Assessment of the state of the Baltic Sea fish community

Understanding the impacts of environmental change to support effective management

Dissertation

With the aim of achieving a doctoral degree at the

Faculty of Mathematics, Informatics and Natural Sciences

Department of Biology of the University of Hamburg

Institute for Marine Ecosystem and Fishery Science

Submitted by Frane Madiraca

Hamburg 2026

The following evaluators recommended the admission of the dissertation:
Prof. Dr. Christian Mollmann (supervisor and evaluator), University of Hamburg
Dr. Saskia A. Otto (co-supervisor and evaluator), University of Hamburg

Commission for the disputation:
Prof. Dr. Christian Mollmann (supervisor and examiner), University of Hamburg
Dr. Saskia A. Otto (co-supervisor and examiner), University of Hamburg
Jun.-Prof. Dr. Flemming Dahlke (chair), University of Hamburg
Prof. Dr. Kai Jensen (deputy chair), University of Hamburg

Date of disputation: 17.4.2026

To my father Pavle,
often admired for his bright mind that was
only outshined by his caring heart.

AUTHOR CONTRIBUTIONS

Chapter 1

Environmentally driven shifts of Baltic fish distributions and their impact on spatiotemporal overlap between species

FM and SO defined the study. **FM** performed the statistical analysis and wrote the original draft. SO substantialy contributed to writing of the final version of the manuscript. All authors reviewed and commented on the manuscript.

Chapter 2

Shifting distributions of Baltic Sea fish under future environmental change

FM and SO defined the study. CD and HEMM shared key data and contributed to defining the study. **FM** performed the statistical analysis and wrote the original draft. SO substantialy contributed to writing of the final version of the manuscript. All authors reviewed and commented on the manuscript.

Chapter 3

Potential mismatches between spatial protection and changing fish community structure and functioning in the Baltic Sea

FM and SO defined the study. **FM** performed the statistical analysis and wrote the original draft. SO substantialy contributed to writing of the final version of the manuscript. All authors reviewed and commented on the manuscript.

Chapter 4

A climate vulnerability assessment of the fish community in the Western Baltic Sea

DM, PP and CM conceptualized the study. DM and NF conducted the literature research underlying the species profiles. HA, UB, UK, TM, MP, VS and HW evaluated and improved species profiles. GP designed and constructed online questionnaires and mapped temperature projections provided by MEEM. **FM** and SO provided species distribution maps. Figure 2 is designed by PK. All authors conducted

sensitivity assessments. Exposure assessments were performed by DM, HHH, **FM**, GP, PP, RV and CM. DM, GP, PP and CM conducted the data analysis. DM, PP and CM provided the initial manuscript. All authors reviewed and commented on the manuscript.

Hamburg, 5.1.2026



Place, Date

Signature
Prof. Dr. Christian Möllmann
Supervisor

SUMMARY

Climate change is rapidly advancing worldwide, causing a multitude of detrimental impacts and changes to ocean ecosystems. Among the many consequences for marine fish, shifts in species distributions and changes in community composition are highly prominent. These often result in fundamental alterations of ecosystem-wide structure and functioning, making the management of natural resources more difficult. Fish communities that are stable in time and space offer a sense of predictability on which foundations of successful industries, especially fisheries, can be built. When this stability is compromised, management must mitigate negative consequences, sometimes jointly across multiple countries, which can further complicate the situation. Adjusting even to positive developments can take time and require significant financial resources. It is therefore not surprising that management efforts are often static, reactive, and burdened by implementation lags. To alleviate these issues, an in-depth understanding of fish community dynamics, species and stock distributions and ecosystem functioning is advantageous. Examining possible shifts under future environmental change can be particularly helpful for establishing proactive and dynamic management plans.

Against this global background, the Baltic Sea represents a highly affected region. As a brackish, semi-enclosed sea and one of the fastest warming large marine ecosystems (LMEs), it is experiencing rapid environmental change. Warming temperatures, expanding hypoxic zones, high eutrophication and intensive fishing have all contributed to major shifts in its ecosystem structure and functioning. Several commercially exploited fish stocks have declined substantially, most notably the two Atlantic cod stocks (*Gadus morhua*) and Atlantic herring (*Clupea harengus*). While cod distributions appear to have contracted, European flounder (*Platichthys flesus*) has expanded its range. Continued environmental change is expected to trigger further distributional shifts, potentially altering spatial overlap among species, with consequences for food web dynamics and ecosystem functioning. Understanding these processes is therefore crucial for anticipating future developments.

To investigate how individual species and stocks respond to changing environmental conditions, advanced species distribution models (SDMs) were developed for eight species (including two cod stocks) for the period between 2001 and 2020 (**Chapter 1**). These models revealed clear spatiotemporal shifts in several taxa, namely European flounder, European plaice, and Eastern Baltic cod, and identified the drivers behind them. They also allowed us to evaluate how spatial overlap among species pairs has changed. We found six cases of significant overlap and five cases of significant separation. Overlap occurred mainly among species and stocks concentrated in a relatively small region (ICES Division IIIa and subdivisions 22-24), whereas separations were more common among those distributed across the wider Baltic Sea. Additionally, eight species pairs showed significant long-term trends in spatial overlap.

Building on this analysis, the same modelling framework was applied to explore how species distributions may develop under future climate (RCP4.5 and RCP8.5) and eutrophication (BSAP and REF) scenarios until 2098 (**Chapter 2**). The projections indicate significant shifts across all scenarios. European plaice, Eastern Baltic cod, and European sprat are likely to benefit from future changes, while common dab, European flounder, Western Baltic cod and whiting are projected to experience negative impacts. Responses of Atlantic herring remained uncertain due to weak model performance. The three-spined stickleback shows mixed responses across scenarios and between time periods (middle and end of the century). It appears to benefit particularly from the environmental conditions projected under RCP8.5. Spatial overlap among species also changes markedly over time under all scenarios, highlighting the need for carefully planned management efforts under future environmental change.

Understanding community-level responses requires going beyond species-level modelling. Therefore, structural and functional ecological indicators were analyzed to assess the spatiotemporal state of the Baltic Sea fish community between 2001 and 2020 (**Chapter 3**). A suite of 10 indicators, including 6 structural and 4 functional indicators, was selected, modeled and spatially predicted, revealing temperature as

the dominant driver across indicators. Derived spatial indices were examined using Multiple Factor Analysis (MFA) to disentangle the contributions of structural versus functional properties and different spatial dimensions. Converting predictions into cumulative Z-scores enabled the identification of areas with the strongest changes in community state. These areas showed limited overlap with HELCOM Marine Protected Areas (MPAs) and a fisheries closure area, and an expansion of wind farms is expected in several of them. These results underscore the importance of integrating spatial and functional dimensions into ecosystem state assessments.

To complement these modelling approaches, the vulnerability of 22 fish species to rising temperatures was evaluated for the Western Baltic Sea using an expert-based assessment (**Chapter 4**). Traditional target species such as cod and herring, as well as species with complex life histories, were identified as particularly sensitive to climate change. Conversely, invasive and better adaptable species may be better positioned to thrive under future warming scenarios.

In summary, this thesis demonstrates that environmental pressures have reshaped the Baltic Sea fish community and are likely to continue doing so. These changes affect both individual species distributions and the structural and functional characteristics of the community. Incorporating these insights into adaptive and forward-looking management strategies will be essential to safeguard the health and productivity of the Baltic Sea ecosystem.

ZUSAMMENFASSUNG

Der Klimawandel schreitet weltweit rasch voran und verursacht eine Vielzahl schädlicher Auswirkungen und Veränderungen in den Ökosystemen der Ozeane. Zu den vielen Folgen für marine Fische zählen insbesondere Verschiebungen der Artenverbreitung sowie Veränderungen in der Zusammensetzung von Lebensgemeinschaften. Diese führen häufig zu grundlegenden Veränderungen der ökosystemweiten Struktur und Funktionsweise und erschweren dadurch das Management natürlicher Ressourcen. Fischgemeinschaften, die zeitlich und räumlich stabil sind, bieten ein Maß an Vorhersagbarkeit, auf dem die Grundlagen erfolgreicher Wirtschaftszweige, insbesondere der Fischerei, aufbauen können. Wird diese Stabilität beeinträchtigt, muss das Management negative Konsequenzen abmildern, teilweise gemeinsam über mehrere Länder hinweg, was die Situation zusätzlich verkomplizieren kann. Selbst die Anpassung an positive Entwicklungen kann Zeit in Anspruch nehmen und erhebliche finanzielle Ressourcen erfordern. Es ist daher nicht überraschend, dass Managementmaßnahmen häufig statisch, reaktiv und durch Verzögerungen bei der Umsetzung belastet sind. Um diesen Problemen entgegenzuwirken, ist ein vertieftes Verständnis der Dynamik von Fischgemeinschaften, der Verteilung von Arten und Beständen sowie der Funktionsweise von Ökosystemen von Vorteil. Die Untersuchung möglicher Verschiebungen unter zukünftigem Umweltwandel kann besonders hilfreich sein, um proaktive und dynamische Managementpläne zu entwickeln.

Vor diesem globalen Hintergrund stellt die Ostsee eine besonders stark betroffene Region dar. Als brackiges, halboffenes Meer und eines der sich am schnellsten erwärmenden großen marinen Ökosysteme (Large Marine Ecosystems, LMEs) erfährt sie rasche Umweltveränderungen. Steigende Temperaturen, sich ausweitende hypoxische Zonen, hohe Eutrophierung und intensive Fischerei haben gemeinsam zu erheblichen Veränderungen der ökologischen Struktur und Funktionsweise beigetragen. Mehrere kommerziell genutzte Fischbestände sind stark zurückgegangen, insbesondere die beiden atlantischen Kabeljaubestände (*Gadus*

morhua) sowie der Atlantische Hering (*Clupea harengus*). Während sich die Verbreitungsgebiete des Kabeljaus offenbar verkleinert haben, konnte der Europäische Flunder (*Platichthys flesus*) sein Areal ausdehnen. Anhaltende Umweltveränderungen werden voraussichtlich weitere Verschiebungen der Verbreitung auslösen und möglicherweise die räumliche Überlappung zwischen Arten verändern, mit Folgen für die Nahrungsnetzdynamik und die Funktionsweise des Ökosystems. Das Verständnis dieser Prozesse ist daher entscheidend, um zukünftige Entwicklungen abschätzen zu können.

Um zu untersuchen, wie einzelne Arten und Bestände auf sich verändernde Umweltbedingungen reagieren, wurden für acht Arten (darunter zwei Kabeljaubestände) für den Zeitraum von 2001 bis 2020 fortgeschrittene Artenverbreitungsmodelle (Species Distribution Models, SDMs) entwickelt (**Kapitel 1**). Diese Modelle zeigten deutliche räumlich-zeitliche Verschiebungen bei mehreren Taxa, namentlich beim Europäischen Flunder, der Europäischen Scholle und dem östlichen Ostseekabeljau, und identifizierten die zugrunde liegenden Treiber. Zudem ermöglichten sie eine Bewertung der Veränderungen der räumlichen Überlappung zwischen Artenpaaren. Es wurden sechs Fälle signifikanter Überlappung und fünf Fälle signifikanter Trennung festgestellt. Überlappungen traten vor allem zwischen Arten und Beständen auf, die in einer relativ kleinen Region konzentriert sind (ICES-Division IIIa und Unterdivisionen 22–24), während Trennungen häufiger bei Arten beobachtet wurden, die über die gesamte Ostsee verbreitet sind. Darüber hinaus zeigten acht Artenpaare signifikante langfristige Trends in ihrer räumlichen Überlappung.

Aufbauend auf dieser Analyse wurde derselbe Modellierungsrahmen verwendet, um zu untersuchen, wie sich Artenverbreitungen unter zukünftigen Klima- (RCP4.5 und RCP8.5) und Eutrophierungsszenarien (BSAP und REF) bis zum Jahr 2098 entwickeln könnten (**Kapitel 2**). Die Projektionen deuten in allen Szenarien auf erhebliche Verschiebungen hin. Die Europäische Scholle, der östliche Ostseekabeljau und der Europäische Sprotte werden voraussichtlich von den zukünftigen Veränderungen profitieren, während für Kliesche, Europäischen Flunder, westlichen Ostseekabeljau

und Wittling negative Auswirkungen prognostiziert werden. Die Reaktionen des Atlantischen Herings blieben aufgrund einer schwachen Modellleistung unsicher. Der Dreistachlige Stichling zeigt gemischte Reaktionen zwischen den Szenarien und zwischen Zeiträumen (Mitte und Ende des Jahrhunderts). Besonders von den unter RCP8.5 projizierten Umweltbedingungen scheint er zu profitieren. Auch die räumliche Überlappung zwischen Arten verändert sich unter allen Szenarien deutlich im Zeitverlauf, was die Notwendigkeit sorgfältig geplanter Managementmaßnahmen unter zukünftigem Umweltwandel unterstreicht.

Das Verständnis von Reaktionen auf Gemeinschaftsebene erfordert ein Vorgehen, das über die Modellierung einzelner Arten hinausgeht. Daher wurden strukturelle und funktionelle ökologische Indikatoren analysiert, um den räumlich-zeitlichen Zustand der Fischgemeinschaft der Ostsee zwischen 2001 und 2020 zu bewerten (**Kapitel 3**). Ein Satz von zehn Indikatoren, darunter sechs strukturelle und vier funktionelle, wurde ausgewählt, modelliert und räumlich vorhergesagt, wobei sich die Temperatur als dominanter Treiber über alle Indikatoren hinweg erwies. Abgeleitete räumliche Indizes wurden mithilfe einer Multiple-Faktoren-Analyse (MFA) untersucht, um die Beiträge struktureller gegenüber funktionellen Eigenschaften sowie unterschiedlicher räumlicher Dimensionen zu entflechten. Die Umwandlung der Vorhersagen in kumulative Z-Scores ermöglichte die Identifikation von Gebieten mit den stärksten Veränderungen im Zustand der Gemeinschaft. Diese Gebiete wiesen nur eine geringe Überlappung mit HELCOM-Meeresschutzgebieten (Marine Protected Areas, MPAs) und einem Fischereisperrgebiet auf, und in mehreren von ihnen wird eine Ausweitung von Offshore-Windparks erwartet. Diese Ergebnisse unterstreichen die Bedeutung der Integration räumlicher und funktioneller Dimensionen in Bewertungen des Ökosystemzustands.

Zur Ergänzung dieser Modellierungsansätze wurde die Vulnerabilität von 22 Fischarten gegenüber steigenden Temperaturen für die westliche Ostsee mithilfe einer expertenbasierten Bewertung untersucht (**Kapitel 4**). Traditionelle Zielarten wie Kabeljau und Hering sowie Arten mit komplexen Lebenszyklen wurden als besonders empfindlich gegenüber dem Klimawandel identifiziert. Im Gegensatz dazu könnten

invasive und besser anpassungsfähige Arten unter zukünftigen Erwärmungsszenarien bessere Voraussetzungen haben, erfolgreich zu sein.

Zusammenfassend zeigt diese Dissertation, dass Umweltbelastungen die Fischgemeinschaft der Ostsee bereits umgestaltet haben und dies voraussichtlich auch weiterhin tun werden. Diese Veränderungen betreffen sowohl die Verbreitung einzelner Arten als auch die strukturellen und funktionellen Eigenschaften der Gemeinschaft. Die Einbindung dieser Erkenntnisse in adaptive und vorausschauende Managementstrategien wird entscheidend sein, um die Gesundheit und Produktivität des Ostseeökosystems langfristig zu sichern.

