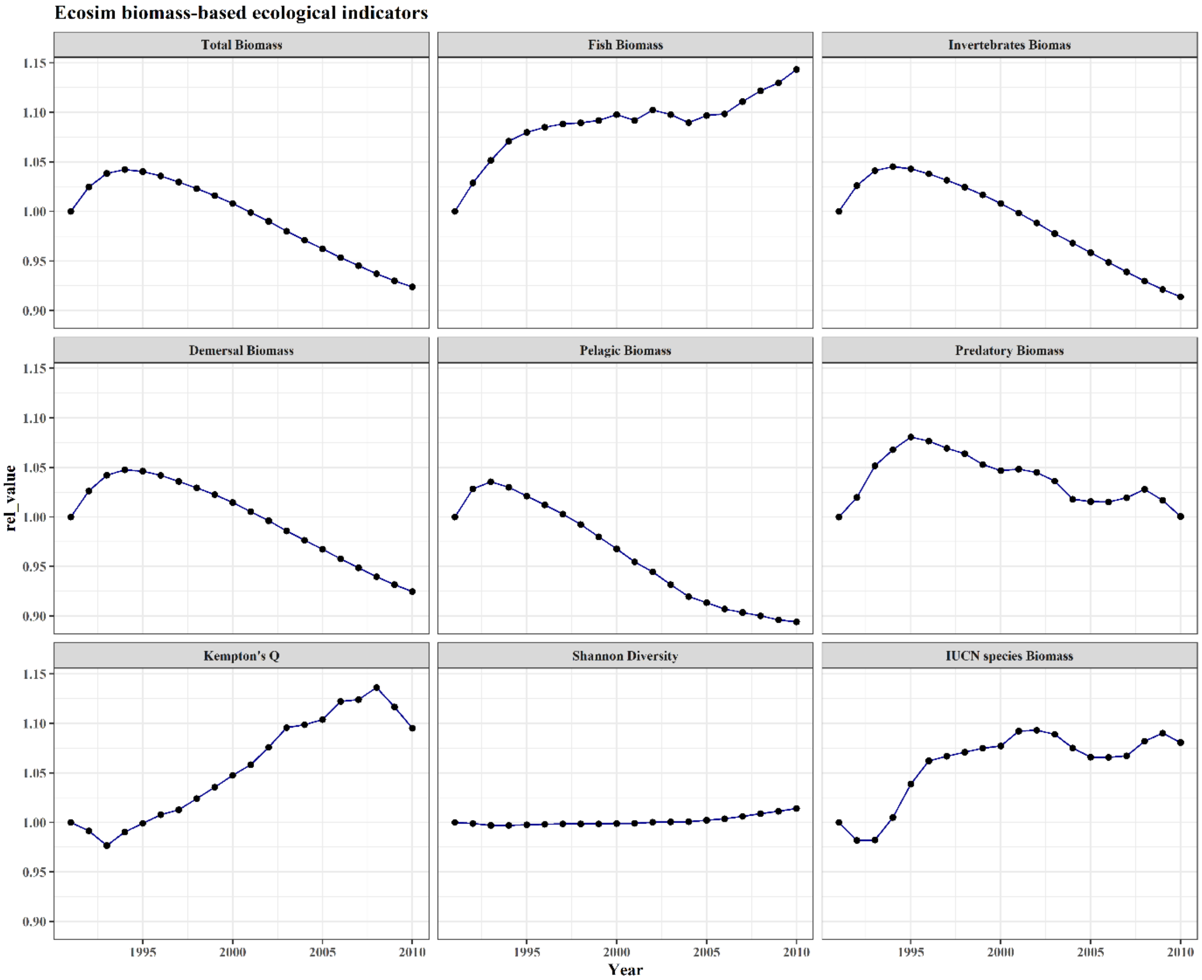
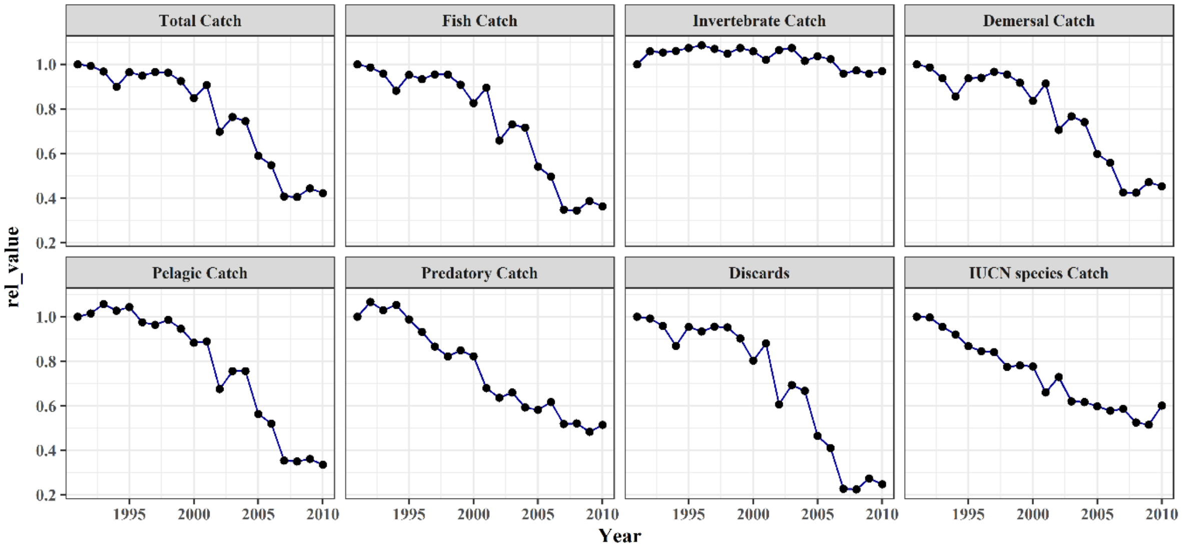


Figure 1.1B: *Sub-set of biomass-based indicators including the species-based biomass trend for IUCN-endangered species. All time series are presented relative to the Ecopath year 1991 for a better comparability among indicators.*

Ecosim catch-based ecological indicators



Ecosim fleets effort time series

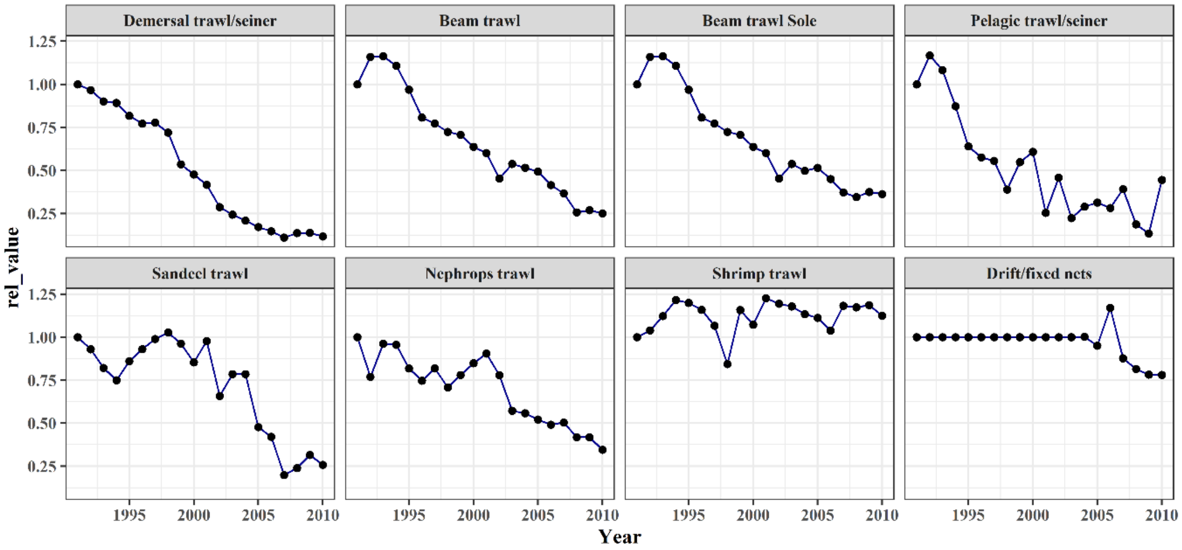


Figure 1.2B: *Upper panel: Sub-set of catch-based indicators including the species-based catch trend for IUCN-endangered species. All time series are presented relative to the Ecopath year 1991 for a better comparability among indicators.* *Lower panel: Effort time series implemented in Ecosim*

B2 Remaining Ecospace results ECOIND

Baseline spatial patterns

For a more lucid presentation, only a subset of spatial patterns of indicators derived from the baseline run with no closures were presented in the paper. Some patterns are reflected well by the maps included in the publication. Others did not show distinct patterns or just minor changes; therefore, they were just presented in this Appendix B. Changes relative to the baseline scenario in trophic levels (TL) were 0.5% and less and therefore not presented in the results section of the paper (Figure 2.3B + 2.4B).

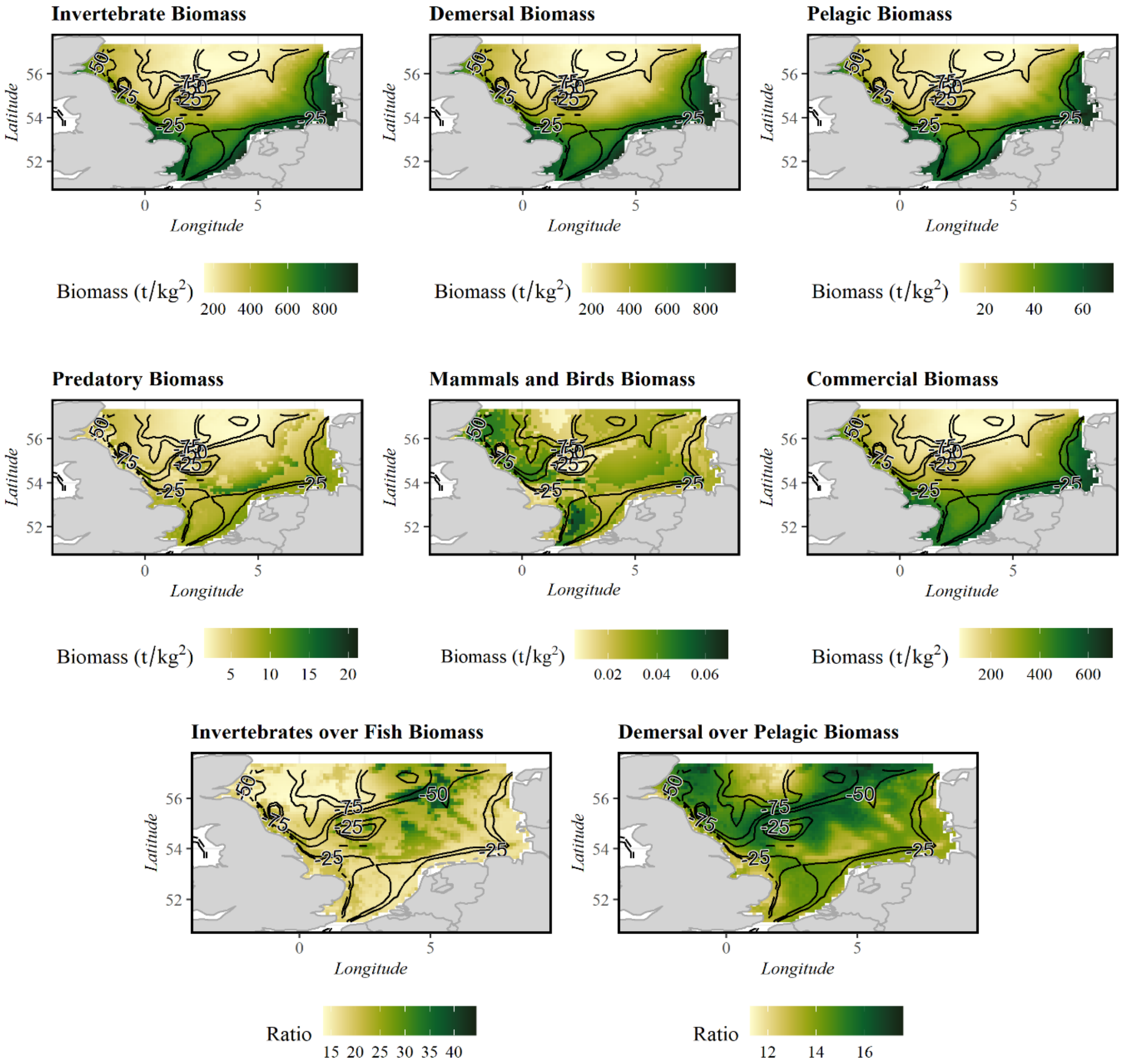


Figure 2.1B: *Spatial patterns of remaining biomass-based indicators derived from the baseline run*