TABLE OF CONTENTS

AUTHOR CONTRIBUTIONS I

SUMMARY III

ZUSAMMENFASSUNG VI

INTRODUCTION 1

CHAPTER 1: Environmentally driven shifts of Baltic fish distributions and their impact on spatiotemporal overlap between species 22

CHAPTER 2: Shifting distributions of Baltic Sea fish under future environmental change 88

CHAPTER 3: Potential mismatches between spatial protection and changing fish community structure and functioning in the Baltic Sea 150

CHAPTER 4: A climate vulnerability assessment of the fish community in the Western Baltic Sea 189

DISCUSSION 229

FUNDING 258

EIDESSTATTLICHE VERSICHERUNG 259

ACKNOWLEDGEMENTS 260

INTRODUCTION

Fish distributions

Fish distributions that are stable in space and time come with many benefits. From a management perspective, knowing where to go, which species will be there, and in roughly what amount is knowledge essential for developing foundations of strong industries, especially fisheries. Generally, spatiotemporal dynamics are shaped by factors such as stochastic variation in abundance, dispersal, and the environment they inhabit (Vellend, 2010). Since the 1850 – 1900 period, global greenhouse emissions from human activities have rapidly risen leading to a temperature increase of 1.1 °C. This has led to what is known as climate change resulting in a multitude of impacts on oceans worldwide. These include sea level rise, warming, increased frequency of heatwaves, acidification, and reduced oxygen levels (IPCC, 2021). Unfortunately, they also interact with other anthropogenic pressures such as pollution and resource overexploitation (Côté *et al.*, 2016). Given the direct and indirect dependence of living organism on their environment, the effects of climate change have already caused changes in species ranges (Priya *et al.*, 2023). In addition, fishing exploitation (Eme *et al.*, 2022) and biotic interactions (Lee-Yaw *et al.*, 2022) can also shape spatiotemporal dynamics.

Species distribution modelling

Species distribution models (SDMs) are tools used to model species occurrence and abundance as they relate to the environment (Waldock *et al.*, 2022). Together with ecological niche models (ENMs), their use has rapidly increased. They are often used for investigating current distribution patterns, predicting how they might change under future climate change, evaluating the potential of invasive species to spread, and even modelling past distributions, among many others. There are three main categories of SDMs: corelative, mechanistic and process-oriented (Melo-Merino *et al.*, 2020). Most popular are correlative models which estimate species requirements by relating their geographical distributions to environmental variables (Araújo and Guisan, 2006; Franklin, 2009). In this category, one can use machine-learning and

Statistical methods, as well as similarity-based and expert-rule approaches (Melo-Merino *et al.*, 2020). Model fitting is followed by model validation and evaluation, and inference and making distribution predictions at the end (Figure 1.)

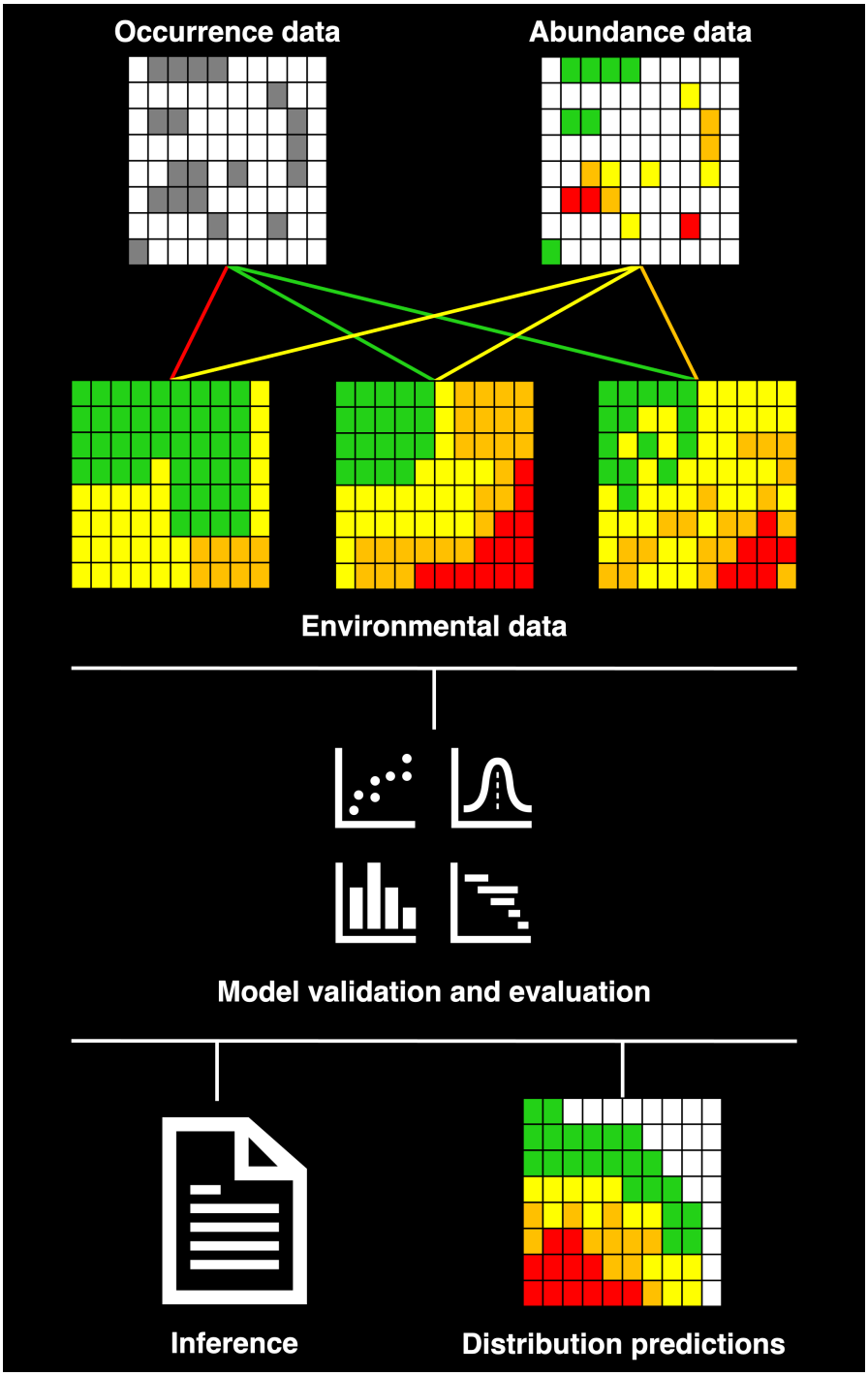


Figure 1. A simplified representation of how a correlative SDM is created and used. Steps include relating occurrence and abundance to environmental data, model validation and evaluation, as well as inference and making distribution predictions.

While valuable tools, SDMs do tend to have certain limitations. Occurrence-based models can be impacted by input data that was collected in a way that might prevent the model to capture the full response of the species as it relates to the environmental conditions it lives in (Phillips *et al.*, 2009). Furthermore, models trained on data from one region might not work in other areas (Randin *et al.*, 2006; Boiffin *et al.*, 2017) and can be misled by presences in non-suitable locations (Van Horne, 1983; Pulliam, 1988; Jenkins *et al.*, 2003) and, vice versa, by absences in suitable ones (Boetsch *et al.*, 2003; Franklin, 2010; Gogol-Prokurat, 2011). To tackle these limitations, validating models with independent data is highly encouraged as it has been found to be even more reliable than using cross-validated AUC based on the different subsets of available locality data that is used for training and evaluating models (Fois *et al.*, 2018; Gregr *et al.*, 2019; McCune *et al.*, 2020). Careful selection of training and testing data (Roberts *et al.*, 2017) as well as exploration of the effects of model parametrization using independent data are encouraged (Fois *et al.*, 2018; McCune *et al.*, 2020). Abundance-based models might be influenced by the fact that abundance, in addition to habitat suitability, might be a result of species' interactions, transient dynamics and stochasticity, metapopulation dynamics, Allee effects, and disturbance (Stevens and Amarilla-Stevens, 2012; Weber *et al.*, 2017; Holt, 2020; Osorio-Olvera *et al.*, 2020). Including estimates of abundance as a predictor, using a two-step approach where abundance is modelled at locations deemed suitable (by modelling probability of presence first) (Potts and Elith, 2006; Boulangeat *et al.*, 2012; Mellin *et al.*, 2012), incorporating demography and other processes influencing abundance (Merow *et al.*, 2014; Ehrlén and Morris, 2015; Evans *et al.*, 2016; Zurell *et al.*, 2016), are some of the recommendations to help alleviate these issues.

Distributional shifts and changes in ecosystem structure and functioning

Redistributions of marine species under anthropogenic change are increasingly documented. In particular, climate change appears to drive poleward increases of abundance and equatorward declines (Hastings *et al.*, 2020). In global fisheries, the signature of ocean warming has been tracked via the increasing mean temperature of the catch (MTC) index (Cheung *et al.*, 2013) and, since the 1970s, species richness has declined at the equator, increased at midlatitudes and shifted north in the

northern hemisphere (Chaudhary *et al.*, 2021). Such changes can greatly influence marine communities and ecosystems, for example by reassembling food webs with potentially dramatic consequences (Pinsky *et al.*, 2020). In addition, altered species distributions have been shown to change production of natural resources required for food security, patterns of disease transmission, and processes of carbon sequestration (Pecl *et al.*, 2017).

Distributional shifts clearly shape the structure of an ecosystem or community but also alter its functioning as a part of the same process. Tropical herbivorous fish expanding into temperate regions have caused overgrazing of temperate macroalgae leading to community phase-shifts (Verges *et al.*, 2014). Functional diversity in marine fish communities is shown to respond to climate change, invasive species, and fisheries (Trindade-Santos *et al.*, 2020; Zhao *et al.*, 2022; Souza *et al.*, 2023). Examples include functional reorganization of marine fish nurseries in the Bay of Somme through changes in composition of life history traits as a result of climate warming (McLean *et al.*, 2019) and the use of specific fishing gears resulting in the selective targeting of specific functional entities (Mbaru *et al.*, 2020).

Challenges for management

The described ecological changes pose serious issues for management efforts. Redistributions have occurred in the North Sea raising concerns on how fisheries could be impacted and community interaction altered (Perry *et al.*, 2005). Alarmingly, over the course of 30 years, 19 fish species encompassing 73 commercial stocks experienced changes in their distribution in the northeast Atlantic with 5 of them shifting across management zones, in turn challenging the current use of relative stability for quota allocation (Baudron *et al.*, 2020). Interestingly, temperature-related expansion of mackerel (*Scomber scombrus*) into Icelandic waters resulted in the formation of a bycatch fishery eventually developing into a direct fishery (Astthorsson *et al.*, 2012). However, even if the effects are positive there is often a need for costly societal adjustments (Weiskopf *et al.*, 2020).

Fisheries themselves might have difficulties adapting to distributional changes due to lagged responses. In the northeast of the United States, fish and invertebrates are shifting polewards but fisheries have shifted only 10 to 30% as much as their target species. It appears that these lags are to a large part a result of economic and regulatory constraints and may lead to overfishing and population declines if not accounted for in management and climate adaptation (Pinsky and Fogarty, 2012). Furthermore, while proactive and flexible adaptation strategies have started being explored in the same country, they are still not prevalent or systematic across the country (Weiskopf *et al.*, 2020).

An additional concern is that shifting species distributions might render Marine Protected Areas (MPAs) ineffective (Cashion *et al.*, 2020). In a global assessment of climate change adaptation in Marine Protected Area (MPA) management plans, it was found that, of all plans published since 2010, only 57% included at least one term related to climate change and that the mean climate change robustness index of climate-considering management was 39% of a total possible score with climate change robustness defined as the degree of incorporation of common climate change adaptation principles (O'Regan *et al.*, 2021). In addition, it was found that when an annual high temperature extreme happens in an exclusive economic zone, on average, 77% of fish and invertebrates therein will decrease in biomass and maximum catch potential will be reduced by 6% (Cheung *et al.*, 2021). These examples, clearly show why ecological changes need to be urgently considered in existing fisheries management strategies and continually understood through further research. In such instances, functional trait-based approaches may prove especially useful for advancing fisheries science and management by improving estimates of population and community dynamics, and rapidly detecting responses to fishing and environmental drivers (Barnett *et al.*, 2019). For example, they can help us understand how fishing may influence the composition of functional traits in a community, especially in cases where these patterns are not mirrored in the species composition (Koutsidi *et al.*, 2016).

Overview of the study area – Baltic Sea

The Baltic Sea (Figure 2), located in Northern Europe, is no exception to the effects of climate change. This brackish, semi-enclosed body of water was crowned with the unfortunate title of the fastest warming Large Marine Ecosystem (LME) between 1982 and 2006 (Belkin, 2009). It is a relatively shallow sea with an average depth of around 53 meters, though it also contains deeper basins such as the Gotland Deep and the Landsort Deep, where depths reach down to 451 meters (HELCOM, 2003). Another interesting aspect of its hydrology is a strong salinity gradient. Saline water enters from the southwest but the water exchange with the North Sea is restricted by narrow straits and shallow sills while in the northeast a freshwater surplus is dominant (The BACC Author Team, 2008). The resulting estuarine gradient allows the coexistence of marine and freshwater species (Frelat *et al.*, 2018). Unfortunately, simulations show a likely temperature rise in the Baltic by 2 to 4 °C and, salinity is expected to decrease given a projected ~30% precipitation increase in the north (Andersson *et al.*, 2015). However, salinity projections still remain highly uncertain (Meier *et al.*, 2021). In addition, the projected increase of precipitation under future climate change is expected to cause increased land runoff of allochthonous organic matter (AOM) and organic pollutants (Andersson *et al.*, 2015). Deoxygenation of the seabed is also a prominent issue in the Baltic. The water column in Baltic Proper is permanently stratified into a brackish surface layer and a more saline deep layer, separated by a strong permanent halocline which limits vertical mixing and prevents oxygen-rich surface waters from reaching the deeper layers (Matthäus and Schinke, 1999). An expansion of hypoxic zones in the Western Baltic Sea (Conley *et al.*, 2007) and the deeper regions of the Baltic Proper and Gulf of Finland (Zillén *et al.*, 2008) occurred as a result of anthropogenic eutrophication, driven by increased inputs of nutrients such as nitrogen and phosphorus, exacerbating oxygen depletion. This restricts marine life in the Baltic to shallower waters and strongly influences the structure of the ecosystem (Conley *et al.*, 2009). A plan to reduce nutrient loads, the Baltic Sea Action Plan (BSAP), was agreed upon by countries sharing the Baltic to combat this issue. Unfortunately, climate change was not taken into account when allowable loads, that would help restore a good ecological status, were calculated (Meier *et al.*, 2021).

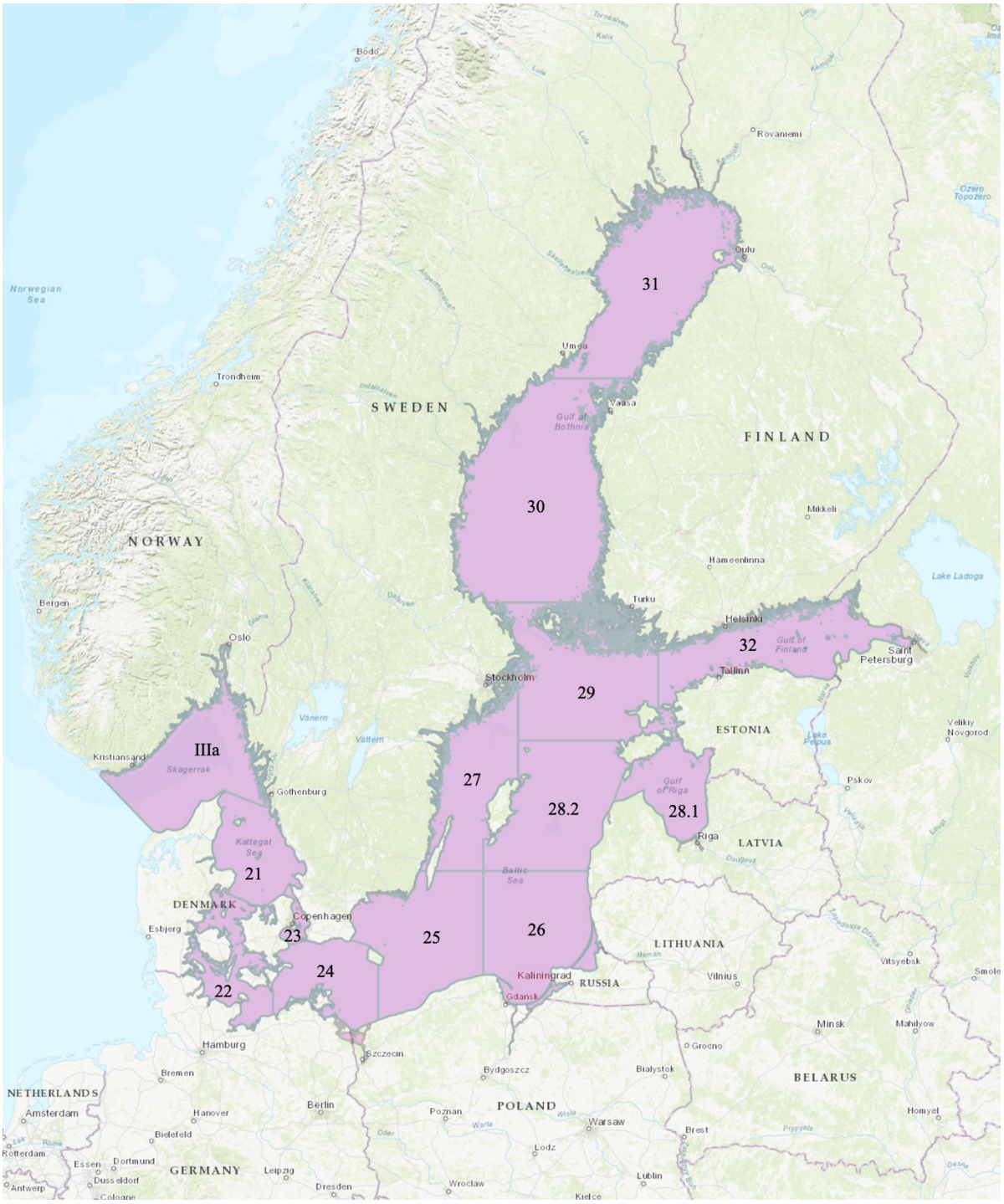


Figure 2. Map of the Baltic Sea including the Kattegat (ICES subdivision 21) and Skagerrak areas (in pink). Together, the two areas comprise ICES division IIIa. ICES subdivisions 22 to 32 are also shown.

In the Baltic, major shifts in ecosystem structure and functioning due to overfishing, expansion of hypoxic zones, increasing temperatures, and high eutrophication have been witnessed (Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020). Other pressures, like

contamination from land-based industries and intense shipping, further stress the ecosystem (Reusch *et al.*, 2018). Commercially important fish stocks experienced significant declines over recent decades due to overexploitation and environmental change (Casini *et al.*, 2008; Möllmann *et al.*, 2009; Tomczak *et al.*, 2022) with Atlantic cod (*Gadus morhua*) serving as a common example. The reduction of its reproductive success has been linked to declining salinity and rising temperatures, leading to stock collapse (Sguotti *et al.*, 2019; Bryhn *et al.*, 2022). In addition, a contraction in the distribution of adult and juvenile cod in the southern Baltic Sea was observed (Orio *et al.*, 2019). Simultaneously, European flounder (*Platichthys flesus*) expanded its distribution (Orio *et al.*, 2019; MacNeil *et al.*, 2025). This seems to have led to an increase in competition overlap between the two (Orio *et al.*, 2020). Atlantic herring (*Clupea harengus*) is another common example of declining populations. This is especially evident in the Western Baltic Sea where overfishing, environmental changes, habitat degradation and eutrophication leading to oxygen depletion in key spawning and nursery areas have negatively impacted the species (Fey *et al.*, 2014; ICES, 2024a). The three species, together with European sprat (*Sprattus sprattus*) and plaice (*Pleuronectes platessa*), account for more than 90% of the fish catches (ICES, 2024b) underscoring their importance to the region's biodiversity and economy. Advancing environmental changes might also allow other species to expand. Such is the case of the three-spined stickleback (*Gasterosteus aculeatus*) which increased dramatically in abundance potentially threating other species (Bergström *et al.*, 2015; Olin *et al.*, 2022). Obviously, there is potential for other species to experience distributional shifts possibly leading to further alterations of spatial overlap patterns. These could lead to substantial changes in biotic interactions and functioning of the fish community within the larger Baltic ecosystem.

Objectives and modelling approach

The overall aims of this thesis are twofold:

i) to investigate spatiotemporal changes of the fish community in the Baltic Sea over recent decades, and

ii) to explore how these changes may develop under future environmental conditions.

These aims are addressed across four chapters. In **chapter 1**, we develop dynamic SDMs for eight species (including two cod stocks) using an advanced modelling framework. We summarize the patterns predicted by the models using a set of five spatial indicators and assess if distributional shifts had occurred over time. In the models, we consider a large array of environmental variables and species- and stock-specific fisheries landings which enable us to identify key drivers of both static and shifting distributional patterns. Lastly, we investigate interannual changes of spatial overlap between pairs of species and stocks as these could likely affect food web dynamics and management.

We develop the SDMs from **chapters 1** and **2** as well as spatiotemporal indicator models from **chapter 3** with the *sdmTMB* R package (Anderson *et al.*, 2022). Here, we fit spatial and spatiotemporal Generalized Linear Mixed Effects Models (GLMMs), and the modelling process uses Template Model Builder (TMB) for efficient model fitting and R-INLA to set up Stochastic Partial Differential Equation (SPDE) matrices. The approach allows for inclusion of spatial and spatiotemporal random fields, typically modeled as Gaussian Random Fields (GRFs), which help account for dependencies resulting from missing covariates or inherent spatial and temporal structures (Anderson *et al.*, 2022). Computing GRFs comes with increased computational intensity, especially with large two- or three-dimensional data. Because of this, the SPDE method is used in order to transform continuous GRFs into Gaussian Markov Random Fields (GMRFs), which have a sparse precision matrix and allow for more efficient computation (Lindgren *et al.*, 2011). Estimation in *sdmTMB* is performed via maximum marginal likelihood which provides a flexible and computationally efficient framework for modeling complex ecological processes.

In **chapter 2** we refit SDMs of the same species and stocks using the same model structures as those created in **chapter 1** to predict their distributions under 4 scenarios of future climate change and eutrophication. Specifically, we look at RCP4.5 and RCP8.5 climate change scenarios coupled with the BSAP and a business-as-usual or reference (REF) eutrophication scenarios (Meier *et al.*, 2021).

We summarize the predictions into the same set of 5 spatial indicators as in **chapter 1** and compare them between scenarios and between 2014-2020, 2053-2059, and 2092-2098 time periods. Lastly, we again investigate the spatial overlap between pairs of species and stocks and how they differ across the scenarios of future environmental change.

As mentioned in **chapter 3**, we use the same spatiotemporal modelling framework but our focus shifts to ecological indicators instead of individual species and stocks. We calculate both indicators representing the biological and functional structure and select an appropriate suite for describing the fish community state. In addition to ecological theory, a 7-step quantitative framework for exploring the considered indicators is an important tool in the selection process. The related scoring system considers a set of performance criteria. Essentially, the indicators should reflect system change, exhibit pressure sensitivity and robustness, link to management, and not be redundant (Otto *et al.*, 2018). After establishing the selections, we use a similar modelling framework as in **chapters 1** and **2** to model them. This allows us to identify the main drivers and create spatiotemporal predictions. Most ecosystem condition assessments tend to neglect the functional aspect of an ecosystem in favor of the structure (Smit *et al.*, 2021). This underscores the importance of evaluating the performance of both structural and functional indicators when choosing an appropriate indicator suite. We also calculate four spatial indices from the predictions and analyze them using the Multiple factor analysis (MFA) to assess the contribution of structural against functional indicators. Later, we convert the spatiotemporal patterns into Z-scores and sum them together into a cumulative state score of the fish community. In this way we develop a state assessment of the fish community that is resolved in both space and time. By incorporating spatiotemporal complexity in this way, we significantly contribute to the existing array of state assessments in the Baltic Sea (Blenckner *et al.*, 2021; HELCOM, 2023). Furthermore, we calculate the difference in mean scores between an early (2001-2005) and a late (2016-2020) period. In this way we find areas that experienced the largest state changes and overlay them with HELCOM MPAs, a fisheries closure area and current and future

wind farms. In doing so, we identify areas where the fish community might require further protection and regulation.

In **chapter 4** we again look at the future of the fish community but focus on the Western Baltic Sea. Herein, we investigate the vulnerability of 22 species to surface and bottom temperature changes under RCP4.5 and RCP 8.5 climate change scenarios (Van Vuuren *et al.*, 2011). The differences are explored for the 2040-2049 and 2080-2089 periods in relation to the reference 2010-2019 period. The study is carried out through an expert judgement assessment framework that largely follows the approach developed for other areas and which combines expert scorings of trait-based sensitivity of species with exposure scorings to locally important climate factors (Hare *et al.*, 2016; Spencer *et al.*, 2019). Essentially, a score of sensitivity of investigated species to local climate impacts is combined with a score of their spatial exposure to said impacts to reproduce an overall vulnerability score. The sensitivity score is based on sensitivity attributes which are biological traits or life history characteristics that show the capacity of a species to respond to a changing environment. The exposure score is based on the comparison of climate exposure and species distribution maps. The overall vulnerability of each species is calculated by multiplying the sensitivity and exposure scores (Hare *et al.*, 2016).

Taken together, our analyses demonstrate that environmental change has already reshaped the distribution and functioning of the Baltic Sea fish community and will continue to do so under all plausible future scenarios. These insights have direct implications for understanding ecosystem functioning and for designing adaptive, ecosystem-based management strategies. The following chapters develop this argument in detail and evaluate its consequences for the future of the Baltic Sea ecosystem.

REFERENCES

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. preprint. Ecology. http://biorxiv.org/lookup/doi/10.1101/2022.03.24.485545 (Accessed 2 January 2024).

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., *et al.* 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO, 44: 345–356.

Araújo, M. B., and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33: 1677–1688.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., and Óskarsson, G. J. 2012. Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. ICES Journal of Marine Science, 69: 1289–1297.

Barnett, L. A. K., Jacobsen, N. S., Thorson, J. T., and Cope, J. M. 2019. Realizing the potential of trait-based approaches to advance fisheries science. Fish and Fisheries, 20: 1034–1050.

Baudron, A. R., Brunel, T., Blanchet, M., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., *et al.* 2020. Changing fish distributions challenge the effective management of European fisheries. Ecography, 43: 494–505.

Belkin, I. M. 2009. Rapid warming of Large Marine Ecosystems. Progress in Oceanography, 81: 207–213.

Bergström, U., Olsson, J., Casini, M., Eriksson, B. K., Fredriksson, R., Wennhage, H., and Appelberg, M. 2015. Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science, 163: 134–142.

Blenckner, T., Möllmann, C., Stewart Lowndes, J., Griffiths, J. R., Campbell, E., De Cervo, A., Belgrano, A., *et al.* 2021. The Baltic Health Index (BHI): Assessing the social–ecological status of the Baltic Sea. People and Nature, 3: 359–375.

Boetsch, J. R., van Manen, F. T., and Clark, J. D. 2003. Predicting rare plant occurrence in Great Smoky Mountains National Park, USA. Natural Areas Journal, 23: 229–237.

Boiffin, J., Badeau, V., and Bréda, N. 2017. Species distribution models may misdirect assisted migration: insights from the introduction of Douglas-fir to Europe. Ecological Applications, 27: 446–457.

Boulangeat, I., Gravel, D., and Thuiller, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters, 15: 584–593.

Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J., *et al.* 2022. Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? Ocean & Coastal Management, 223: 106154.

Cashion, T., Nguyen, T., Ten Brink, T., Mook, A., Palacios-Abrantes, J., and Roberts, S. M. 2020. Shifting seas, shifting boundaries: Dynamic marine protected area designs for a changing climate. PLOS ONE, 15: e0241771.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B: Biological Sciences, 275: 1793–1801.

Chaudhary, C., Richardson, A. J., Schoeman, D. S., and Costello, M. J. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. Proceedings of the National Academy of Sciences, 118: e2015094118.

Cheung, W. W. L., Watson, R., and Pauly, D. 2013. Signature of ocean warming in global fisheries catch. Nature, 497: 365–368.

Cheung, W. W. L., Frölicher, T. L., Lam, V. W. Y., Oyinlola, M. A., Reygondeau, G., Sumaila, U. R., Tai, T. C., *et al.* 2021. Marine high temperature extremes amplify the impacts of climate change on fish and fisheries. Science Advances, 7: eabh0895.

Conley, D. J., Carstensen, J., Ærtebjerg, G., Christensen, P. B., Dalsgaard, T., Hansen, J. L. S., and Josefson, A. B. 2007. LONG-TERM CHANGES AND

IMPACTS OF HYPOXIA IN DANISH COASTAL WATERS. Ecological Applications, 17. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/05-0766.1 (Accessed 16 January 2025).

Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., *et al.* 2009. Hypoxia-related Processes in the Baltic Sea. Environmental Science & Technology, 43: 3412–3420.

Côté, I. M., Darling, E. S., and Brown, C. J. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences, 283: 20152592.

Ehrlén, J., and Morris, W. F. 2015. Predicting changes in the distribution and abundance of species under environmental change. Ecology Letters, 18: 303–314.

Eme, D., Rufino, M. M., Trenkel, V. M., Vermard, Y., Laffargue, P., Petitgas, P., Pellissier, L., *et al.* 2022. Contrasted spatio-temporal changes in the demersal fish assemblages and the dominance of the environment vs fishing pressure, in the Bay of Biscay and Celtic Sea. Progress in Oceanography, 204: 102788.

Evans, M. E., Merow, C., Record, S., McMahon, S. M., and Enquist, B. J. 2016. Towards process-based range modeling of many species. Trends in Ecology & Evolution, 31: 860–871. Elsevier.

Fey, D. P., Hiller, A., Margonski, P., Moll, D., Nilsson, H., Pongolini, L., Stybel, N., *et al.* 2014. HERRING Impact Report Herring spawning areas - present and future challenges.

Fois, M., Cuena-Lombraña, A., Fenu, G., and Bacchetta, G. 2018. Using species distribution models at local scale to guide the search of poorly known species: Review, methodological issues and future directions. Ecological Modelling, 385: 124–132. Elsevier.

Franklin, J. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press. https://scholar.google.com/scholar_lookup?title=Mapping%20Species%20Distributions%3A%20Spatial%20Inference%20and%20Prediction&author=J.%20Franklin&publication_year=2009 (Accessed 17 December 2025).

Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions, 16: 321–330.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Gogol-Prokurat, M. 2011. Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecological Applications, 21: 33–47.

Gregr, E. J., Palacios, D. M., Thompson, A., and Chan, K. M. A. 2019. Why less complexity produces better forecasts: an independent data evaluation of kelp habitat models. Ecography, 42: 428–443.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., *et al.* 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PLOS ONE.

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., and Genner, M. J. 2020. Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species. Current Biology, 30: 1572-1577.e2.

HELCOM. 2003. Baltic Sea Environment Proceedings No. 87.

HELCOM. 2023. State of the Baltic Sea. Third HELCOM holistic assessment 2016-2021. Baltic Sea Environment Proceedings n°194.

Holt, R. D. 2020. Reflections on niches and numbers. Ecography, 43: 387–390.

ICES. 2024a. Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Herring_i_Clupea_harengus_i_in_subdivisions_20_24_spring_spawners_Skagerrak_Kattegat_and_western_Baltic_/25019273 (Accessed 16 January 2025).

ICES. 2024b. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports. https://ices-library.figshare.com/articles/report/Baltic_Fisheries_Assessment_Working_Group_WGBFAS_/25764978 (Accessed 9 October 2024).

IPCC. 2021, August 9. Climate change widespread, rapid, and intensifying – IPCC. IPCC PRESS RELEASE.

Jenkins, C. N., Powell, R. D., Bass Jr, O. L., and Pimm, S. L. 2003. Why sparrow distributions do not match model predictions. *In* Animal Conservation forum, pp. 39–46. Cambridge University Press. https://www.cambridge.org/core/journals/animal-conservation-forum/article/why-sparrow-distributions-do-not-match-model-predictions/C3187E2A89B881043662A57CD21D80A4 (Accessed 15 December 2025).

Koutsidi, M., Tzanatos, E., Machias, A., and Vassilopoulou, V. 2016. Fishing for function: the use of biological traits to evaluate the effects of multispecies fisheries on the functioning of fisheries assemblages. ICES Journal of Marine Science, 73: 1091–1103.

Lee-Yaw, J. A., McCune, J. L., Pironon, S., and Sheth, S. N. 2022. Species distribution models rarely predict the biology of real populations. Ecography, 2022: e05877.

Lindgren, F., Rue, H., and Lindström, J. 2011. An Explicit Link between Gaussian Fields and Gaussian Markov Random Fields: The Stochastic Partial Differential Equation Approach. Journal of the Royal Statistical Society Series B: Statistical Methodology, 73: 423–498.