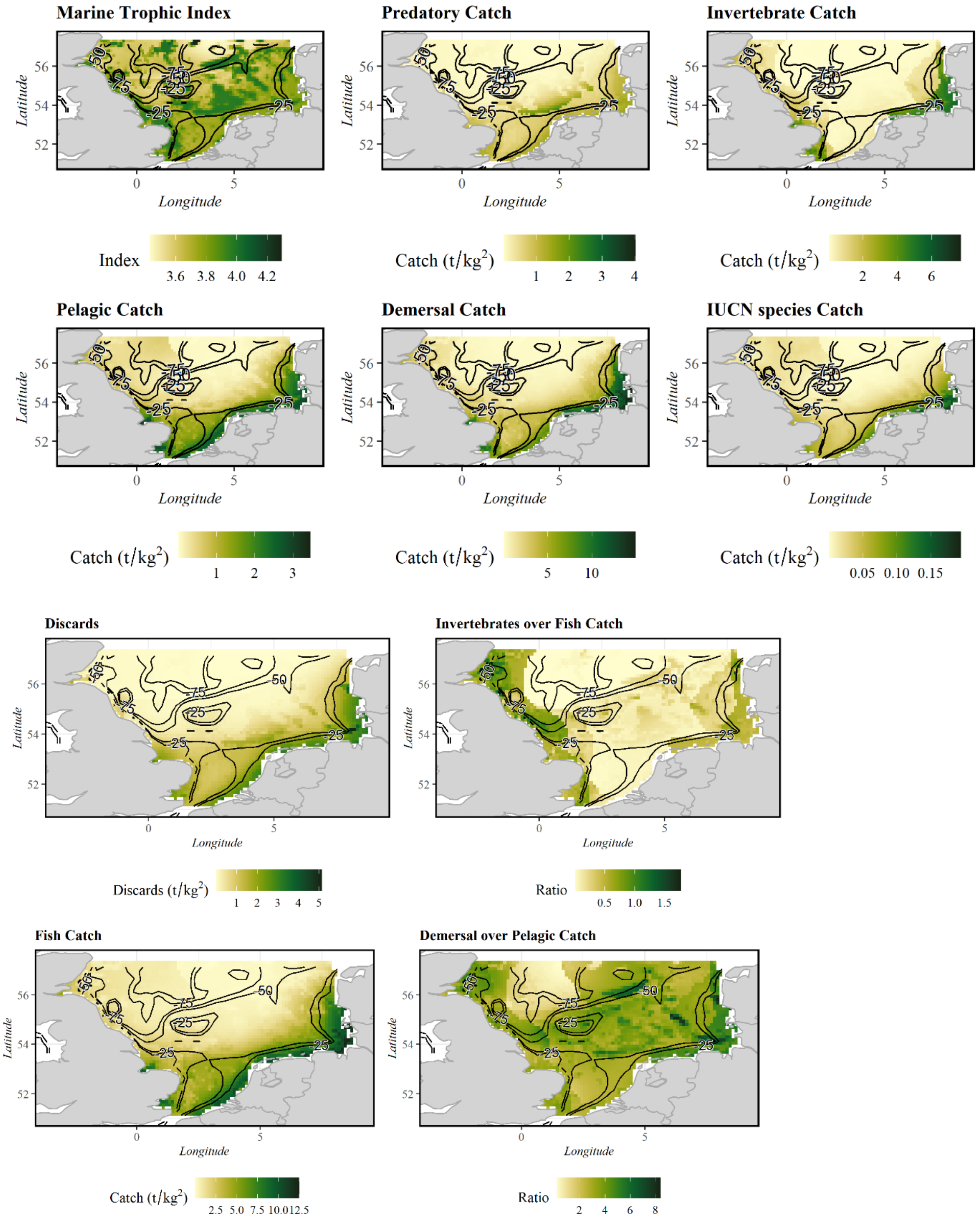


Figure 2.2B: *Spatial patterns of remaining catch-based indicators derived from the baseline run*

Trophic levels

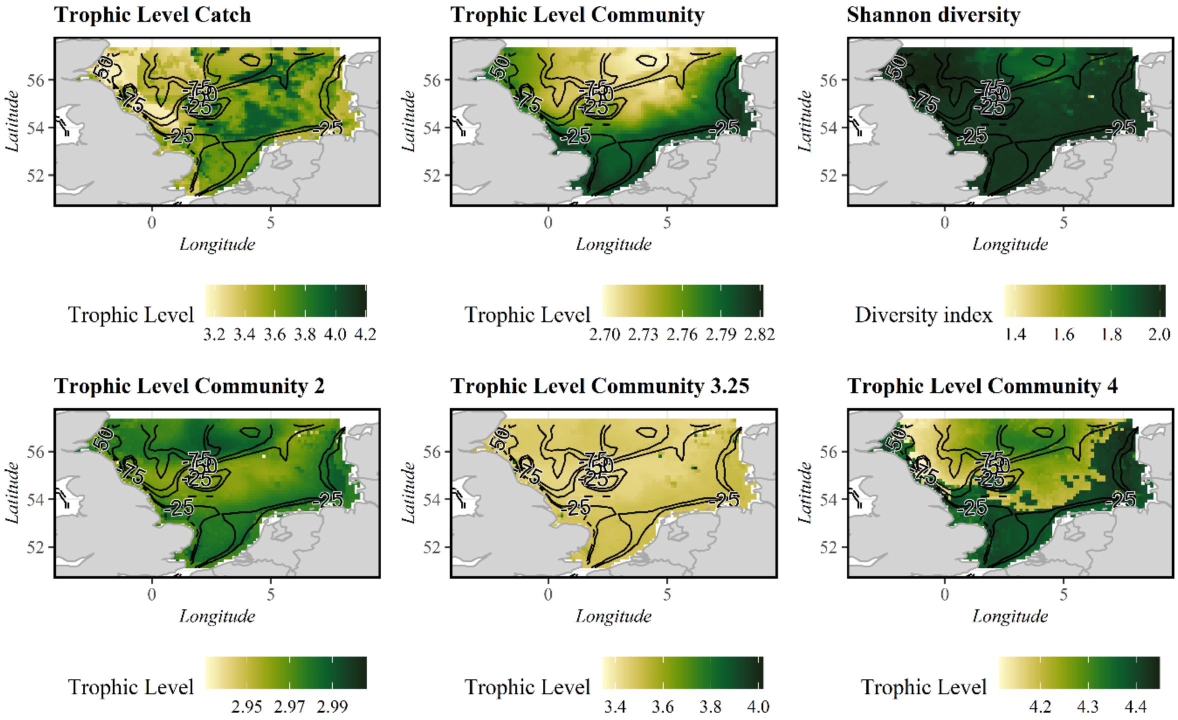


Figure 2.3B: *Spatial patterns of remaining trophic level and species-based indicators derived from the baseline run*

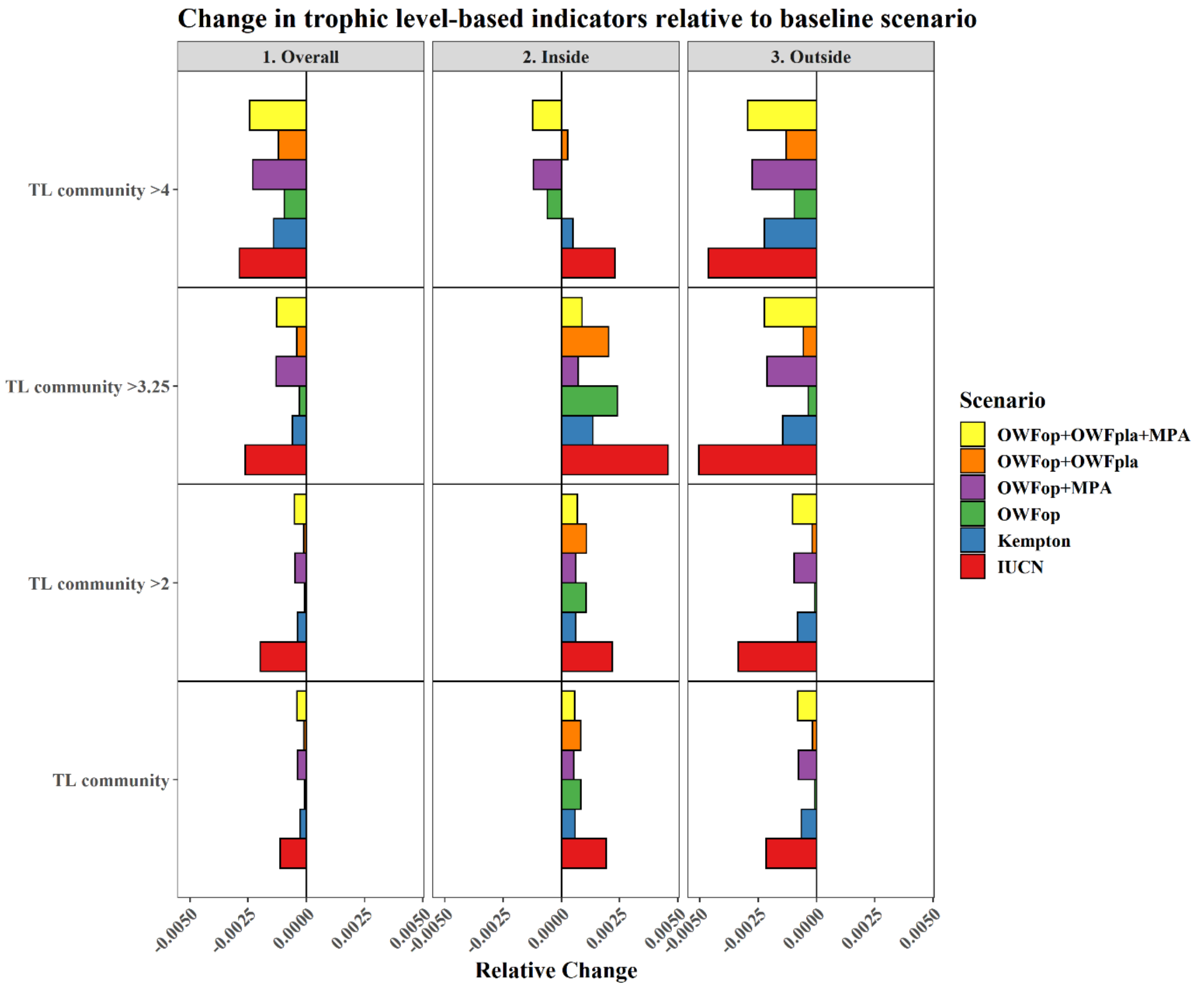
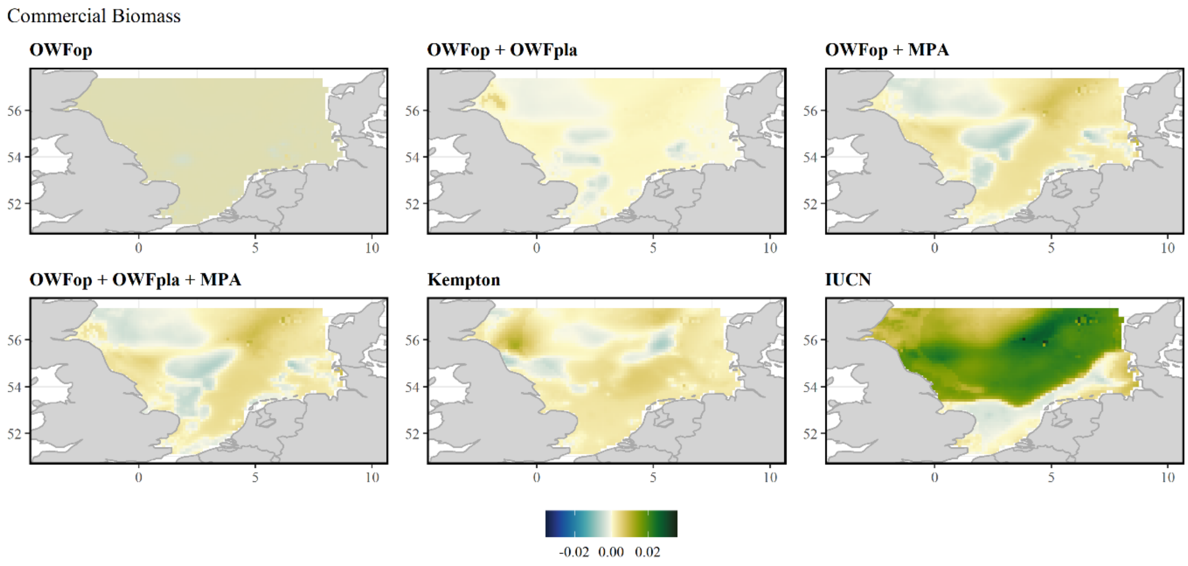
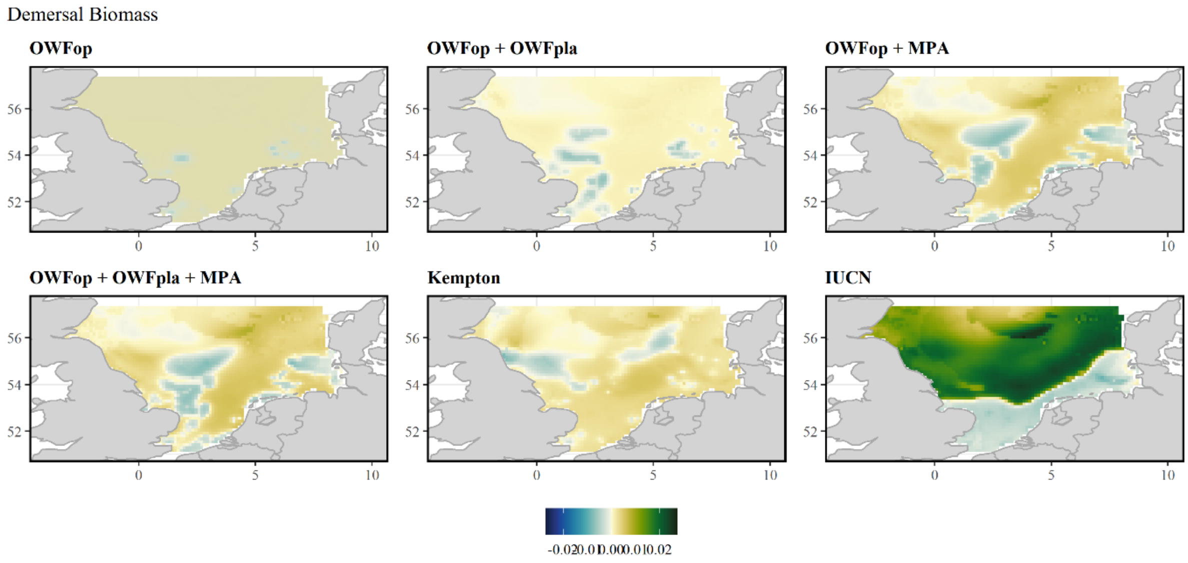