MacNeil, L., Madiraca, F., Otto, S., and Scotti, M. 2025. Spatial Change of Dominant Baltic Sea Demersal Fish Across Two Decades. Ecology and Evolution, 15: e71309.

Matthäus, W., and Schinke, H. 1999. The influence of river runoff on deep water conditions of the Baltic Sea. *In* Biological, Physical and Geochemical Features of Enclosed and Semi-enclosed Marine Systems, pp. 1–10. Ed. by E. M. Blomqvist, E. Bonsdorff, and K. Essink. Springer Netherlands, Dordrecht. http://link.springer.com/10.1007/978-94-017-0912-5_1 (Accessed 16 January 2025).

Mbaru, E. K., Graham, N. A. J., McClanahan, T. R., and Cinner, J. E. 2020. Functional traits illuminate the selective impacts of different fishing gears on coral reefs. Journal of Applied Ecology, 57: 241–252.

McCune, J. L., Rosner-Katz, H., Bennett, J. R., Schuster, R., and Kharouba, H. M. 2020. Do traits of plant species predict the efficacy of species distribution models for finding new occurrences? Ecology and Evolution, 10: 5001–5014.

McLean, M. J., Mouillot, D., Goascoz, N., Schlaich, I., and Auber, A. 2019. Functional reorganization of marine fish nurseries under climate warming. Global Change Biology, 25: 660–674.

Meier, H. E. M., Dieterich, C., and Gröger, M. 2021. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. Communications Earth & Environment, 2: 50.

Mellin, C., Russell, B. D., Connell, S. D., Brook, B. W., and Fordham, D. A. 2012. Geographic range determinants of two commercially important marine molluscs. Diversity and Distributions, 18: 133–146.

Melo-Merino, S. M., Reyes-Bonilla, H., and Lira-Noriega, A. 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecological Modelling, 415: 108837.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., *et al.* 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography, 37: 1267–1281.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., and Bergström, U. 2022. Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback. ICES Journal of Marine Science, 79: 1419–1434.

O'Regan, S. M., Archer, S. K., Friesen, S. K., and Hunter, K. L. 2021. A Global Assessment of Climate Change Adaptation in Marine Protected Area Management Plans. Frontiers in Marine Science, 8: 711085.

Orio, A., Bergström, U., Florin, A., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap between interacting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Osorio-Olvera, L., Yañez-Arenas, C., Martínez-Meyer, E., and Peterson, A. T. 2020. Relationships between population densities and niche-centroid distances in North American birds. Ecology Letters, 23: 555–564.

Otto, S. A., Kadin, M., Casini, M., Torres, M. A., and Blenckner, T. 2018. A quantitative framework for selecting and validating food web indicators. Ecological Indicators, 84: 619–631.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., *et al.* 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., *et al.* 2020. Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography, 43: 197–208.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308: 1912–1915.

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., and Ferrier, S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications, 19: 181–197.

Pinsky, M. L., and Fogarty, M. 2012. Lagged social-ecological responses to climate and range shifts in fisheries. Climatic Change, 115: 883–891.

Pinsky, M. L., Selden, R. L., and Kitchel, Z. J. 2020. Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science, 12: 153–179.

Potts, J. M., and Elith, J. 2006. Comparing species abundance models. Ecological modelling, 199: 153–163. Elsevier.

Priya, A. K., M, M., Rajamanickam, S., Sivarethinamohan, S., Gaddam, M. K. R., Velusamy, P., R, G., *et al.* 2023. Impact of climate change and anthropogenic

activities on aquatic ecosystem – A review. Environmental Research, 238: 117233.

Pulliam, H. R. 1988. Sources, Sinks, and Population Regulation. The American Naturalist, 132: 652–661.

Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M., and Guisan, A. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography, 33: 1689–1703.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances, 4: eaar8195.

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., *et al.* 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography, 40: 913–929.

Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Ryberg, M. P., Lindegren, M., Durant, J. M., *et al.* 2019. Catastrophic dynamics limit Atlantic cod recovery. Proceedings of the Royal Society B: Biological Sciences, 286: 20182877.

Smit, K. P., Bernard, A. T. F., Lombard, A. T., and Sink, K. J. 2021. Assessing marine ecosystem condition: A review to support indicator choice and framework development. Ecological Indicators, 121: 107148.

Souza, A. T., Dias, E., Antunes, C., and Ilarri, M. 2023. Disruptions caused by invasive species and climate change on the functional diversity of a fish community. NeoBiota, 88: 211–244.

Spencer, P. D., Hollowed, A. B., Sigler, M. F., Hermann, A. J., and Nelson, M. W. 2019. Trait-based climate vulnerability assessments in data-rich systems: An application to eastern Bering Sea fish and invertebrate stocks.

Stevens, R. D., and Amarilla-Stevens, H. N. 2012. Seasonal environments, episodic density compensation and dynamics of structure of chiropteran frugivore guilds in Paraguayan Atlantic forest. Biodiversity and Conservation, 21: 267–279.

The BACC Author Team. 2008. Assessment of Climate Change for the Baltic Sea Basin.

Tomczak, M. T., Müller-Karulis, B., Blenckner, T., Ehrnsten, E., Eero, M., Gustafsson, B., Norkko, A., *et al.* 2022. Reference state, structure, regime shifts, and regulatory drivers in a coastal sea over the last century: The Central Baltic Sea case. Limnology and Oceanography, 67. https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.11975 (Accessed 16 January 2025).

Trindade-Santos, I., Moyes, F., and Magurran, A. E. 2020. Global change in the functional diversity of marine fisheries exploitation over the past 65 years. Proceedings of the Royal Society B: Biological Sciences, 287: 20200889.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management: 893–901. JSTOR.

Van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., *et al.* 2011. The representative concentration pathways: an overview. Climatic Change, 109: 5–31.

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology, 85: 183–206.

Verges, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Jr, K. L. H., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts.

Waldock, C., Stuart-Smith, R. D., Albouy, C., Cheung, W. W. L., Edgar, G. J., Mouillot, D., Tjiputra, J., *et al.* 2022. A quantitative review of abundance-based species distribution models. Ecography, 2022: ecog.05694.

Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F., and Grelle, C. E. V. 2017. Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography, 40: 817–828.

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., *et al.* 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Science of The Total Environment, 733: 137782.

Zhao, K., Gaines, S. D., García Molinos, J., Zhang, M., and Xu, J. 2022. Climate change and fishing are pulling the functional diversity of the world's largest

marine fisheries to opposite extremes. Global Ecology and Biogeography, 31: 1616–1629.

Zillén, L., Conley, D. J., Andrén, T., Andrén, E., and Björck, S. 2008. Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. Earth-Science Reviews, 91: 77–92.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., *et al.* 2016. Benchmarking novel approaches for modelling species range dynamics. Global Change Biology, 22: 2651–2664.

CHAPTER 1

Environmentally driven shifts of Baltic fish distributions and their impact on spatiotemporal overlap between species

Frane Madiraca[1], Liam MacNeil[2], Marco Scotti[2,3], Christian Möllmann[1], and Saskia A. Otto[1]

[1] Institute of Marine Ecosystem and Fishery Science, Center for Earth System Research and Sustainability (CEN), Hamburg University, Hamburg, Germany

[2] Marine Ecology Research Division, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

[3] Institute of Biosciences and Bioresources, National Research Council of Italy, Firenze, Italy

ABSTRACT

The Baltic Sea is among the world's most ecologically threatened and commercially significant marine ecosystems, facing long-standing pressures from eutrophication, pollution, climate change, and overfishing. Climate change, in particular, is expected to exacerbate existing challenges, intensifying the need to understand how these stressors interact and impact fish populations. A critical aspect of this preparation involves examining the spatial and temporal dynamics of fish distributions, their environmental drivers, and the ecological and management implications of such changes. In this study, we developed species distribution models (SDMs) for eight fish species, including 2 cod stocks, using a novel modelling framework. These models allowed us to 1) analyze spatial distribution patterns and detect temporal shifts, 2) identify key drivers behind these patterns, and 3) evaluate spatial overlap among species. Our results revealed clear spatiotemporal shifts in European flounder, European plaice, and Eastern Baltic cod, driven primarily by rising temperatures and shifting oxygen levels. We also identified notable trends in interannual spatial overlap,

highlighting potential changes in competition and trophic interactions. These findingsprovide valuable insights into the ecological impacts of climate change andother stressors in the Baltic Sea. We discuss their implications for food web dynamics andfisheries management, emphasizing the need for adaptive strategies to address the challenges posed by species redistributions and overlaps in a rapidly changing ecosystem.

Keywords: Baltic Sea, species distribution model, climate change, eutrophication, fishing exploitation, spatiotemporal patterns

INTRODUCTION

Changes in species distributions have become a key focus of ecological research, as these shifts are increasingly recognized for their profound impact on ecosystems (Pecl *et al.*, 2017). Climate change is one of the most significant drivers of species redistribution, interacting with other factors such as habitat degradation, overexploitation, and pollution (Sunday *et al.*, 2012; Hastings *et al.*, 2020; Chaudhary *et al.*, 2021; Priya *et al.*, 2023). As species move in response to warming temperatures, altered precipitation patterns, and shifting ocean currents, both terrestrial and marine ecosystems are undergoing transformations (Weiskopf *et al.*, 2020; Jackson, 2021). For example, terrestrial species like European ungulates are shifting to higher altitudes (Büntgen *et al.*, 2017), while marine species such as Atlantic mackerel (*Scomber scombrus*) and Atlantic cod (*Gadus morhua*) have extended their ranges northward into Arctic waters (Perry *et al.*, 2005; Astthorsson *et al.*, 2012). These climate-driven redistributions are not isolated; they can have cascading effects on food webs as biotic interactions between overlapping species are altered. As species interact in new ways, predator-prey dynamics, competition, and mutualistic relationships are reshaped, affecting ecosystem structure and function (Hollowed *et al.*, 2013; Vergés *et al.*, 2014). This is especially problematic for static Marine Protected Areas (MPAs), which may no longer cover the habitats of the species they were designed to protect (Edgar *et al.*, 2014). For fisheries, these shifts pose substantial challenges, as the movement of non-commercial species into areas

targeted by fisheries for specific species is likely to lead to increased bycatch, complicating management strategies and affecting the sustainability of fish stocks (Baudron *et al.*, 2020). A signature of such climate-change effects on fisheries catches has already been demonstrated over the past four decades on a global scale (Cheung *et al.*, 2013).

In the Baltic Sea, understanding changes in fish distributions is particularly important, as this semi-enclosed brackish water body has already undergone major shifts in ecosystem structure and functioning due to overfishing, the expansion of hypoxic zones, increasing temperatures, and high eutrophication (Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020). Additional pressures, such as contamination from land-based industries and intense shipping, further stress the ecosystem (Reusch *et al.*, 2018). Climate projections suggest continued increases in temperature, land runoff of organic matter, decreases in salinity, and the spread of bottom-water anoxia (Andersson *et al.*, 2015), with cyanobacterial blooms likely worsening due to rising temperatures and phosphorus release from sediments. These cumulative impacts are expected to alter fish distribution patterns in the Baltic, potentially disrupting established species interactions that underpin ecosystem properties and processes (Lang and Benbow, 2013).

Several commercially exploited fish stocks have declined significantly due to overexploitation and environmental changes in recent decades (Casini *et al.*, 2008; Möllmann *et al.*, 2009; Tomczak *et al.*, 2022). Atlantic cod (*Gadus morhua*) has been particularly affected, with reduced reproductive success linked to declining salinity and rising temperatures, leading to stock collapse (Sguotti *et al.*, 2019; Bryhn *et al.*, 2022) and a contraction in the distribution of adult and juvenile cod in the southern Baltic Sea (Orio *et al.*, 2019). At the same time European flounder (*Platichthys flesus)* showed an expansion in its distribution (Orio *et al.*, 2019; MacNeil *et al.*, 2025), leading to an increase in competition overlap between the two species (Orio *et al.*, 2020). Atlantic herring (*Clupea harengus*) populations have also declined, especially in the Western Baltic Sea, due to overfishing, environmental changes, habitat degradation and eutrophication leading to oxygen depletion in key spawning and nursery areas

(Fey *et al.*, 2014; ICES, 2024a). Together with European sprat (*Sprattus sprattus*) and plaice (*Pleuronectes platessa*) these species are vital for the region's biodiversity and economy, accounting more than 90% of the fish catches (ICES, 2024b). Rapid environmental changes may allow opportunistic species to proliferate, potentially causing large impacts on the ecosystem. This is seen in the case of the three-spined stickleback (*Gasterosteus aculeatus*), a pelagic mesopredator that has dramatically increased in abundance by 4- to 45-fold over recent decades, posing a growing threat to herring, sprat, and other coastal fish predators (Bergström *et al.*, 2015; Olin *et al.*, 2022). Other species such as common dab (*Limanda limanda*) and the benthopelagic whiting (*Merlangius merlangus*), which are typically confined to areas with higher salinities, may also shift their distribution, competing with cod, flounder, and plaice.

In this study, we develop dynamic species distribution models (SDMs) for these eight species (Table 1) to understand and predict changes in their distributions and species overlaps over space and time. Using 20 years of high-resolution trawl survey data for demersal and benthopelagic species and 7 years of data for pelagic species, we adopt a novel, geostatistical approach implemented in the R package *sdmTMB*, that is computationally fast and efficient (Anderson *et al.*, 2022). We fit the SDMs using Generalized Linear Mixed Effect Models (GLMMs) with spatial and spatiotemporal latent Gaussian Markov Random Fields (GMRFs) based on the Stochastic Partial Differential Equations (SPDE) approach (Lindgren *et al.*, 2011). Both species occurrence and abundance are modeled as functions of hydrographical conditions, depth, and substrate type, while fisheries landings are incorporated as covariates to account for exploitation and density-dependent dynamics. Two modeling strategies are tested: one modeling occurrence and abundance separately in two steps, and another modeling them jointly. We use a validation-set approach, with the first years as the training period and the last years as the test period, to assess predictive performance and derive spatial indicators. The specific aims of the study are to i) evaluate changes in the spatial distribution of these fish stocks over time, ii) identify key environmental and anthropogenic drivers, and iii) quantify changes in spatial overlap between species. We also explore the implications of these findings for food web dynamics and fisheries management.

MATERIALS AND METHODS

Study area

The Baltic Sea, located in Northern Europe, is a brackish, semi-enclosed water body with an average depth of around 53 meters, though it contains also deeper basins such as the Gotland Deep and the Landsort Deep, where depths reach up to 451 meters (HELCOM, 2003). Water exchange with the North Sea is restricted by narrow straits and shallow sills, creating a strong salinity gradient - saline water enters from the southwest, while a freshwater surplus dominates in the northeast (The BACC Author Team, 2008). This estuarine gradient allows the coexistence of marine and freshwater species (Frelat *et al.*, 2018). The water column of the Baltic Proper is permanently stratified into a brackish surface layer and a more saline deep layer, separated by a strong permanent halocline. This halocline limits vertical mixing and prevents oxygen-rich surface waters from reaching the deeper layers (Matthäus and Schinke, 1999). Anthropogenic eutrophication, driven by increased inputs of nutrients such as nitrogen and phosphorus, has exacerbated oxygen depletion, leading to the spread of hypoxic zones in the Western Baltic Sea (Conley *et al.*, 2007) and the deeper regions of the Baltic Proper and Gulf of Finland (Zillén *et al.*, 2008). These hypoxic and anoxic conditions restrict marine life to the more oxygenated, shallower waters and strongly influence the Baltic's ecological structure (Conley *et al.*, 2009). For the purpose of our study, we consider the Baltic Sea as the traditionally defined area with the addition of ICES Division IIIa.

Data and data processing

Trawl survey data

For the demersal and benthopelagic species (see Table 1), including both western and eastern Baltic cod stocks, we used data from the Baltic International Trawl Survey (BITS), a multi-decadal program coordinated by the International Council for the Exploration of the Sea (ICES) (ICES, 2017). Since 2001, the survey has been carried out with a harmonized sampling scheme and a standard gear designed to sample the demersal fish community in the Baltic Sea. The sampling scheme consists of trawl hauls with a duration of 30 minutes on average, carried out at a speed of

three knots with demersal otter trawl gears optimized for sampling species such as gadoids and flatfish (TVL 930 meshes, TVS 520 meshes). Sampling occurs twice annually: in quarter 1 (between 15th February and 31st March) and quarter 4 (primarily between 1st and 30th November, with additional samplings in October and December, and occasional sampling in September). Due to inconsistent sampling in September, hauls from this month were excluded. In total, our dataset comprised of catch per unit of effort (CPUE) data from 10,489 hauls carried out between 2001 and 2020, with an average of 524 hauls per year. This dataset provided good spatial coverage from the Kattegat (ICES subdivision (SD) 21) to the northern Baltic proper (ICES SD 29). The original dataset was downloaded from the ICES Database on Trawl Surveys (DATRAS), [Date accessed: 02.06.2023], ICES, Copenhagen, Denmark (https://datras.ices.dk).