Figure 2.4B: *Changes in trophic level-based indicators relative to the baseline run for the different closure scenarios. Left: Results for the entire model area. Middle: Results inside the closed areas. Right: Results outside the closed areas in the different scenarios.*

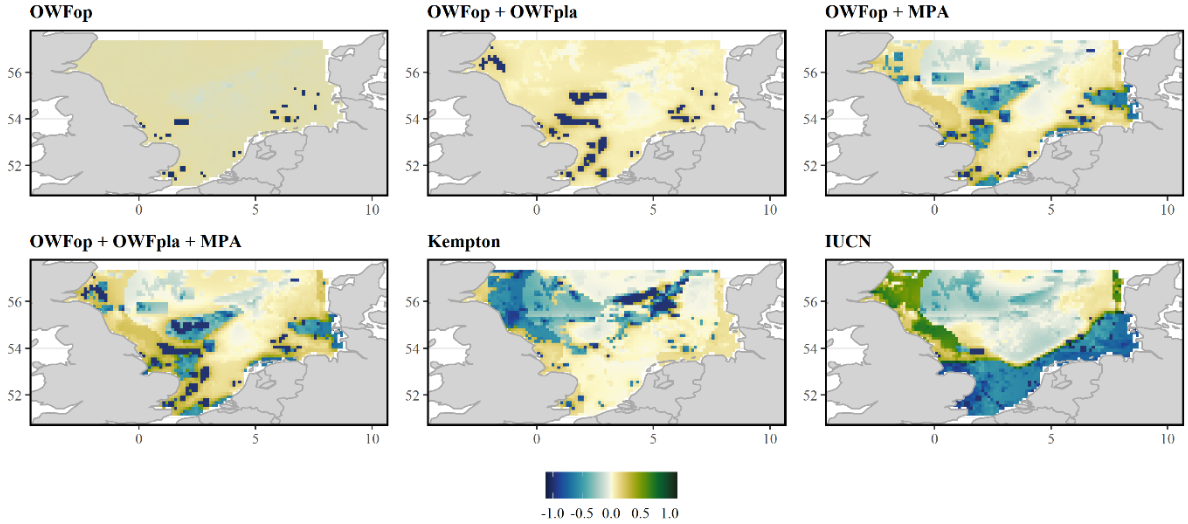
Shifts in spatial patterns

Similar to the spatial patterns of the baseline run, not all results could be included in the paper. The remaining results are presented in Figure 2.5B.





Demersal Catch



OWFop

OWFop + OWFpla

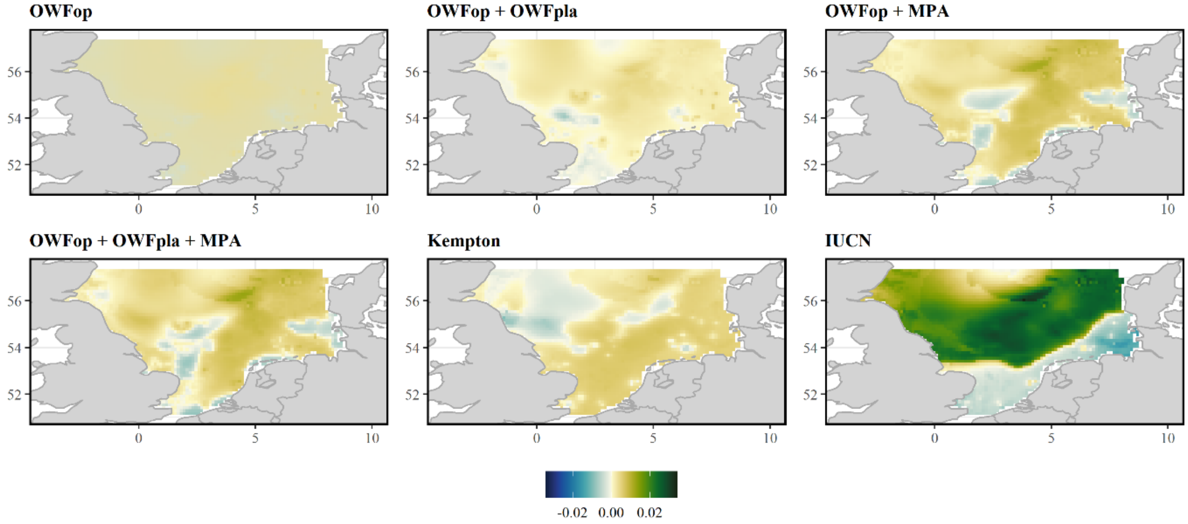
OWFop + MPA

OWFop + OWFpla + MPA

Kempton

IUCN

Demersal vs. Pelagic Biomass



OWFop

OWFop + OWFpla

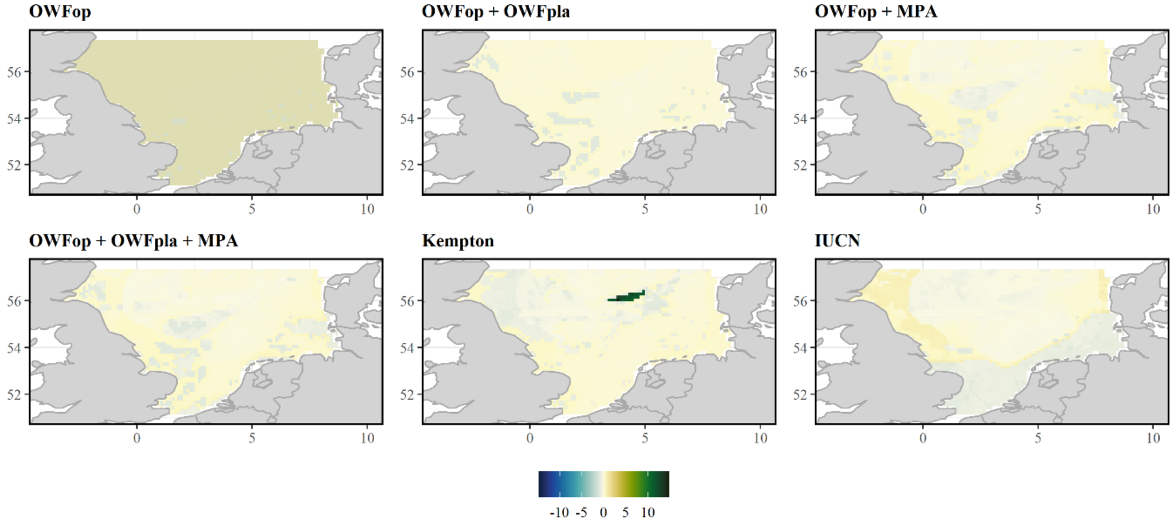
OWFop + MPA

OWFop + OWFpla + MPA

Kempton

IUCN

Demersal vs. Pelagic Catch



OWFop

OWFop + OWFpla

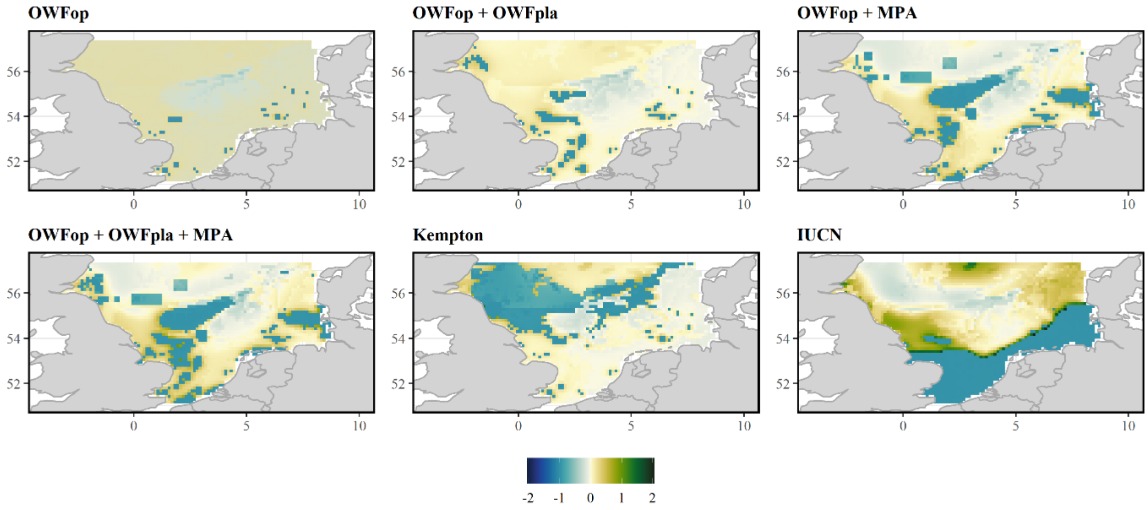
OWFop + MPA

OWFop + OWFpla + MPA

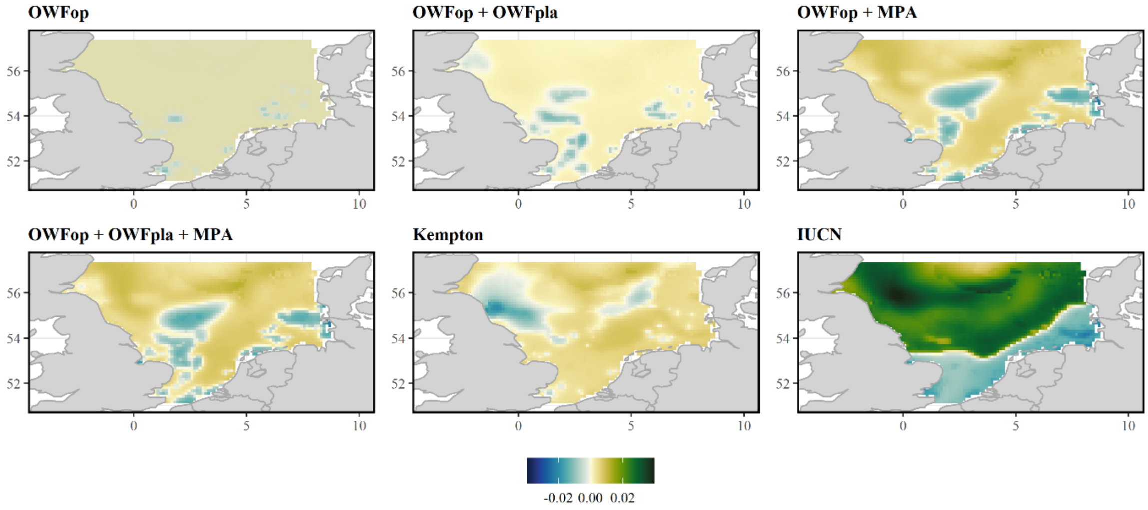
Kempton

IUCN

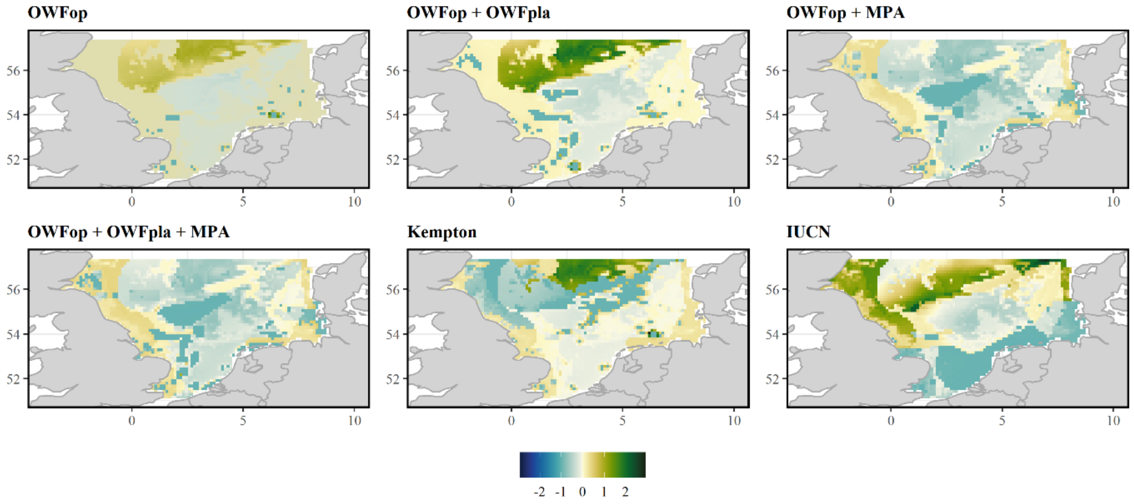
Discards



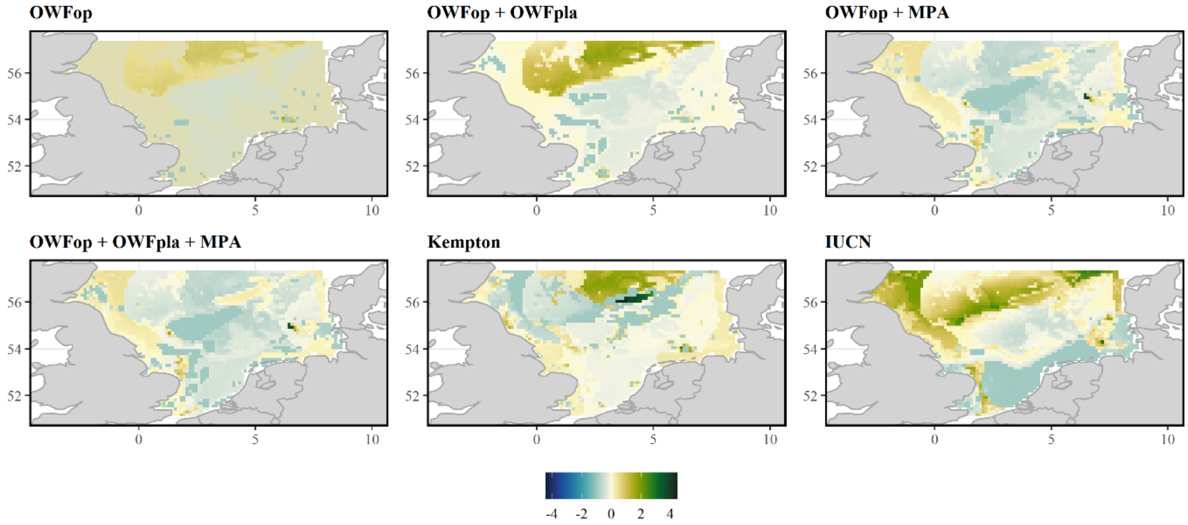
Invertebrates Biomass



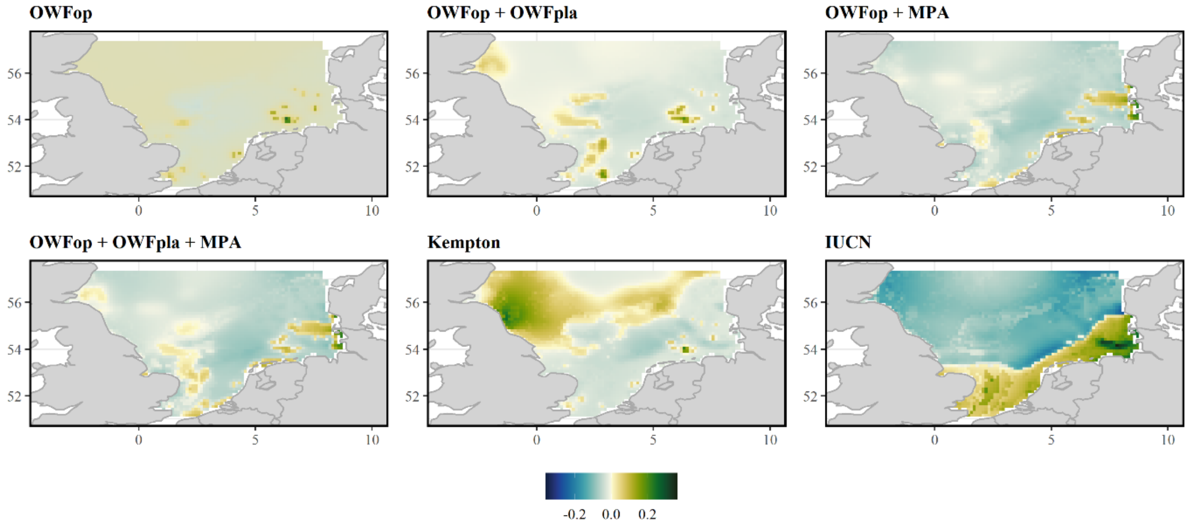
Invertebrates Catch



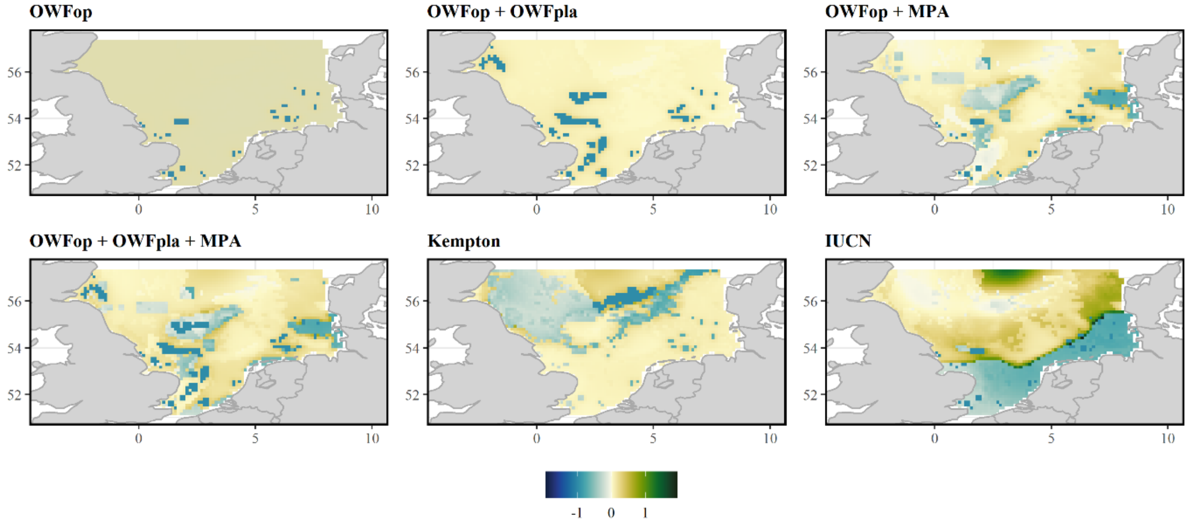
Invertebrates vs. Fish Catch



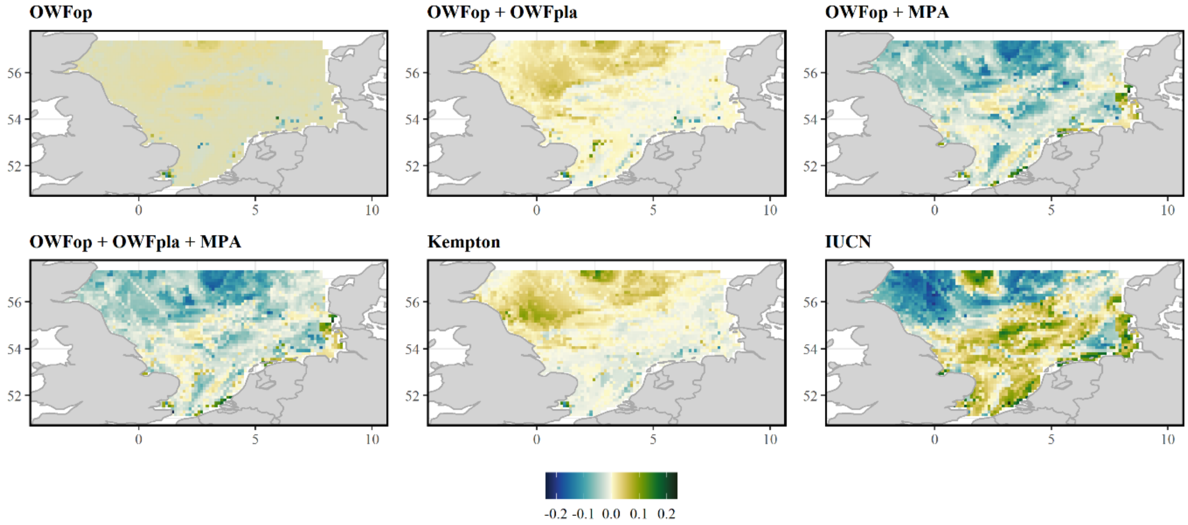
IUCN species Biomass



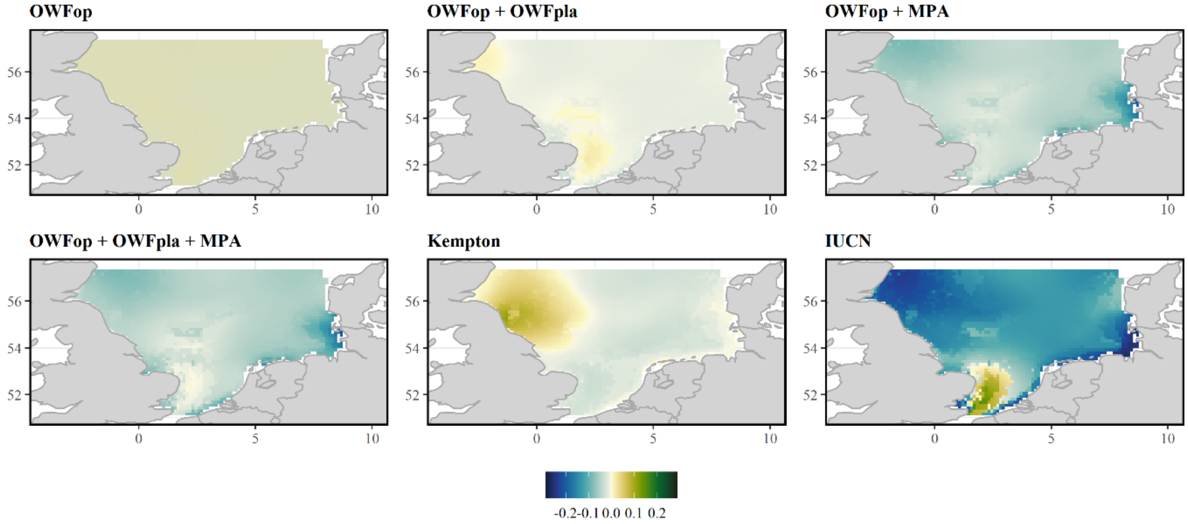
IUCN species Catch



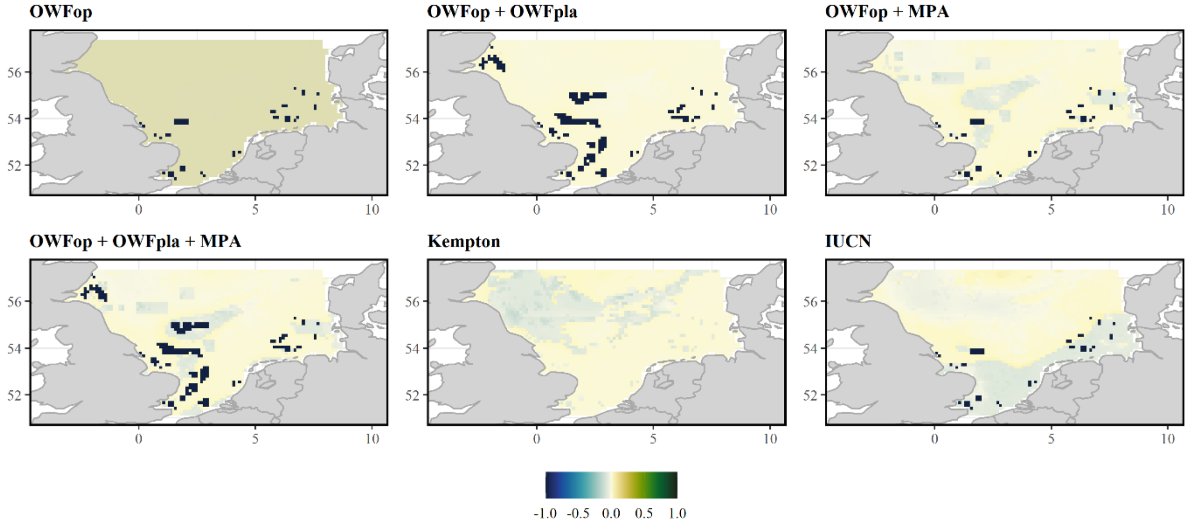
Kempton's Q



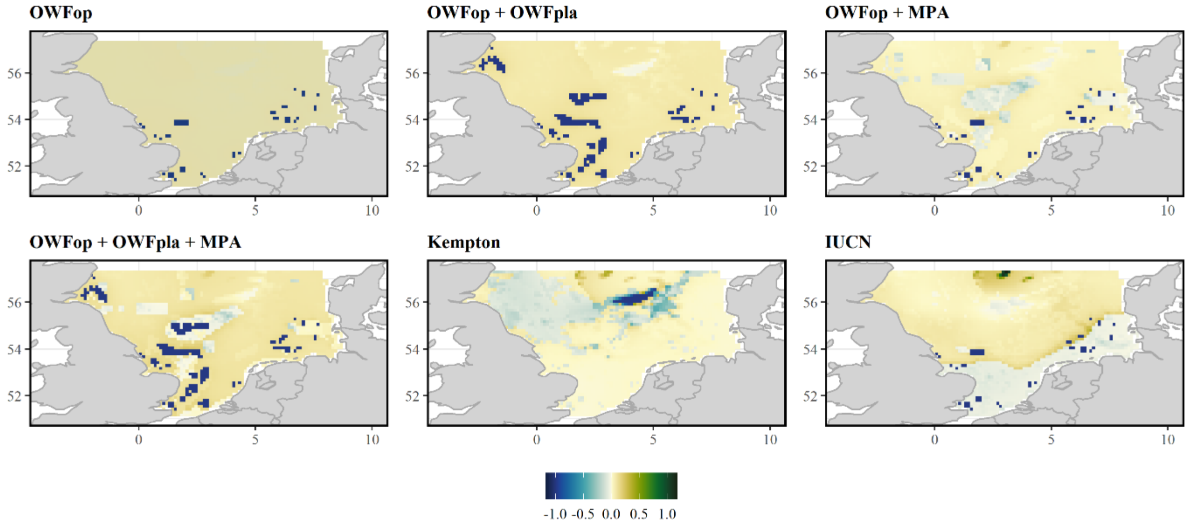
Mammals and Birds Biomass



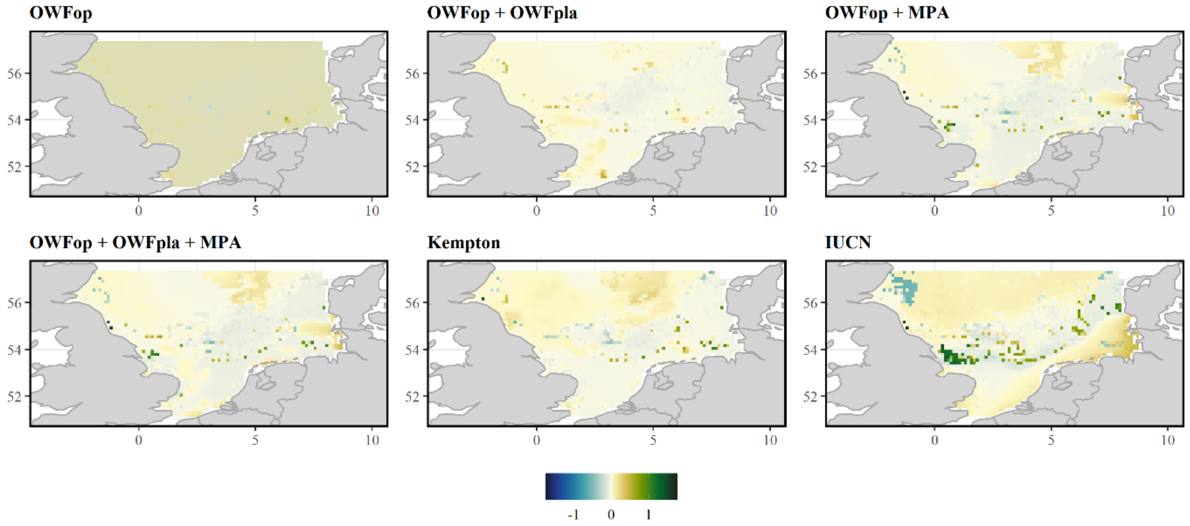
Marine Trophic Index



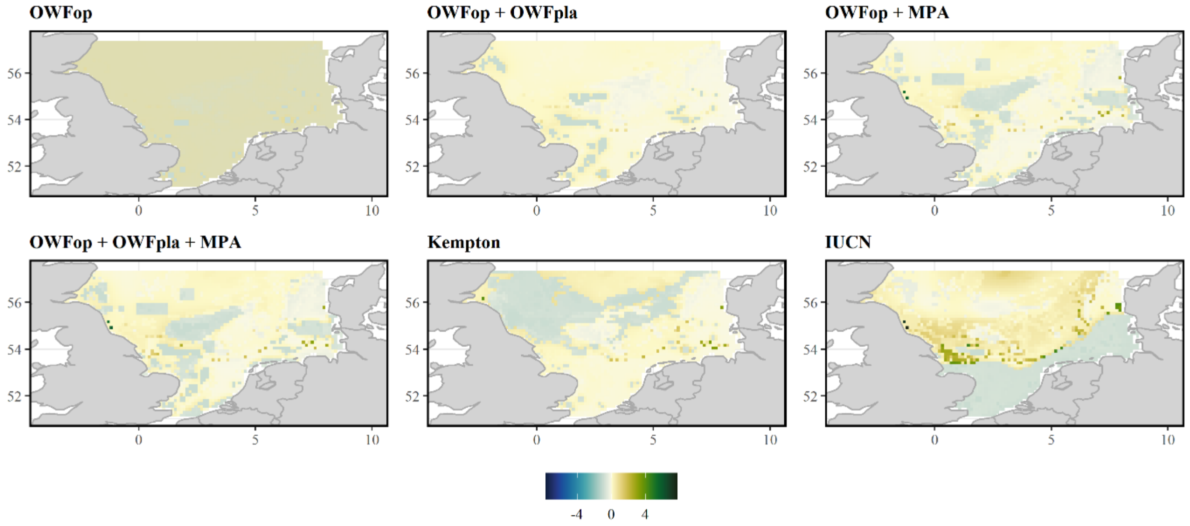
Pelagic Catch



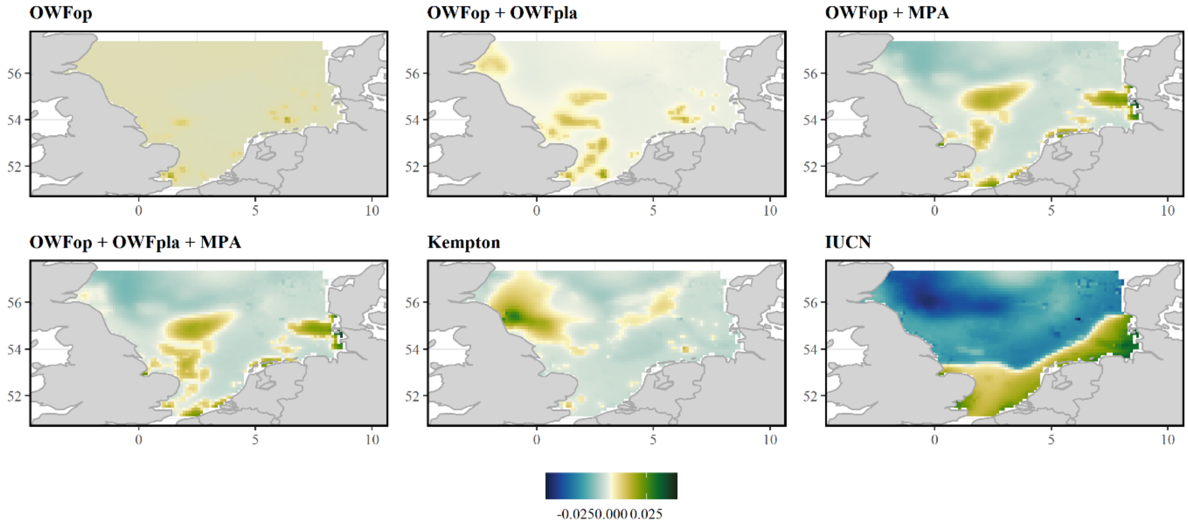
Predatory Biomass



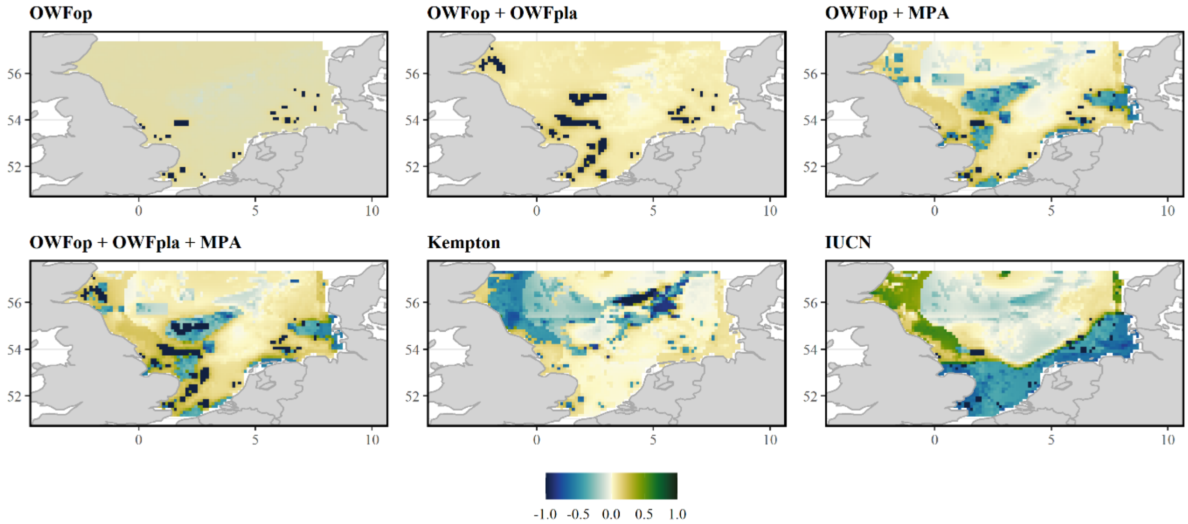
Predatory Catch



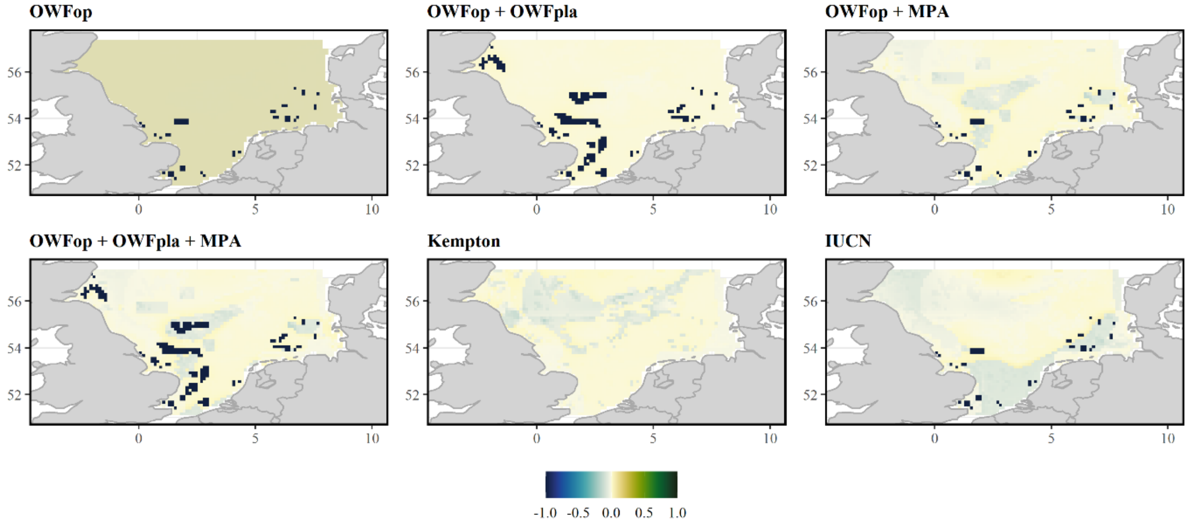
Shannon Diversity



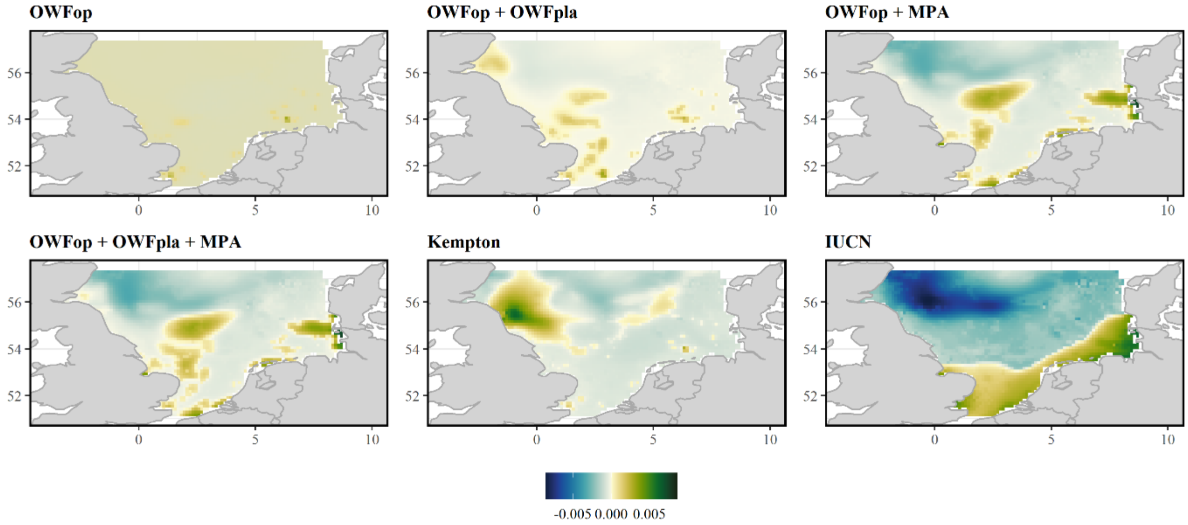
Total Catch



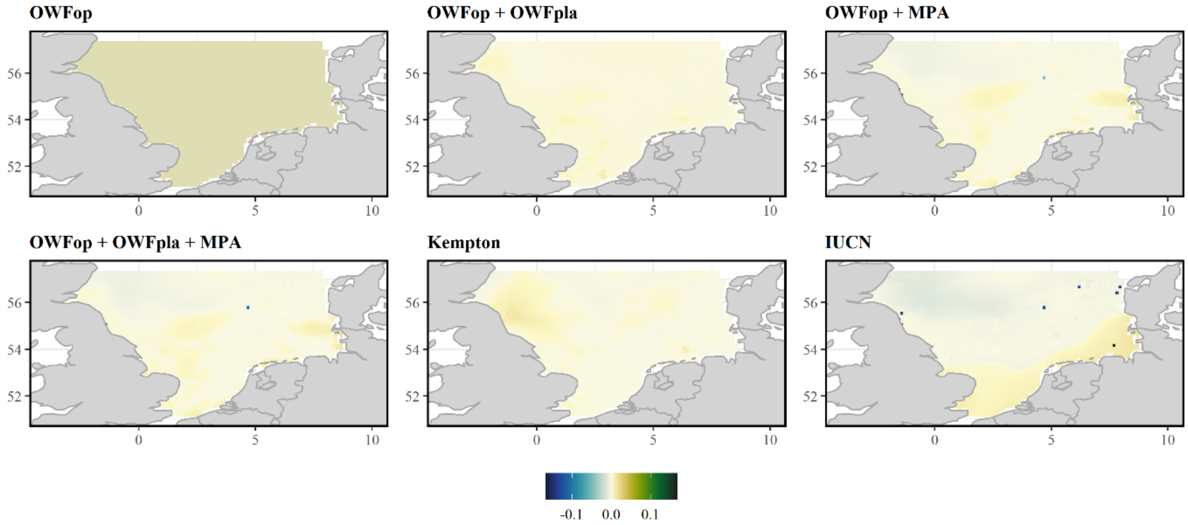
Trophic Level Catch



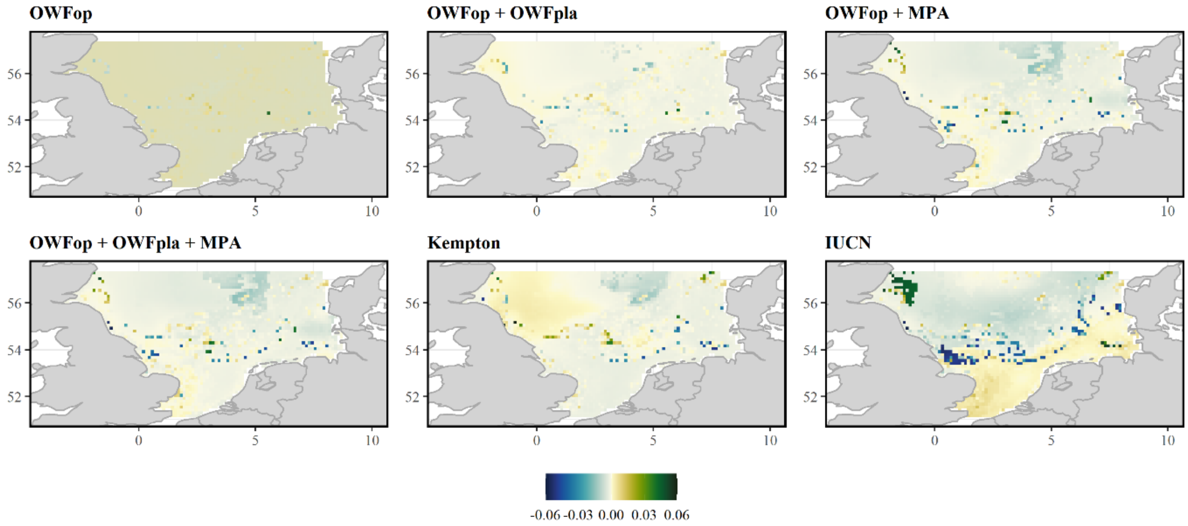
Trophic Level Community 2



Trophic Level Community 3.25



Trophic Level Community 4



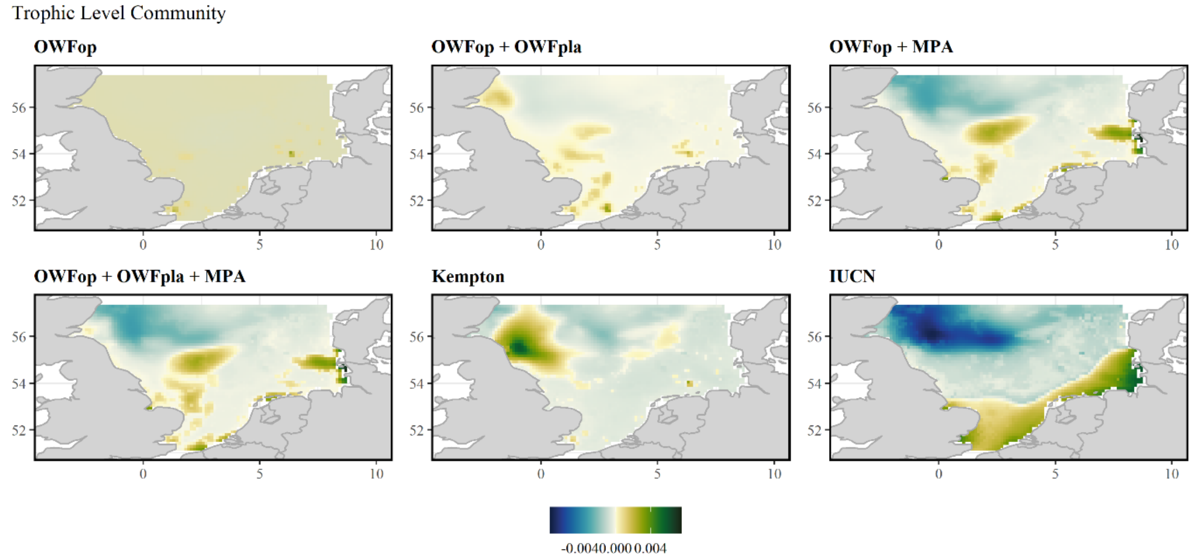


Figure 2.5B: *Changes in remaining ecological indicators for each of the six scenarios. Changes are relative to baseline scenario with no closures with increases displayed by yellow to greenish colors and a decrease displayed by blue.*