For the pelagic species, we used data from the Baltic International Acoustic Survey (BIAS), downloaded from the ICES Acoustic data portal, [Date accessed: 21.04.2021], ICES, Copenhagen, Denmark (https://acoustic.ices.dk) The BIAS survey covers the whole Baltic area, including ICES Division IIIa (see Fig. 1), and is based on ICES statistical rectangles. The survey is conducted regularly in September and October of each year, with trawl-based sampling in both midwater and near-bottom areas using different trawl gears and haul durations (ICES, 2009). In our study, we used data from 2015 to 2020, as this period fully covered the study area. Data from 2014 was also included despite limited coverage in the western Baltic Sea. However, hauls conducted in November were excluded due to infrequent coverage. In total, our dataset contained catch per unit of effort (CPUE) data from 1,416 hauls carried out between 2014 and 2020, with an average of 202 hauls per year. The following expression was applied

$$CPUE_{species} = \left(\frac{Abundance_{species}}{Duration\ of\ the\ haul}\right) \times 30\ minutes \qquad (1)$$

to standardize species abundance per haul to a 30-minute duration. Observations were excluded from both datasets if the haul duration was less than 15 minutes or if

haul depth was not recorded. Standardized CPUE data for juvenile and adult fish were pooled together and aggregated by species or stock (Atlantic cod). Aggregation was performed by calculating the median CPUE per spatial grid cell, defined as 0.1° longitude by 0.1° latitude, for each month and year. The median CPUE data were then converted to presence/absence data for the occurrence-based models and log-transformed for the abundance-based models.

Table 1. An overview of fish populations studied, related data sources, and presumed drivers of their distributions.

Common name	*Scientific name*	*Range*	*Habitat*	*Data source*	*Presumed important drivers that were used in this study*
Common dab	*Limanda limanda*	Baltic Sea	Demersal	BITS	Salinity, sediment and depth (Heessen *et al.*, 2015; Rau *et al.*, 2019)
European flounder	*Platichthys flesus*	Baltic Sea	Demersal	BITS	Temperature, eutrophication and prey organisms (both proxied by chlorophyll *a*), salinity, oxygen, depth (Heessen *et al.*, 2015; Orio *et al.*, 2017, 2019; Rau *et al.*, 2019)
European plaice	*Pleuronectes platessa*	Baltic Sea	Demersal	BITS	Temperature, salinity, prey organisms (proxied by chlorophyll *a*), sediment, depth (Heessen *et al.*, 2015; Rau *et al.*, 2019)
Atlantic cod	*Gadus morhua*	Western Baltic Sea (WBS)	Bentho-pelagic	BITS	Temperature, salinity, oxygen, eutrophication (proxied by chlorophyll *a*), exploitation (proxied by landings), habitat, depth (Heessen *et al.*, 2015; Bryhn *et al.*, 2022)
Atlantic cod	*Gadus morhua*	Eastern Baltic Sea (EBS)	Bentho-pelagic	BITS	Temperature, salinity, oxygen, eutrophication (proxied by chlorophyll *a*), exploitation (proxied by landings), habitat, depth (Heessen *et al.*, 2015; Orio *et al.*, 2019; Bryhn *et al.*, 2022), population size (also proxied by landings) (Bartolino *et al.*, 2017)
Whiting	*Merlangius merlangus*	Baltic Sea	Bentho-pelagic	BITS	Depth, salinity (based on available distribution maps) (Heessen *et al.*, 2015)
Atlantic herring	*Clupea harengus*	Baltic Sea	Pelagic	BIAS	Temperature (Arula *et al.*, 2019; Dodson *et al.*, 2019; Polte *et al.*, 2021; Ory *et al.*, 2022), salinity, prey availability (proxied by chlorophyll *a*), population size (proxied by landings) (Casini *et al.*, 2010; Illing *et al.*, 2016; Rajasilta *et al.*, 2019), exploitation (also proxied by landings) (Froese *et al.*, 2022)
European sprat	*Sprattus sprattus*	Baltic Sea	Pelagic	BIAS	Temperature, salinity, oxygen, biological production and prey (proxied by chlorophyll *a*), density (proxied by landings) (Cardinale *et al.*, 2002; MacKenzie and Köster, 2004; MacKenzie *et al.*, 2008; Petereit *et al.*, 2008; Ojaveer and Kalejs, 2010)
Three-spined stickleback	*Gasterosteus aculeatus*	Baltic Sea	Pelagic	BIAS	Temperature, eutrophication and resources (proxied by chlorophyll *a*) (Lefébure *et al.*, 2014; Olin *et al.*, 2022)

Environmental and landings data

We selected environmental variables based on their potential or known effects on the studied fish species, specifically focusing on depth, substrate type, local hydrographic conditions, and primary productivity (Table 1). Seabed depth data for each grid cell was extracted from a data compilation that provided a digitized topography of the Baltic Sea (Seifert *et al.*, 2001). Photic and non-photic mean percentages of mud, sand and hard bottom complex substrate, based on the BALANCE Interim Report No. 10 (Al-Hamdani and Reker, 2007), were provided by Hans-Harald Hinrichsen. To obtain total substrate percentages for each grid cell, we summed the photic and non-photic components of each substrate type. Seven variables concerning local hydrographic conditions and primary productivity were extracted from the Copernicus Marine Environmental Service (CMEMS) as product of the coupled NEMO-Nordic ice-ocean and Swedish Coastal and Ocean Biogeochemical (SCOBI) models (Eilola *et al.*, 2009; Liu *et al.*, 2017). CMEMS provided monthly values of temperature, salinity, oxygen, and chlorophyll *a*, with a horizontal resolution of 1 nautical mile and 56 vertical layers. For demersal and benthopelagic species, bottom conditions (temperature, salinity, and oxygen) were calculated as median values for the bottom 5 meters. For pelagic species, surface conditions were additionally calculated as median values for the upper 10.6 meters of the water column. Chlorophyll *a* concentration was used as an indicator of primary productivity, and proxy for eutrophication and prey availability across all species. The eight variables were aggregated to the same 0.1° x 0.1° grid cells as the fish observational data, and only grid cells where trawling occurred during that month were retained.

Additionally, spatially non-resolved yearly landings data related to the studied fish species and stocks were extracted from the ICES Stock Assessment Graphs database using the icesSAG R package (Millar *et al.*, 2023). These data were used to account for the effects of density-dependent internal dynamics and fisheries exploitation. Landings data were available for all populations except whiting and three-spined stickleback and were lagged by one year to capture delayed relationships between fisheries exploitation and population responses. When

necessary, landings from different areas were aggregated to provide a comprehensive estimate.

All variables were normalized to a mean of zero and a standard deviation of one to alleviate numerical issues during model fitting. Prior to fitting the models, we evaluated the collinearity of candidate covariates. Variables with high collinearity ($R > 0.7$, variance-inflation factor (VIF) > 10) were removed. Due to high collinearity, we excluded sand as a covariate because mud had a stronger contribution in the study area. Additionally, oxygen was removed from the model for Western Baltic Sea (WBS) cod, and salinity and depth were discarded for Eastern Baltic Sea (EBS) cod, due to collinearity.

Modelling approach

Species Distribution Models

We adopted a SDM approach using the *sdmTMB* R package to fit spatial and spatiotemporal Generalized Linear Mixed Effects Models (GLMMs). The modelling process utilized Template Model Builder (TMB) for efficient model fitting and R-INLA to set up Stochastic Partial Differential Equations (SPDE) matrices. This approach allowed for the inclusion of spatial and spatiotemporal random fields, accounting for dependencies that arise due to missing covariates or inherent spatial and temporal structures (Anderson *et al.*, 2022). These random fields are typically modeled as Gaussian Random Fields (GRFs) and included as random effect in models. However, due to the computational intensity of GRFs - especially with large datasets in two or three dimensions- the SPDE method was employed to transform continuous GRFs into Gaussian Markov Random Fields (GMRFs), which have a sparse precision matrix and allow for more efficient computation (Lindgren *et al.*, 2011). Estimation in *sdmTMB* was performed via maximum marginal likelihood, providing a flexible and computationally efficient framework for modeling complex ecological processes.

Following Lee-Yaw *et al.* (2022), we modeled both occurrence and abundance (represented as log-CPUE for grid cells, where the population is present) and

combined their results to improve predictions and overcome limitations of individual approaches. We applied two modelling strategies:

- **Two-step-approach:** in this approach, occurrences and abundances were separately modeled for each species population, and their predictions were then combined for the final predictions of CPUE (see Figure 1). This allowed us to include different covariates and random fields in each model. To determine species presence, we used a threshold based on the **Kappa criterion** (Freeman and Moisen, 2008), rather than the default value of 0.5, as it maximizes the accuracy of presence/absence predictions.
- **One-step approach**: two methods were used. The first involved fitting occurrence and abundance models simultaneously, sharing the same covariates and random fields, with outputs combined internally by the *sdmTMB* R package. The second method fit models on the original data directly using a Tweedie distribution. Both methods did not require a threshold value for presence/absence.

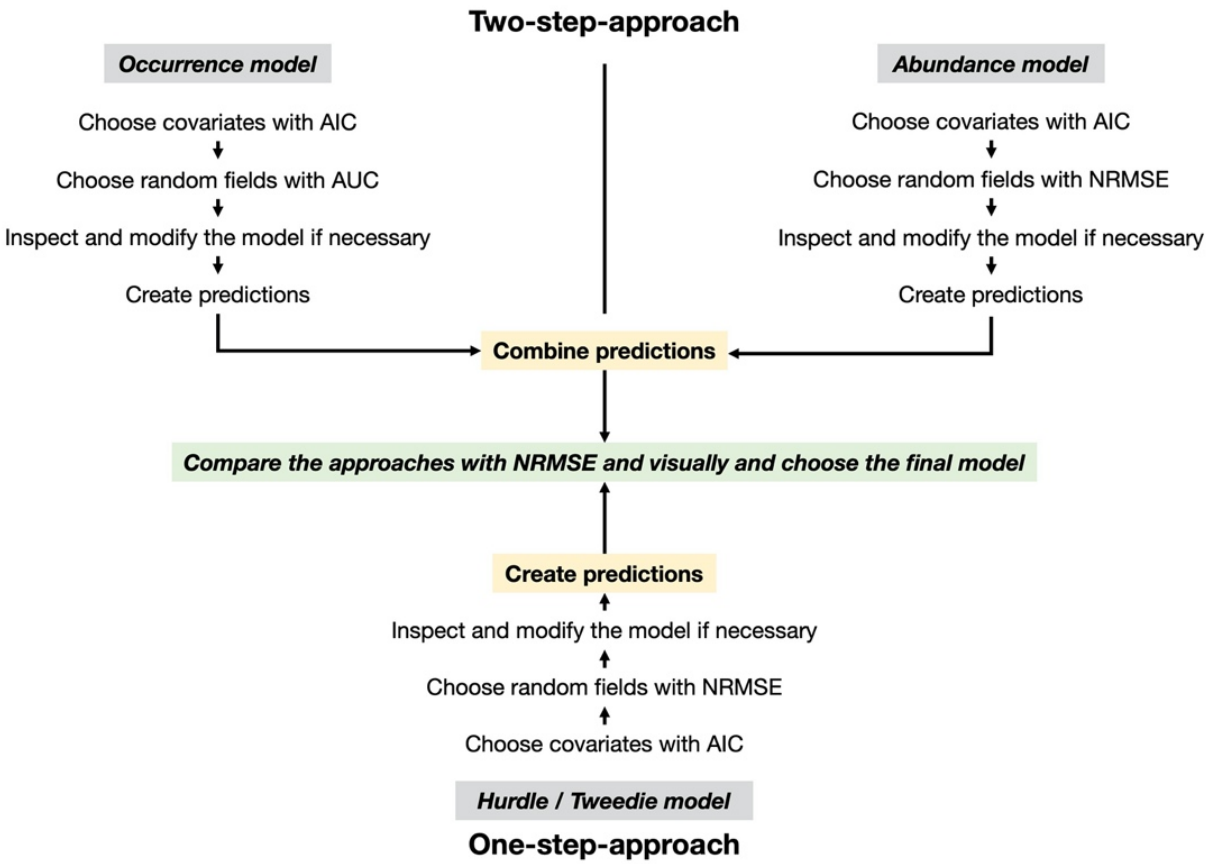


Figure 1. Overview of the modeling strategy applied in this study. The two-step approach models species occurrences and abundances separately, with final predictions combining both. The one-step approach simultaneously models occurrences and abundances, sharing covariates and random fields. Both strategies incorporate spatial and spatiotemporal random fields to account for dependencies in the data.

Model training and selection

We used a validation-set approach, splitting the time period evenly into a 50% training set and a 50% testing set. For demersal and benthopelagic species, models based on **BITS data** were trained using data from 2001 to 2010 and tested on data from 2011 to 2020. Models for pelagic species based on **BIAS data** were trained on data from 2014 to 2017, with 2018 to 2020 used as out-of-sample testing data.

Both modeling strategies began with a full model, including linear effects of all covariates (depth, percentages of hard bottom complexes and mud, bottom

hydrographical conditions, chlorophyll *a*, and population-specific landings). Given that the associated BIAS survey is carried out in the midwater and in the near bottom, the same covariates were used for pelagic species, excluding substrate type. A separate full model was fitted with surface hydrographical conditions and without substrate type and depth. We compared several error distributions and found that **log-normal** and **Gamma** distributions were most suitable for abundance-based models. For the one-step approach, we also tested models using the **Tweedie distribution**, which allowed us to model zero-inflated density data instead of combining internally the output of the occurrence- and abundance-based models. Covariate selection was carried out using a backwards-selection process based on the AIC ($\Delta \geq 2$) (Akaike, 1974). Spatial and spatiotemporal (first-order auto regressive – AR(1), and independent and identically distributed - IID) random fields were added after selecting the most parsimonious models component. This led to six candidate models:

1) Model with only fixed effects,
2) Model with fixed effects and spatial random fields,
3) Model with fixed effects and AR1 spatiotemporal random fields,
4) Model with fixed effects and IID spatiotemporal random fields,
5) Model with fixed effects, spatial and AR1 spatiotemporal random fields,
6) Model with fixed effects, spatial and IID spatiotemporal random fields.

Model selection was based on the out-of-sample testing data and varied depending on the modelled response variable. For occurrence-based models in the two-step-approach we used the approximation of the area under the ROC curve with a Mann-Whitney U statistic (AUC) criterion (DeLong *et al.*, 1988), while for abundance models and one-step models, we used the Normalized Root Mean Squared Error (NRMSE) (Otto, 2019). In cases of similar NRMSE values, we further compared the predictive performance in the training period.

Model evaluation

All models underwent a sanity check using functionalities available in the *sdmTMB* package. This is a quick diagnostic tool that inspects a fitted model for obvious issues and is thus useful for ensuring that it is working correctly. If a model failed a sanity check, it was improved by passing one or more covariates as smoothers to account for non-linear effects. If this did not resolve the issues, the model was excluded. The residual patterns of all final models were examined visually for non-linearity, and smoothers were applied to covariates where necessary. If applying smoothers negatively affected model performance or caused the model to fail a sanity check, we reverted to using non-smoothed covariates. Response curves were also visually inspected to ensure their validity. If landings were found to have a positive effect on the response variable, the covariate was excluded, as this would imply an unrealistic relationship—higher exploitation leading to higher abundance. We interpreted this as higher abundance in independent surveys coinciding with increased landings due to larger fish stock sizes, despite the one-year lag in the covariate.

Lastly, when fitting the cod models, data from ICES subdivision 24 were excluded due to mixing of the two cod stocks, which made it unclear which stock each record belonged to. However, the models were used to predict CPUE for this area, which may have impaired predictive performance since models trained in one region may not generalize well to others (Lee-Yaw *et al.*, 2022).