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Publication 4. - *Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea*

Appendix

This Appendix is divided into part A and part B. Part A describes small changes that were made to the original EwE model for the southern part of the North Sea. Part B shows the remaining results that were not featured in the publication.

Appendix A

A Ecosim and Ecospace adaptations

The main adaptation applied to the model was applied to the group info included in Ecosim. The group info includes information such as feeding time under predation risk or handling time of prey (Christensen et al., 2008). Feeding time adjustment rates are implemented to stabilize consumption rates per biomass, best practice recommendations suggest an adjustment of feeding rates only for marine mammals and potentially juvenile stanza groups (Christensen et al., 2008). The EwE model for the southern part of the North Sea was build on the basis of the EwE model for the entire North Sea and thus included feeding times implemented in this model (Mackinson & Daskalov, 2007). However, for Ecospace these feeding rates were reset to 0 for all functional groups, except for the functional groups included in the recommendations, to stabilize multi-stanza interactions (Table A1).

Table A1: *Adapted feeding time adjustment rates*

Functional groups	*Feeding time adjustment rate*
Toothed whales	0.5
Seals	0.5
Cod (juvenile)	0.5
Whiting (juvenile)	0.5

Haddock (juvenile)	0.1
Herring (juvenile)	0.5
Plaice (juvenile)	0.5
Sole (juvenile)	0.5
Crangon (below 5cm)	1