Spatial indices

We calculated a set of indices based on model predictions for the whole period to summarize interannual changes in spatial pattern. These indices include total CPUE, habitat size (previously referred to as positive area), center of gravity (Woillez *et al.*, 2009), and the Morisita index of intraspecific aggregation (Morisita, 1959, 1962). To detect potential breakpoints in the distributional patterns of individual populations, which may indicate spatiotemporal shifts, we applied constrained hierarchical clustering to sets of associated time series of the mentioned indices normalized to a mean of zero and a standard deviation of one (Legendre *et al.*, 1985). The broken stick method was used to determine the number of the breakpoints, and we visually

inspected time series of the indices and interannual distribution maps, to evaluate the validity of the breakpoints. To assess potentially significant spatial overlap between the modeled populations, we calculated the Spatial overlap index (SOI) (Otto *et al.*, 2016) for each year. We tested the resulting time series for significant trends by using a sieve-bootstrap version of the local regression-based WAVK test, which accounts for potential autocorrelation in the data (Wang *et al.*, 2008). Definitions and equations for the selected indices are described below.

Habitat size

Habitat size is typically calculated as the number of grid cells with positive values (in our case, where CPUE > 0). However, we modified this indicator to include only the top 95% of positive observations, discarding the lowest 5%. This threshold was chosen because many of the modelled populations exhibited positive CPUE values in nearly every grid cell each year, making the lower range less informative.

Center of gravity (COG)

The COG represents the mean location of a population and is calculated as follows

$$COG_j = \frac{\sum_{i=1}^{n} x_{ij} z_{ij}}{\sum_{i=1}^{n} z_{ij}} \quad (2)$$

where j represents the year, n is the number of observations, i is the grid cell, x is either longitude or latitude, and z is the CPUE value.

Morisita index of intraspecific aggregation (Imor)

Imor measures intraspecific aggregation and ranges from 0 to *n.* Values from 0 to 1 indicate uniform (hyperdispersed) patterns, while values greater than 1 indicate clumped distributions. The index is calculated as

$$Imor = \frac{n\Sigma {x_{ij}}^2 - \Sigma x_{ij}}{\Sigma {x_{ij}}^2 - \Sigma x_{ij}} \quad (3)$$

where n is the number of samples, and x_{ij} is the CPUE in grid cell i and year j.

Spatial overlap index (SOI)

The SOI measures the overlap between species or stock distributions. An SOI < 0.8 indicates a population separation, SOI > 1.2 suggests overlap in some grid cells, and SOI between the two values indicates a uniform or random distribution of either of the two. It is calculated as

$$SOI_j = \frac{\Sigma_{i=1}^{n}(P1_{ij}P2_{ij})N}{\Sigma_{i=1}^{n}(P1_{ij})\Sigma_{i=1}^{n}(P2_{ij})} \quad (4)$$

where $P1$ and $P2$ represent the two fish populations and N is the number of sampled grid cells.

Software and sources

All statistical analyses were conducted in the programming environment R 4.1.2 (R Core Team, 2023, version 4.3.1). The cleaned datasets, R-scripts with details on used R packages will be made available upon the successful publishment of this article at https://github.com/franemadiraca/.

RESULTS

Final models – Performance and drivers

The final SDMs for the eight fish species (including two cod stocks inhabiting the Baltic Sea) demonstrated significant spatial and spatiotemporal patterns across the study area. Overall, most models showed strong predictive performance, with high accuracy in capturing both the occurrence and abundance of each population. Notably, except for European plaice, the highest-performing models were one-step models, suggesting that both occurrences and abundances could be effectively explained by the same covariates and error structures, albeit with varying levels of importance. Spatial and spatiotemporal fields were included in most models, except for common dab, whiting, and three-spined stickleback. This is due to the three not

passing the sanity checks if the random fields were applied. An overview of the used modelling framework, NRMSE values associated with the training and testing datasets, used distribution, used random effects, and estimated covariate coefficients of the final models are provided in Table 2.

Table 2. Overview of the final SDMs' structure. "Train" denotes the training and "Test" the testing dataset, "SP" denotes spatial random effects, "SPT" spatiotemporal random effects, "Temp." temperature, "Sal." salinity, "Oxy." Oxy, "Chl." Chlorophyll *a*, "Hard bott." hard bottom complexes, and "Land." denotes landings. The numbers reported in the table represent coefficient estimates obtained from the models, those noted with "*****" and in bold are deem statistically significant ($p \leq 0.05$). Response curve types are written underneath covariate coefficients: "Sc" stands for S-shaped curve, "Cv" for convex, "Cc" for concave, and "Li" for linear. "Sm" stands for a smoother.

Model	*Modelling framework*	*NRMSE*	*Submodel*	*Distribution*	*Random effects*	*Temp.*	*Sal.*	*Oxy.*	*Chl.*	*Depth*	*Hard bott.*	*Mud*	*Land.*
Common dab	1-step	Train: 0.40 Test: 0.43	Occurrence	Bernoulli	None	**-0.35*** **Cv**	**3.29*** **Sc**	0.30 Cv	**0.57*** **Sc**	**-4.04*** **Sc**	-0.04 Li	**0.58*** **Cv**	
			Density	Lognormal		0.02 Li	**0.35*** **Cv**	**0.09*** **Li**	0.01 Li	-**1.30*** Cv	**0.08*** **Li**	**0.09*** **Li**	
European flounder	1-step	Train: 0.77 Test: 0.94	Occurrence	Bernoulli	SPT-AR1	**-0.86*** **Cc**	0.05 Li	**0.66*** **Cc**	0.12 Li	**-0.92*** **Cc**	-0.14 Li	0.14 Li	-0.07 Li
			Density	Lognormal		**-0.08*** **Li**	**0.26*** **Cv**	**0.06*** **Li**	**0.10*** **Cv**	**0.12*** **Cv**	0.01 Li	**0.05*** **Li**	-0.01 Li
European plaice	2-step	Train: 0.51 Test: 0.74	Occurrence	Bernoulli	SP + SPT-AR1	**0.42*** **Cc**	0.01 Li	**1.18*** **Sc**	-0.17 Li	**1.38*** **Sc**	0.17 Li	**0.19*** **Li**	
			Density	Lognormal	SPT-AR1	0.07 Sm	**0.29*** **Cv**	**0.19*** **Cv**	**0.04*** **Li**	**0.16*** **Li**	**0.07*** **Li**	0.01 Li	-0.05 Li

WBS cod	1-step	Train: 0.81 Test: 0.93	Occurrence	Bernoulli	SP	**-0.29*** **Cc**	0.35 Cc			3.30 Cc	0.37 Cc	0.08 Li
			Density	Gamma		**-0.04*** **Li**	0.09 Li			0.34 Li	-0.01 Li	-0.03 Li
EBS cod	1-step	Train: 0.71 Test: 0.88	Occurrence	Bernoulli	SPT-AR1	**1.02*** **Cc**		**1.66*** **Sc**	-0.09 Li		0.33 Cc	**0.86*** **Cc**
			Density	Lognormal		**0.26*** **Cv**		**0.19*** **Cv**	**-0.11*** **Cv**		0.00 Li	**0.04*** **Li**
Whiting	1-step	Train: 0.51 Test: 0.57	Density	Tweedie	None	**1.56*** **Sm**	**37.73*** **Sm**	**0.26*** **Cv**	**0.08*** **Cv**	-12.14 Sm	**0.08*** **Li**	**0.13*** **Li**
Atlantic herring	1-step	Train: 0.80 Test: 0.92	Occurrence	Bernoulli	SP		-0.53 Cc			**3.78*** **Cc**		
			Density	Gamma			0.01 Li			0.01 Li		
European sprat	1-step	Train: 0.56 Test: 0.80	Occurrence	Bernoulli	SPT-AR1	-0.45 Li	**-2.81*** **Cc**		1.68 Cc			
			Density	Gamma		**0.08*** **Li**	-0.03 Li		0.02 Li			
Three-spined stickleback	1-step	Train: 0.65 Test: 0.85	Occurrence	Bernoulli	None	**-2.43*** **Sc**	-126.60 Sm		-0.03 Li			
			Density	Lognormal		**-0.10*** **Li**	3.24 Sm		-0.03 Li			

Demersal species

The results from the SDMs for demersal species indicate that the occurrence of all three flatfish species is primarily driven by temperature and depth, with depth consistently showing the largest effect size, influencing their abundances as well. European plaice favors warmer and deeper areas, while common dab and European flounder are more likely to occur in colder, shallower regions. Interestingly, although flounder is less likely to be present in deeper areas, its abundance increases with depth. Salinity is another critical driver, positively affecting the abundance of all three flatfish species, particularly plaice and flounder. In addition, the distributional range of dab is strongly associated with more saline waters. Oxygen influences both the occurrence and abundance of flounder as was expected (see Table 2). However, we also found significant effects on the dab abundance and plaice occurrence as well as abundance. Chlorophyll *a* was anticipated to be important for the abundance of flounder and plaice, but it also significantly affects the occurrence of common dab. Among the tested substrate types, mud proved to be important for all three flatfish species.

Benthopelagic species

For WBS cod, our final model identifies temperature as the only significant driver (Table 2). Other covariates that were presumed important (Table 1) were either not significant in our model or removed due to collinearity during the covariate selection process. Temperature is also an important driver for EBS cod, where it has the largest effect size in the abundance model. However, unlike for WBS cod, the relationship with temperature in EBS cod is positive. For whiting, temperature is also significant and positive, though its size effect cannot be directly compared with other covariates as it is modeled using a smoother. The distributions of EBS cod and whiting share oxygen, chlorophyll *a*, and the percentage of mud as important drivers. For EBS cod, oxygen is particularly critical for its occurrence, showing the largest effect size among significant covariates. However, other covariates such as depth, salinity and landings, which we hypothesized to be important (Table 1), were either not significant or excluded due to collinearity. In the case of whiting, salinity and hard bottom complexes are additional significant drivers. Interestingly, although depth was

expected to be an important factor (Table 1), it was not supported by the model results.

Pelagic species

Despite the wide range of presumed important drivers listed in Table 1, the final model for Atlantic herring identified depth as the only significant factor, and this was limited to the occurrence model. No covariates were significant in the density model (Table 2). For European sprat the model highlighted surface temperature and surface salinity as key drivers (Table 2), while other expected covariates (Table 1) were not significant or removed during the covariate selection process. In the case of the three-spined stickleback, surface temperature was confirmed as significant, but surface salinity and chlorophyll *a* were not significant in the final model (Table 2).

Spatiotemporal patterns and shifts in predicted species distributions

Demersal species

As predicted by the model, common dab shows the highest density in ICES Division IIIa and SD 22 and 23 in the western Baltic Sea. This pattern remains consistent over time (Figure 2a). A Imor value of 1 indicates a highly aggregated distribution, with little change in aggregation over time (Figure S15e, Supplementary material).

The predicted distribution of European flounder exhibits temporal variability (Figure 2b), with two distinct hotspots: one in northern ICES Division IIIa and another along the coast of Latvia in ICES SD 28.2. Compared to the 2006–2010 period, CPUE density in the eastern hotspot declined notably during the 2011–2015 and especially the 2016–2020 periods. Areas of low density, to which we refer as “coldspots”, were observed west and east of Gotland in earlier periods, but these regions showed increased densities in later periods. This suggests that conditions in the eastern Baltic coastal areas are becoming less favorable for flounder, while previously less suitable areas now show improved habitat conditions. Constrained hierarchical clustering (Figure S19, Supplementary material) and visual examination of the spatial indices time series reveals a prominent breakpoint in 2007-2008, indicating a spatiotemporal shift marked by increased CPUE, habitat size, and a westward shift in the

population's center of gravity (COG). The Imor also indicates greater population dispersion after 2008 (Figure 3a–e). Although additional breakpoints were identified in 2002–2003, 2009-2010 and 2013–2014, we are less confident these represent true shifts in distributions.

Model predictions for European plaice show the highest CPUE values in ICES Division IIIa, with a noticeable expansion along the Polish coast and eastward (SDs 25 and 26) during the 2010s, along with sporadic increases further north at low densities (Figure 2c). In the Belt Sea (SD 22) and the Arkona basin (SD 24), CPUE density initially rose before declining over time. Based on the constrained hierarchical clustering (Figure S20, Supplementary material) and visual examination of the spatial indices time series, a prominent breakpoint for European plaice was identified in 2008-2009 and a potential one was found in 2016–2017, though we are less confident in the latter one. Time series and breakpoints are shown in Figure 3. The model predicts increasing habitat size and total CPUE, along with a more dispersed, though still aggregated, population as indicated by the Imor. The center of gravity (COG) points to a southward and eastward shift in distribution (Figure 3f–j). Interestingly, while the model predicts a decline in total CPUE after 2015, in the actual data show continued increases in CPUE over the years (Figure S17, Supplementary material).

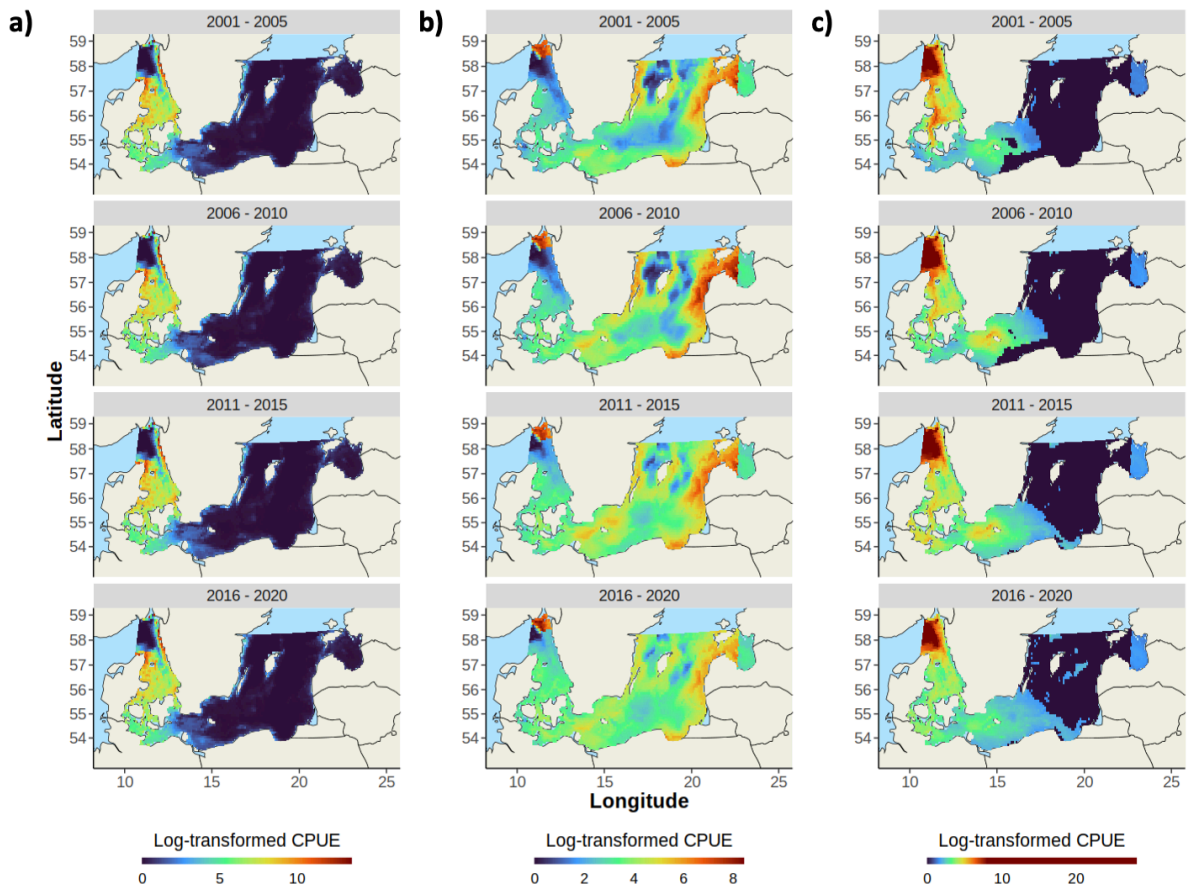


Figure 2. Predicted distribution of the demersal populations in the Baltic Sea expressed as median CPUE over 5-year periods between 2001 and 2020: a) common dab, b) European flounder, and c) European plaice. The scale for European plaice was adjusted to better highlight changes between periods.