Functional responses were included in the model to drive the foraging capacity in relation to changing temperatures in Ecospace. These responses were structured based on temperature affinities of the individual species included. Four temperature values were used to designate the trapezoid shape of the functional response: total minimum and maximum and preferred minimum and maximum temperatures, defining the optimum temperature range. When these ranges are exceeded for certain functional groups, their consumption rate is decreased (Christensen et al., 2014). Table A2 displays the functional groups for which temperature values in 2050 already exceed this optimum range.

Table A2: *Mean and max temperatures for both RCP scenarios in 2050. Red x indicates a mismatch between temperatures and the optimum temperature range for the functional group. Only functional groups are shown, that are impacted by the increasing temperatures.*

Functional group	*RCP4.5 2050 Mean = 11.4*	*RCP8.5 2050 Mean = 11.7*	*RCP4.5 2050 Max= 13.7*	*RCP8.5 2050 Max=14.2*
Brill	O	O	O	O
Cod	O	O	X	X
Dab	O	O	X	X
Haddock	O	O	X	X
Halibut	X	X	X	X
Herring	O	O	X	X
Large crabs	O	O	X	X
Lemon sole	O	O	X	X
Long-rough dab	X	X	X	X
Norway pout	O	O	X	X
Other gadoids (large)	O	O	X	X
Plaice	O	O	X	X
Sandeels	O	O	X	X

Seals	O	O	X	X
Shrimp	X	X	X	X
Sprat	O	O	X	X
Starry ray & others	X	X	X	X
Turbot	O	O	X	X
Whiting	O	O	X	X
Witch	O	O	X	X
Sessile epifauna	O	O	X	X
Small mobile epifauna	O	O	X	X
Epifaunal macrobenthos	O	O	X	X

Appendix B

B Remaining model outputs

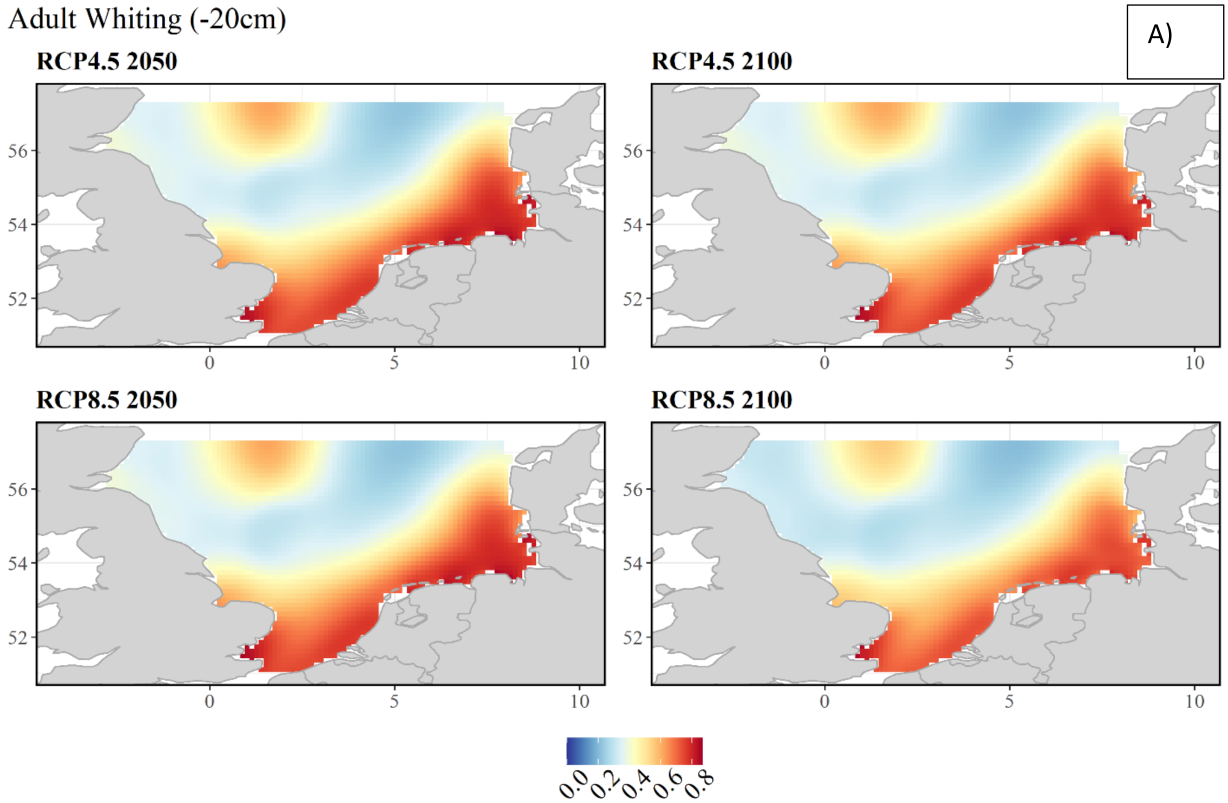
For all ecological indicators, a shift in center of gravity was calculated by calculating the weighted mean of latitude and longitude of each indicator (Table B1).

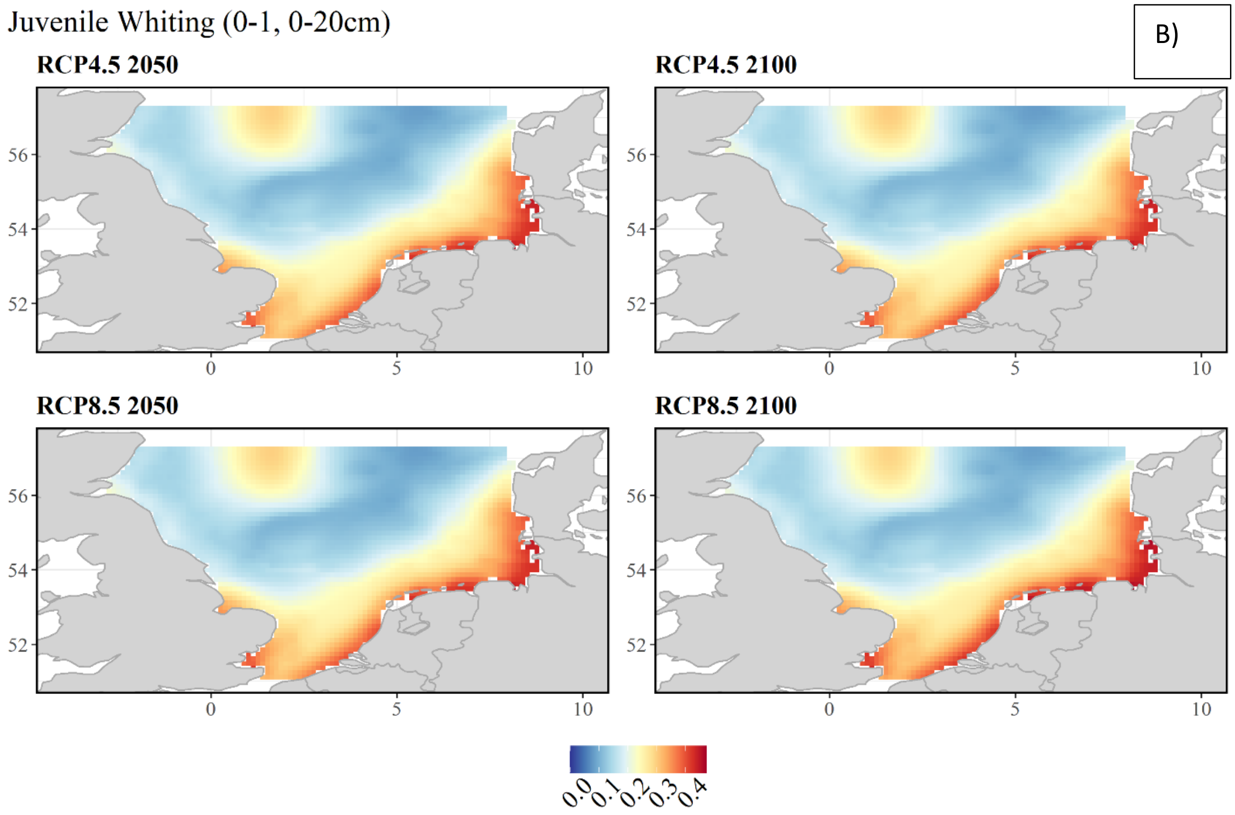
Table B1: *Shift in center of gravity for analyzed ecological indicators*

Ecological Indicator	*Maximum shift*	*Shift direction*
Commercial Biomass	0.02405755	South
Demersal/Pelagic Biomass	0.02524366	South
Demersal/Pelagic Catch	0.09190089	North
Demersal Biomass	0.03540548	South
Demersal Catch	0.23093507	North
Discards	0.15911062	North
Fish Biomass	0.14302166	North
Fish Catch	0.21753025	North
Invertebrate Catch	0.05184663	North
Invertebrate/Fish Biomass	0.15982196	South
Invertebrate/Fish Catch	0.07744897	South

Invertebrate Biomass	0.04141015	South
IUCN species Biomass	0.08596035	North
IUCN species Catch	0.04073435	South
Kempton's Q	0.02232061	North
Mammals & Birds Biomass	0.0755559	North
Mammals & Birds Catch	0.03941174	North
Marine Trophic Index	0.07538419	South
Pelagic Biomass	0.03996581	South
Pelagic Catch	0.02828206	South
Predatory Biomass	0.00992816	South
Predatory Catch	0.09704661	North
Shannon diversity	0.17584345	South
Trophic level catch	0.24788044	South
Trophic level community	0.03153206	North
Trophic level community 2	0.02410517	South
Trophic level community 3.25	0.00399217	South
Trophic level community 4	0.00282296	South
Total Biomass	0.00478225	South
Total Catch	0.194079274	North

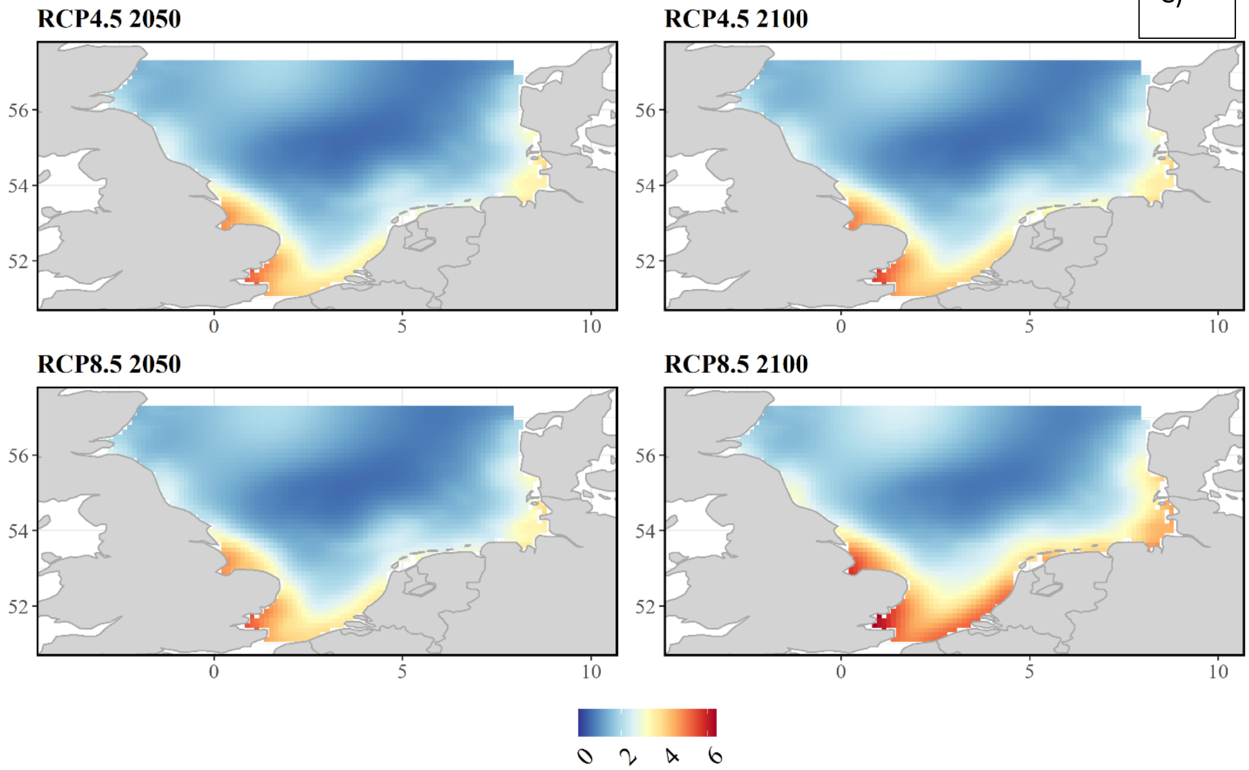
In the publication, only the distribution patterns of the stanzas with the greatest overall change were displayed. In the following, the remaining distribution shifts of the five analyzed commercial species are displayed (Figure B1).


Adult Whiting (-20cm)
A)
RCP4.5 2050
RCP4.5 2100
RCP8.5 2050
RCP8.5 2100
56
54
52
0
5
10
0.0
0.2
0.4
0.6
0.8


Juvenile Whiting (0-1, 0-20cm)
B)
RCP4.5 2050
RCP4.5 2100
RCP8.5 2050
RCP8.5 2100
56
54
52
0
5
10
0.0
0.1
0.2
0.3
0.4

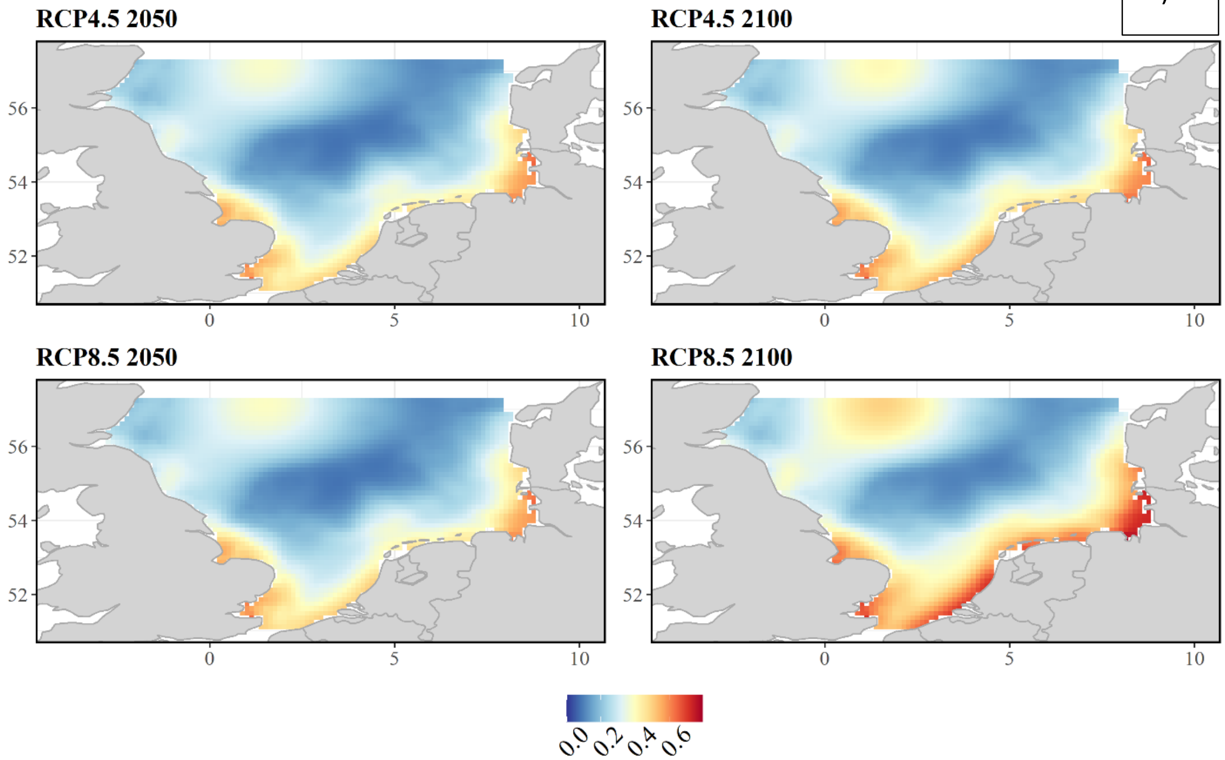
Herring (adult)

C)