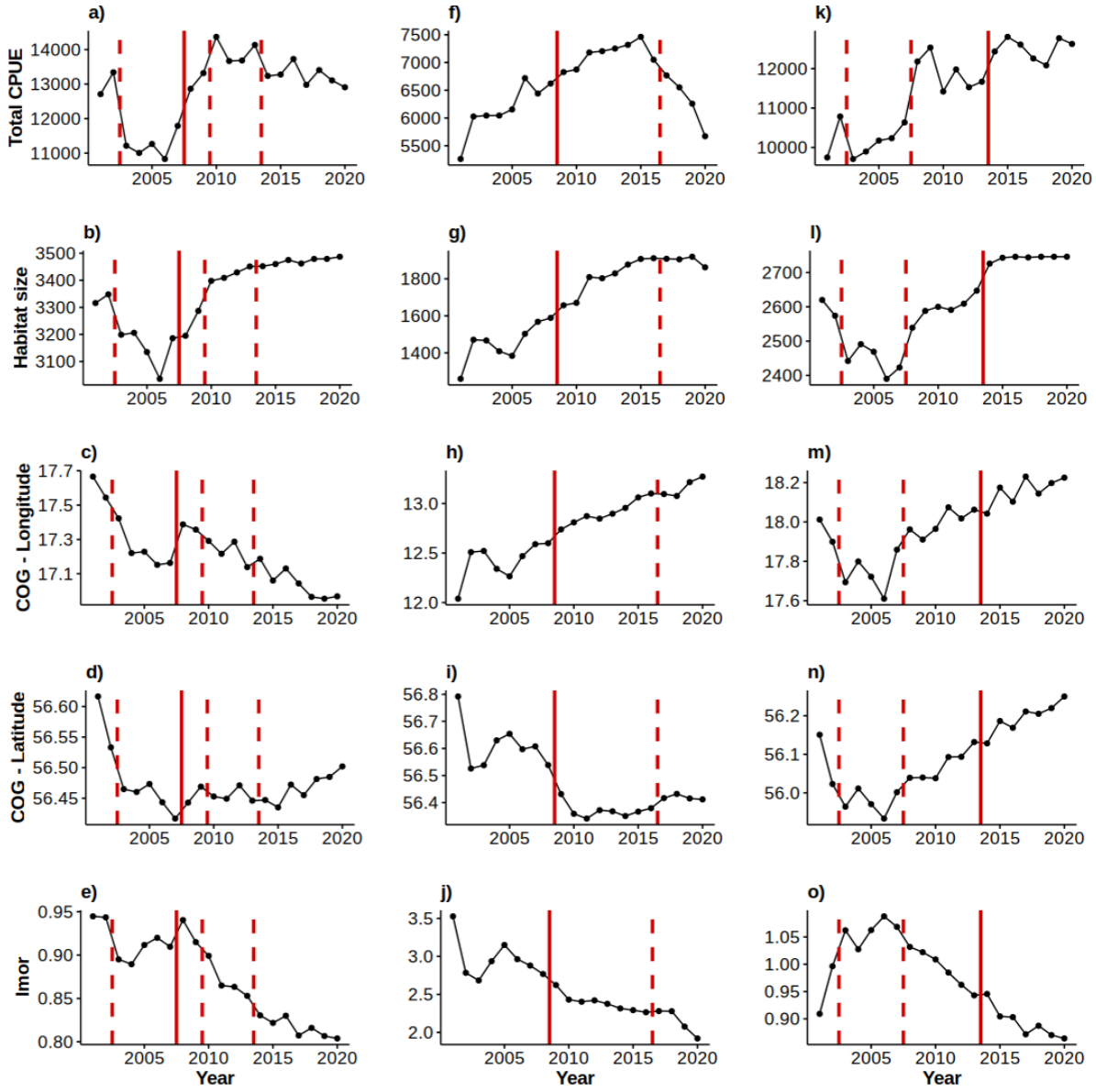


Figure 3. Indices summarizing spatiotemporal patterns in the distributions of European flounder (a-e), European plaice (f-j), and EBS cod (k-o) distributions. Solid red lines represent breakpoints identified using constrained hierarchical clustering, which are considered highly likely to reflect true shifts in distributional patterns. Dashed red lines represent breakpoints that are deemed less likely to indicate actual shifts.

Benthopelagic species

The predicted spatial distribution of WBS cod remains stable over time, with the highest densities found in the southwest, particularly in the Sound (SD 23) and the Little Belt and southern part of the Belt Sea (SD 22). No clear changes in distributional

patterns were observed over time for (Figure 4a). Imor indicates that WBS cod is highly dispersed throughout its distributional range (i.e., SDs 22–24) (Figure S15j, Supplementary material). However, the predicted intermediate densities in the Arkona Basin (SD 24) should be interpreted with caution, as the model was not trained for this area due to the mixing with the EBS cod stock. As a result, distributional patterns in this region are extrapolated and therefore uncertain.

For the EBS cod stock (Figure 4b), a high-density area located in the Arkona Basin (SD 24) and Bornholm Basin (SD25) remained relatively stable, though it diminished in the 2016–2020 period. Similar to the WBS cod model, the distributional patterns in the Arkona Basin should be treated cautiously due to uncertainty from extrapolation. Interestingly, we found a small “coldspot” east of Bornholm Island in the Bornholm Basin, which remained consistent over time. During 2016–2020, we observe increasing densities in previously depleted areas, suggesting greater dispersal of the stock, particularly west and east of Gotland (SD 27 and 28). Comparing the 2001–2005 and 2006–2010 periods, we also note a rise in density, with a new hotspot forming in the southeast Baltic Proper (SD26), along the coasts of Lithuania and Kaliningrad (Russia). Results from the constrained hierarchical clustering (Figure S22, Supplementary material) and visual examination of the spatial indices provide strong evidence of a spatiotemporal shift for EBS cod in 2013-2014, and additional ones in 2002-2003 and 2007-2008. Since 2007, both total CPUE and habitat size have increased, and the population has become more dispersed as indicated by the Imor (Figure 3k–o). Concurrently, the center of gravity (COG) has shifted eastward and northward.

The predicted spatial distribution of whiting (Figure 4c) remains consistent over time, with the highest densities in ICES Division IIIa and the Western Baltic Sea (SD 21, 22, and 23), as well as the offshore area in the Arkona Basin (SD 24). The Imor indicates that whiting is highly aggregated within its distributional range (Figure S15o, Supplementary material).

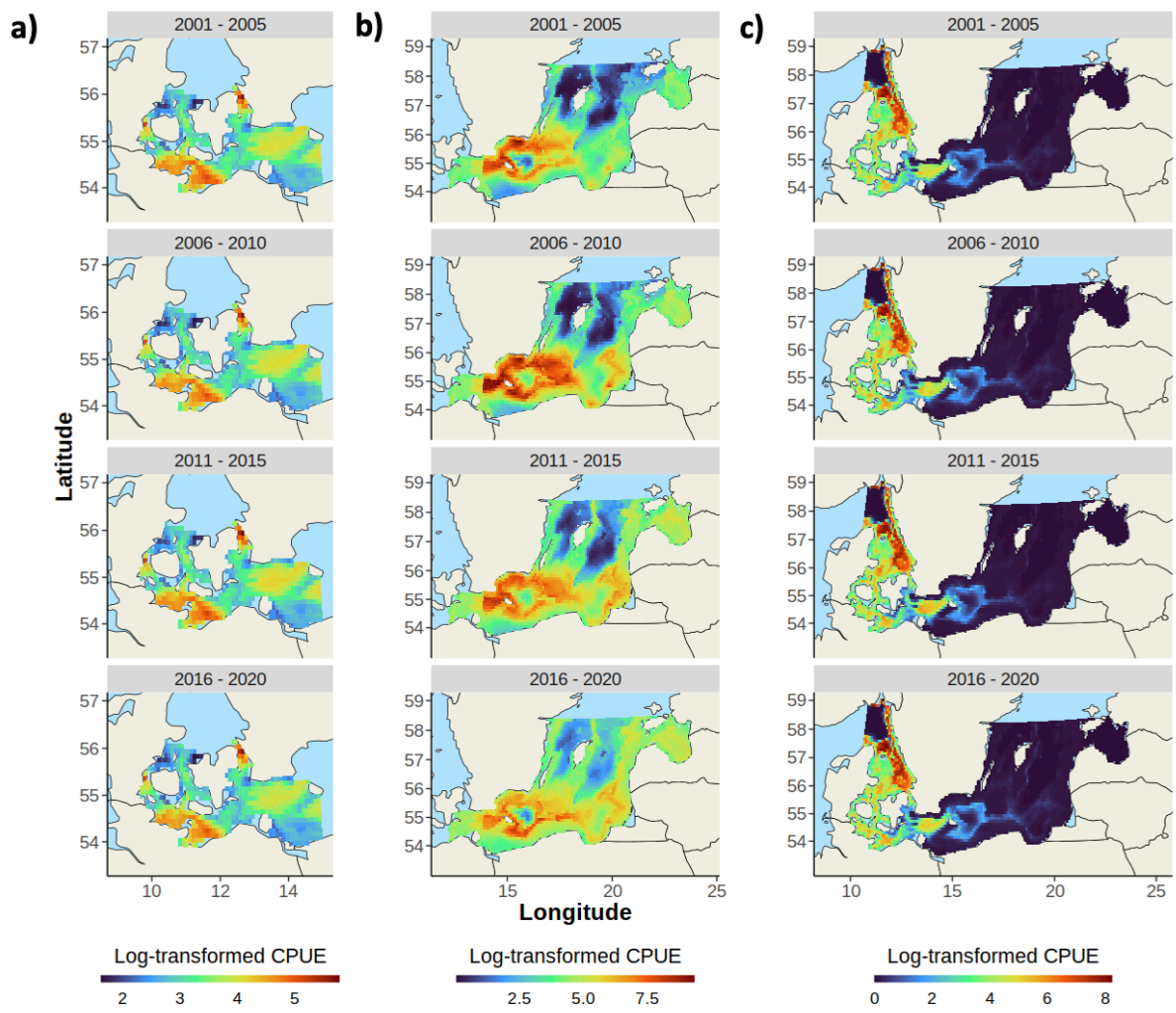


Figure 4. Predicted distribution of the benthopelagic populations in the Baltic Sea, expressed as median CPUE over 5-year periods between 2001 and 2020: a) WBS cod, b) EBS cod, and c) whiting.

Pelagic species

The predicted distribution of Atlantic herring remains relatively constant throughout the modeling period, with above average densities in Division IIIa, the Southern Baltic Proper (SD 24-26), the Bothnian Sea (SD 30) and Gulf of Finland (SD 32) (Figure 5a). Two "coldspots" are predicted by the model: one along the Danish coast of the Great belt (SD22) and Kattegat (SD21) and one at the coast near the Border between Kaliningrad (Russia) and Lithuania (SD26). The spatial patterns of European sprat also remain fairly stable over time, with higher densities concentrated in the Arkona Basin near the island Rügen and along the eastern coastline of the Baltic Proper (SD 26 and 28.2) into the Gulf of Riga (SD 28.1) and Gulf of Finland (Figure 5b). For the three-

spined stickleback, higher densities are predicted only in the Northeastern areas of the Baltic Sea, i.e., the Gulf of Riga, Gulf of Finland, and Gulf of Bothnia, with spatial patterns around Gotland expanding and retracting across periods (Figure 5c).

The results of the constrained hierarchical clustering Constrained hierarchical clustering (Figure S24-26, Supplementary material) and visual examination of spatial indices (Figure S16, Supplementary material) provided no strong evidence of distributional shifts for any of the pelagic species. According to the Imor of intraspecific aggregation, Atlantic herring and European sprat are considered dispersed within the study area, while the three-spined stickleback exhibits an aggregated distribution (Figure S16, Supplementary material).

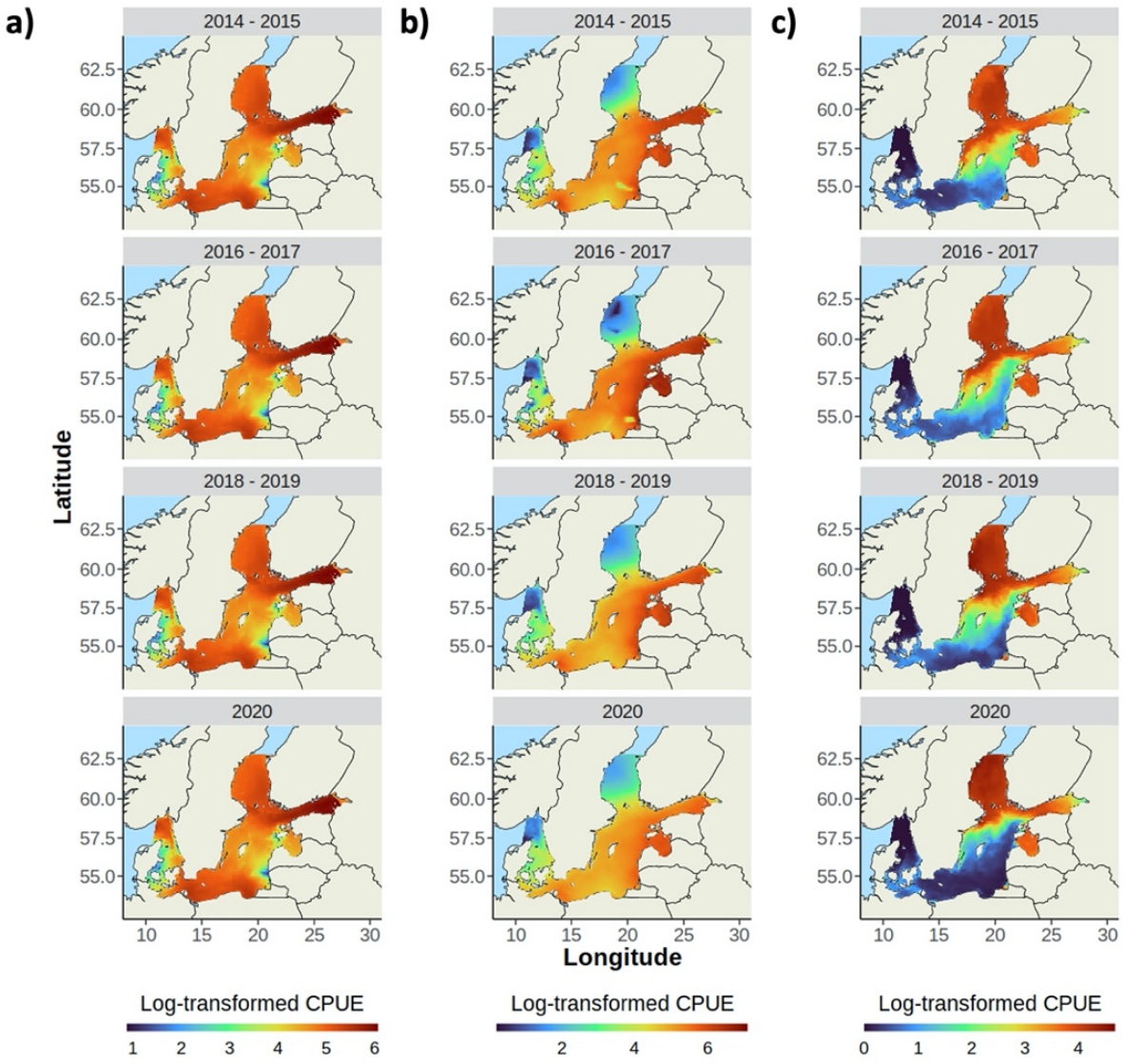


Figure 5. Predicted distribution of the pelagic populations in the Baltic Sea expressed as median CPUE over 2-year periods between 2014 and 2019 and in 2020: a) Atlantic herring, b) European sprat, and c) three-spined stickleback.

Spatial overlap index

After calculating the SOI for 27 species pairs, we identified 6 cases of distinct population overlaps involving common dab, European plaice, WBS cod, and whiting (Figure 6a), with common dab and whiting exhibiting the greatest overlap. In contrast, there were 5 cases of clear separation involving common dab, European plaice, WBS cod, EBS cod, whiting and three-spined stickleback. For other 16 pairs, SOI values fell between 0.8 and 1.2, suggesting a nearly uniform or random distribution of the two populations.