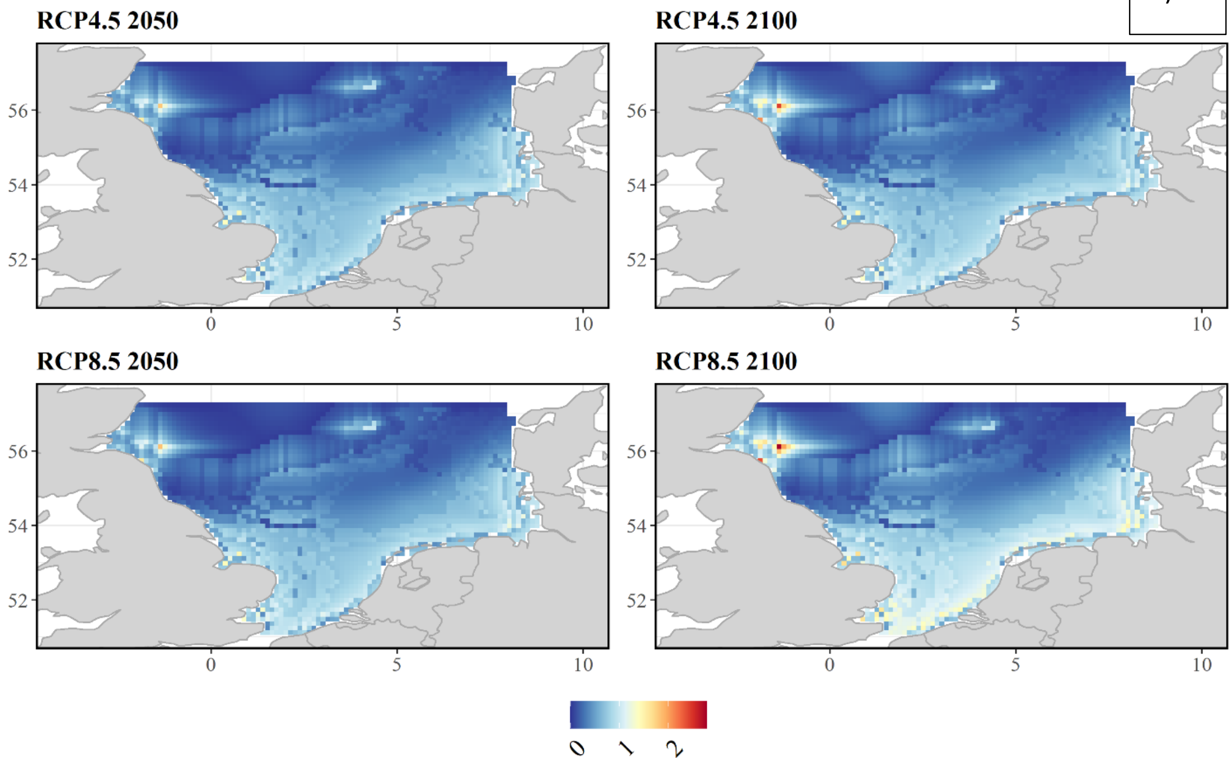
Herring (juvenile 0, 1)

D)



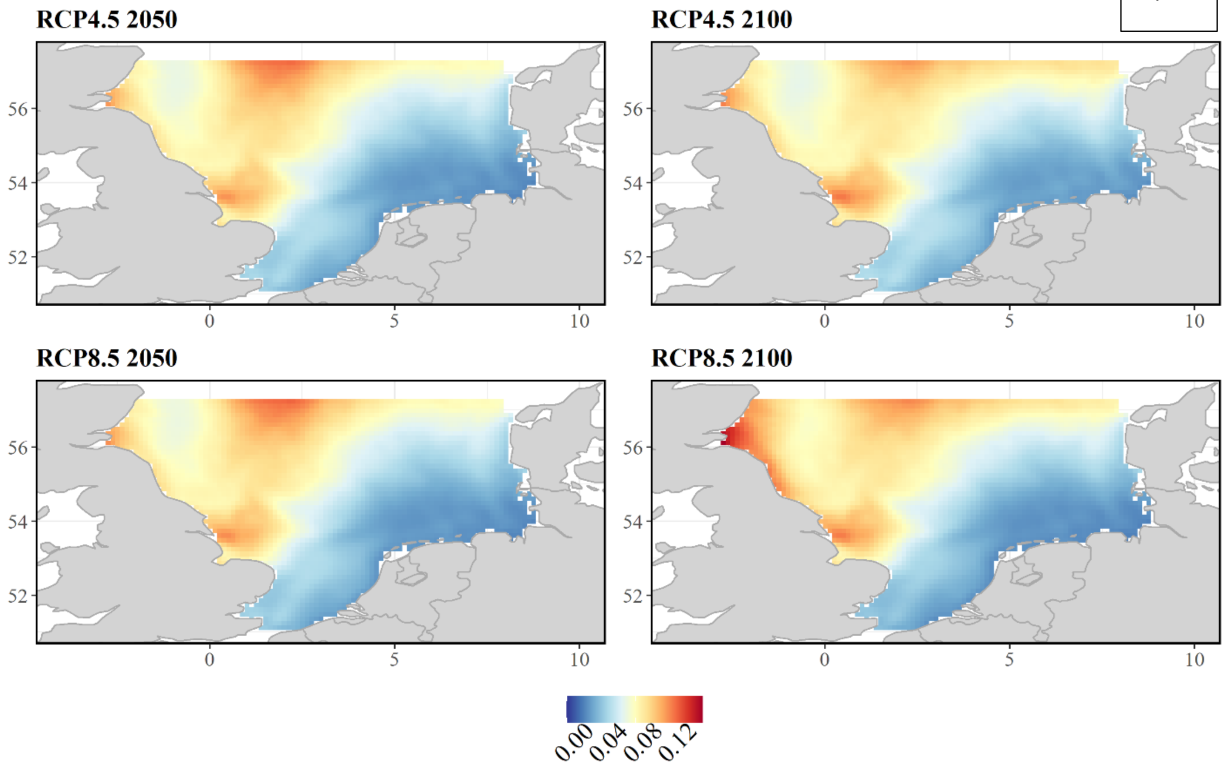
Sole (adult)

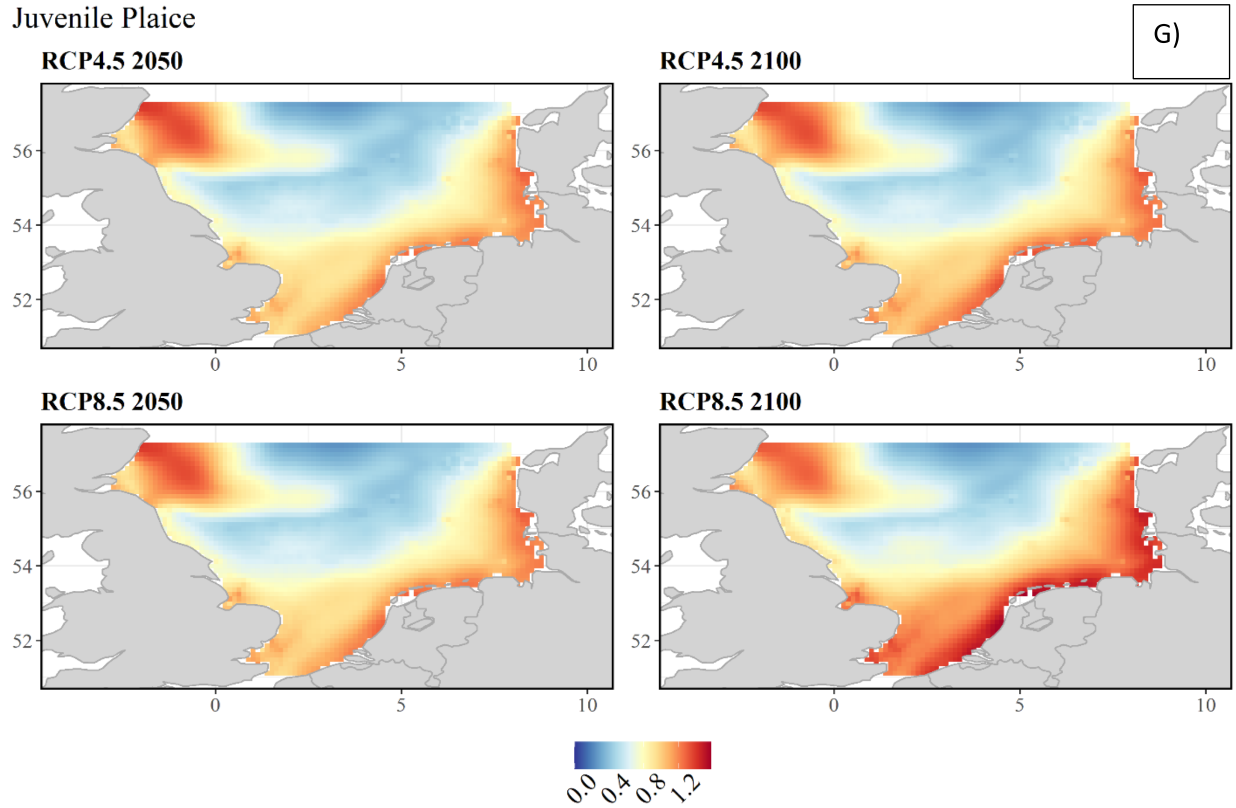
E)



Juvenile Cod(0-2, 0-40cm)

F)





Juvenile Plaice

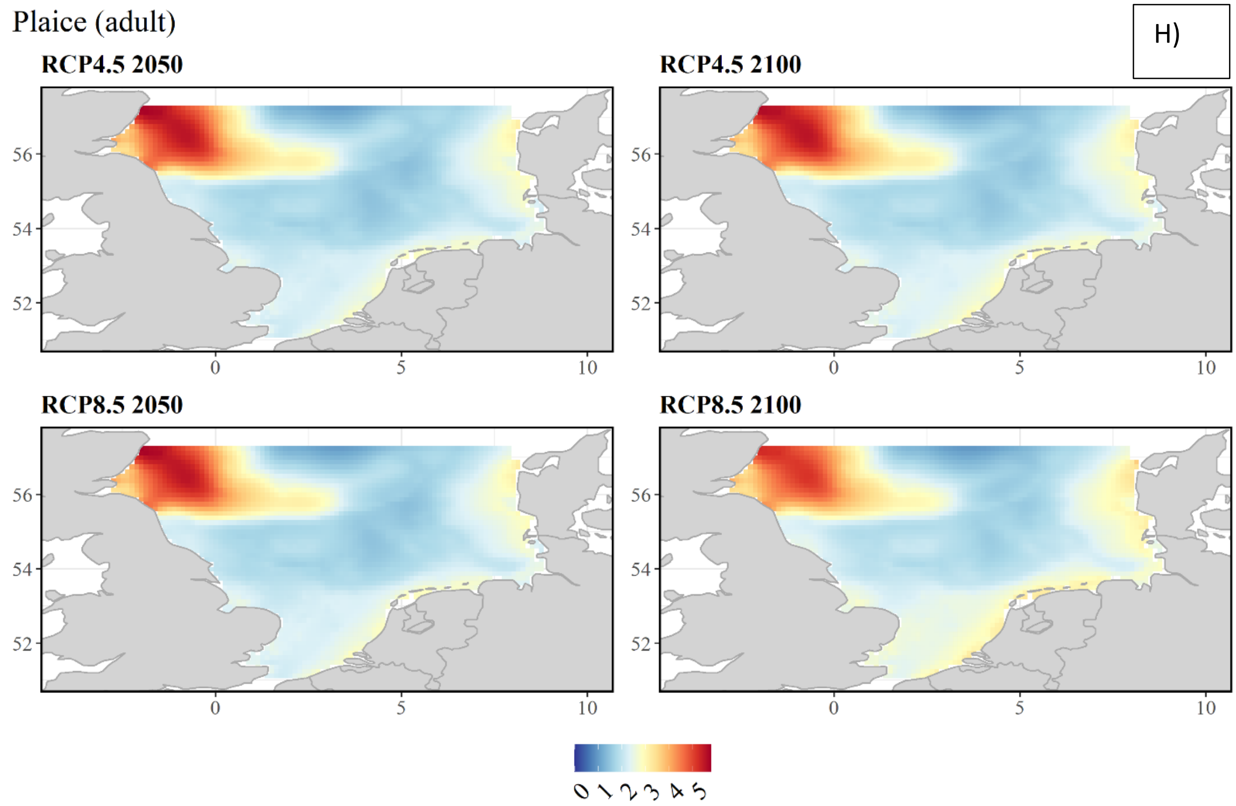
G)

RCP4.5 2050

RCP4.5 2100

RCP8.5 2050

RCP8.5 2100



Plaice (adult)

H)

RCP4.5 2050

RCP4.5 2100

RCP8.5 2050

RCP8.5 2100

Figure B1: *Plots A-H display the biomass distributions of the commercial species focused on in the publication.*

References for Appendix A & B

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., & Walters, C. J., 2014. Representing Variable Habitat Quality in a Spatial Food Web Model. *Ecosystems*, *17*(8). https://doi.org/10.1007/s10021-014-9803-3

Christensen, V., Walters, C. J., Pauly, D., & Forrest, R., 2008. Ecopath with Ecosim version 6 User Guide. *Fisheries Centre, University of British Columbia, Vancouver, Canada*, *281*(November), 1–235. http://sources.ecopath.org/trac/Ecopath/wiki/UsersGuide

Mackinson, S., & Daskalov, G., 2007. An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation. *Science Series*, *142*, 196pp.

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Declaration on Oath

I hereby declare upon oath that I have written the present dissertation "Evaluating spatial processes and management strategies under changing anthropogenic influences on the ecosystem of the southern part of the North Sea" independently and have not used further resources or aids than stated.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift dissertation "Evaluating spatial processes and management strategies under changing anthropogenic influences on the ecosystem of the southern part of the North Sea" selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Miriam Püts

Bremen, 11.11.2021 Miriam Püts