Among the SOI time series, significant trends were identified in eight cases using the sieve-bootstrap version of the WAVK test. Of these, three exhibited small magnitude of change. Of the remaining five, four showed constant significant overlap between populations. Overlap between plaice and dab, as well as plaice and whiting, decreased over time. Dab and WBS cod showed a gradual decline in overlap, with a short-term increase around 2013 and 2014. Meanwhile, dab and whiting maintained consistently high levels, with a slight peak around 2007 to 2013. Even though their populations showed separation at the beginning of the times series, European plaice and flounder exhibit a consistent increase in their spatial overlap over time. This increase has led their case being classified in between significant separation and significant overlap starting from 2010. This trend appears slow and gradual but does not show any indication of changing in the future (Figure 6b).

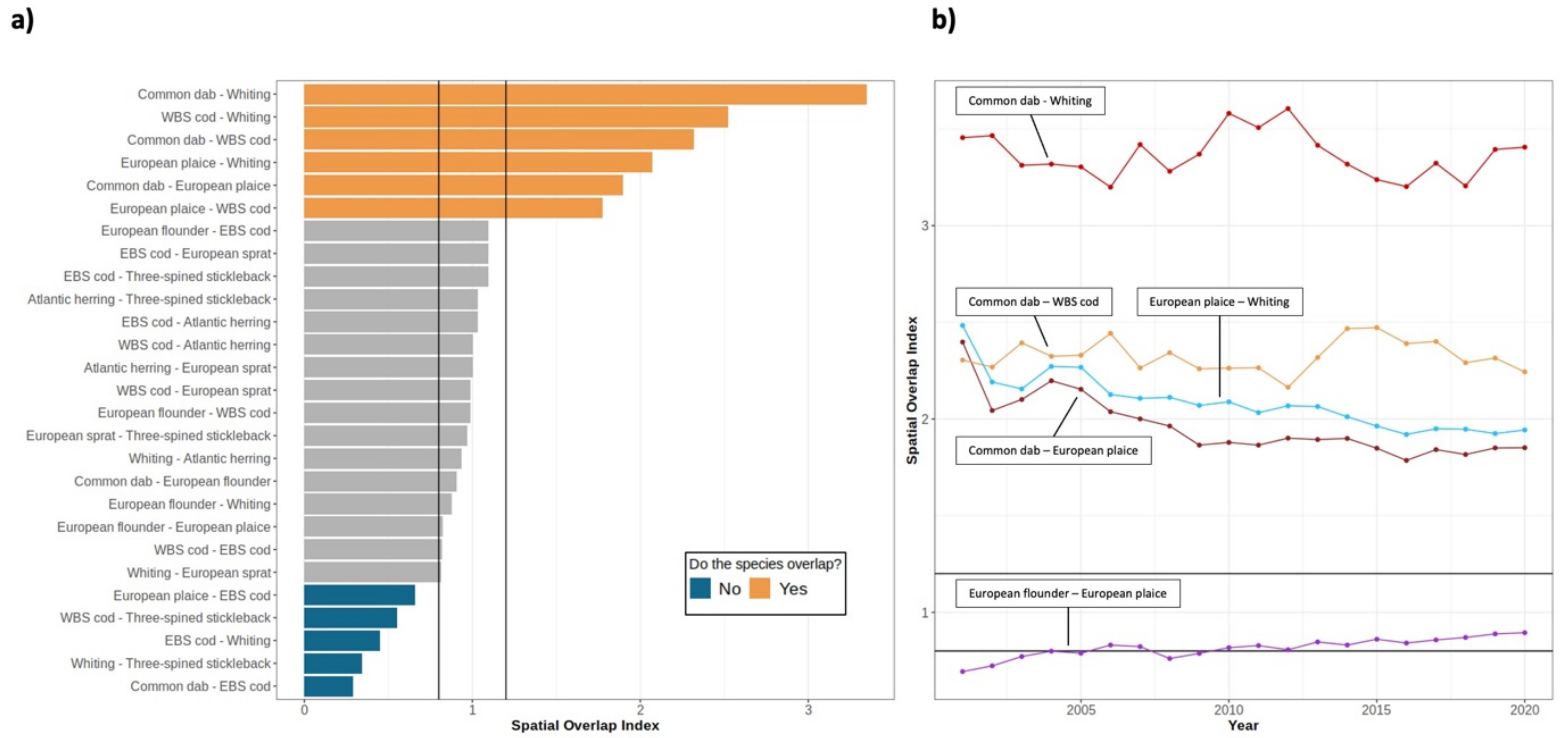


Figure 6. Calculated Species Overlap Index (SOI) in the Baltic Sea for the species investigated in this study: a) median SOI values over the entire study periods, with cases of overlap (in orange), separation (in blue) and of uniform or random distributions (in grey) indicated, b) interannual changes in SOI time series where significant trends were detected. The two solid black lines represents SOI = 0.8 (left in a) and down in b)) and SOI = 1.2 (right in a) and up in b)); values of SOI > 1.2 indicate overlapping populations, while SOI < 0.8 indicates separated populations. In b), the following cases are not shown due to small magnitude of change of SOI: WBS cod and Atlantic herring, WBS cod and European sprat, and Atlantic herring and three-spined stickleback.

DISCUSSION

Spatiotemporal shifts and environmental drivers

This study highlights significant spatiotemporal distributional shifts in European flounder, European plaice, and EBS cod in the Baltic Sea, driven by key environmental factors. Our advanced SDMs revealed increases in habitat size and dispersal for these species, alongside declining abundances in historic hotspots during the autumn/winter period. For instance, European flounder exhibited a pronounced abundance hotspot along the eastern coasts of the Baltic States, which diminished over time. This decline in abundance is consistent with biomass losses reported by MacNeil *et al.* (2025) for the same region. Orio et al. (2019), however, suggested that in earlier periods, flounder distribution was more concentrated along the southern Baltic coast. Rising temperatures played a pivotal role in these shifts, influencing both the presence and density of flounder. This finding aligns with Rau et al. (2019), who identified temperature as a primary driver for flatfish distributions in the western Baltic Sea. The observed broader and more uniform spatial distribution of flounder in the last decade likely reflects a combination of warming waters and changes in oxygen concentrations (Figures S2a and S2c, Supplementary material).

EBS cod exhibited westward and northward shifts in distribution, coupled with an increase in habitat size. This pattern contrasts with the contraction described by Orio et al. (2019), attributed to hypoxia and predation risk in shallow waters. While our models do not explicitly account for predator-prey interactions, oxygen concentration emerged as a significant factor in cod distributions, aligning with findings from Orio *et al.* (2019). Increasing oxygen concentrations in areas such as east of Gotland and rising temperatures likely drove the observed spatiotemporal shifts in EBS cod, highlighting the interplay of dynamic abiotic factors. These findings also support broader observations that cod populations are sensitive to environmental constraints, including oxygen and temperature, as documented by Bryhn et al. (2022) and Heessen et al. (2015).

European plaice showed consistent high densities in the western Baltic similar to findings from MacNeil *et al.* (2025), with expansion toward the south and east. Unlike other flatfish, plaice appears less constrained by low salinity, as reflected in its ability to inhabit brackish environments. Temperature and salinity, in line with the literature (Heessen *et al.*, 2015; Rau *et al.*, 2019), as well as oxygen are among key drivers of its distribution, thus emphasizing the importance of dynamic abiotic factors and underpinning the sensitivity of flatfish to changing environmental conditions.

The spatiotemporal shifts we detected, especially the increases of habitat size and dispersal fit well with globally observed patterns. Among others, examples include Atlantic mackerel (*Scomber scombrus*) expanding into Icelandic waters (Astthorsson *et al.*, 2012) and tropical herbivorous fish extending into temperate regions leading to overgrazing of temperate macroalgae (Verges *et al.*, 2014). Such developments could potentially impact ecosystem functioning and structure (Hollowed *et al.*, 2013).

Stationary distributions

In contrast, no evidence of spatiotemporal shifts was found for common dab, WBS cod, whiting, Atlantic herring, European sprat, or three-spined stickleback. These species exhibited relatively stable distributions, indicating that their habitat preferences and tolerances were largely met during the study period. Common dab distributions were strongly influenced by salinity and depth, consistent with Heessen *et al.* (2015) and Rau *et al.* (2019). This reliance on specific salinity gradients underscores the stability of its ecological niche. Whiting showed a broader suite of environmental drivers than expected, with no significant role for depth. This adaptability may explain its stable distribution, although unmodeled factors such as prey availability or species interactions could play a role. WBS cod, in contrast, displayed only a negative relationship with temperature, consistent with Bryhn et al. (2022). This suggests that increasing temperatures may constrain the habitat suitability for WBS cod, contrasting with the positive relationship observed for EBS cod.

The pelagic species—herring, sprat, and three-spined stickleback—also demonstrated stable distributions. Depth was the only significant covariate for herring occurrence, while no environmental drivers were identified for its abundance. Given the high model performance for both training and test period suggests that other dynamics captured by the spatial field might explain the abundance of the species. For instance, competition for prey items might also be an important factor as there is evidence that, at high sprat abundance, herring growth is considerably lower (Casini *et al.*, 2010). Sprat, on the other hand, showed a preference for areas with decreasing salinity, while rising temperatures had a significant positive effect on its abundance. This aligns with findings by Ojaaver and Kalejs (2010), who observed that conditions favorable for sprat often hinder the reproduction of its main predator, cod. Temperature and salinity also play essential roles in sprat recruitment and early-life development, as documented in studies by MacKenzie and Köster (2004), MacKenzie et al. (2008), and Petereit et al. (2008). Salinity further influences sprat condition variability (Cardinale *et al.*, 2002), reinforcing its importance in shaping the species' distribution. Three-spined stickleback distribution was influenced solely by temperature, emphasizing its strong link to warming trends in the Baltic Sea. However, species interactions could play a critical role, as its abundance increases when populations of northern pike (*Esox lucius*) and European perch (*Perca fluviatilis*) decline, as noted by Bergström *et al.* (2015) and Eriksson *et al.* (2021).

Spatial Overlap

This study significantly expands on the topic of spatial overlap between species in the Baltic Sea, revealing six cases of significant overlap and five cases of significant separation. The overlap cases appear between species most abundant in ICES Division IIIa and subdivisions 22–24. These regions represent a relatively small portion of the total study area, making increased overlap more likely due to the concentration of populations (Deane, 2022). Conversely, cases of spatial separation often involve species with more dispersed distributions across the broader Baltic Sea, where environmental gradients such as salinity and temperature likely play a stronger role in driving species distributions (Frelat *et al.*, 2017).

A notable example is the case between European flounder and EBS cod, which can be compared to findings by Orio et al. (2020). Our analysis does not identify neither significant separation not significant overlap between the two but does however show the highest SOI value among such cases, implying high potential for overlap. Orio *et al.* (2020) applied a more nuanced approach, showing that competition overlap for cod has increased, whereas the overlap between cod and large flounder has decreased. This reduction in overlap may have facilitated the expansion of flounder abundance and habitat in recent decades. These shifts are consistent with broader observations of climate-driven redistributions that influence interspecific interactions, as highlighted by Pecl *et al.* (2017). Additionally, studies on predator-prey dynamics in overlapping distributions, such as those by (Brodeur *et al.*, 2008), emphasize the role of spatial overlap in shaping ecological interactions and competitive outcomes.

Using the sieve-bootstrap version of the WAVK test, we identified eight time series with significant trends. Among these, European plaice showed particularly interesting dynamics. Its eastward and southward expansion appears to have reduced overlap with dab and whiting, two species that favor more saline environments in the western Baltic. This reduction in overlap may lead to decreased competition and predation among the three species, aligning with observations that climate-induced range shifts can alter interspecific interactions and community structures (Pecl *et al.*, 2017). Simultaneously, overlap between flounder and plaice, which currently sits between separation and overlap, is gradually increasing. This trend suggests that future interactions between these species may intensify, potentially altering competitive dynamics in line with observations of expanding overlap networks (Pie and Caron, 2022). The impact of potential trophic competition between species and stocks stemming from increased spatial overlap should not be disregarded. For example, in Floridas' Biscayne National Park, there is evidence that increased abundance of invasive Indo-Pacific lionfishes (*Pterois* spp.) could have reduced the breadth of resource use of the graysby (*Cephalopholis cruentata*) and also led to interspecific niche segregation between the two (Curtis *et al.*, 2017).

Management Implications and limitations

This study provides critical insights into the spatial and temporal dynamics of fish species distributions in the Baltic Sea, with significant implications for fisheries management and conservation. The differential responses of WBS and EBS cod to temperature emphasize the need for nuanced management approaches that account for physiological and ecological differences between stocks. While the positive relationship between temperature and EBS cod observed in this study might suggest a potential benefit, this finding should be interpreted with caution. Existing evidence indicates that rising temperatures are generally detrimental to cod stocks across the region (Bryhn *et al.*, 2022), particularly during warmer months not captured by the ICES surveys (BITS and BIAS). Revising survey protocols to include summer data and expanding coverage to shallow coastal areas are critical steps for improving data accuracy and model predictions.

The results also highlight the critical role of species overlap and trophic interactions in shaping ecosystem dynamics. The eastward and southward expansion of European plaice, for instance, may reduce overlap and competition with dab and whiting, species that favor more saline environments in the western Baltic. Conversely, increasing overlap between plaice and flounder could intensify interactions, potentially altering competitive and trophic dynamics. Similarly, significant overlap between WBS cod and species such as dab, plaice, and whiting raises concerns about trophic competition. Given the already depleted state of WBS cod stocks, such interactions could further hinder their recovery, emphasizing the need for management strategies that address these dynamics. This is critical to understand given that, for example, fisheries-induced mesopredator releases can even have dramatic cross-ecosystem impacts (Eriksson *et al.*, 2011). While the models employed in this study incorporate spatiotemporal dependencies that can capture some indirect effects of species interactions (Anderson *et al.*, 2022), they do not explicitly account for direct trophic or competitive relationships. This limitation underscores the importance of integrating interaction terms in future modeling efforts to better understand and predict ecosystem-level impacts.

Climate-induced shifts highlight the need for flexible, adaptive management frameworks. Rising temperatures and declining salinity are expected to favor sprat while further constraining herring, exacerbating competitive dynamics and habitat loss. Adaptive measures such as dynamic spatial closures and habitat protection will be essential to mitigate these impacts. However, the interplay between environmental changes and fisheries exploitation remains challenging to quantify. Spatially non-resolved fisheries data limit the ability to disentangle these effects. Historical overexploitation, particularly of Baltic cod stocks, has likely left populations vulnerable to current environmental pressures (Bryhn *et al.*, 2022). Reconstructing spatially resolved fisheries data will be critical for understanding long-term drivers and informing sustainable management strategies.

Conclusion

This study provides critical insights into the spatiotemporal dynamics of fish species in the Baltic Sea, revealing key drivers of distributional shifts and stable patterns. Climate-induced changes and historical exploitation have shaped current fish populations, highlighting the importance of adaptive management strategies. Future efforts should integrate spatially resolved fisheries data, expand survey protocols, and enhance modeling frameworks to include biotic interactions. Collaborative approaches across Baltic nations will be essential to develop effective, ecosystem-based management strategies that safeguard the biodiversity and productivity of the Baltic Sea.

REFERENCES

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19: 716–723.

Al-Hamdani, Z., and Reker, J. 2007. Towards marine landscapes in the Baltic Sea. BALANCE interim report #10: 116.

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. preprint. Ecology. http://biorxiv.org/lookup/doi/10.1101/2022.03.24.485545 (Accessed 2 January 2024).

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., *et al.* 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO, 44: 345–356.

Arula, T., Shpilev, H., Raid, T., and Sepp, E. 2019. Thermal conditions and age structure determine the spawning regularities and condition of Baltic herring (Clupea harengus membras) in the NE of the Baltic Sea. PeerJ, 7: e7345.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., and Óskarsson, G. J. 2012. Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. ICES Journal of Marine Science, 69: 1289–1297.

Bartolino, V., Tian, H., Bergström, U., Jounela, P., Aro, E., Dieterich, C., Meier, H. E. M., *et al.* 2017. Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. PLOS ONE, 12: e0172004.

Baudron, A. R., Brunel, T., Blanchet, M., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., *et al.* 2020. Changing fish distributions challenge the effective management of European fisheries. Ecography, 43: 494–505.

Bergström, U., Olsson, J., Casini, M., Eriksson, B. K., Fredriksson, R., Wennhage, H., and Appelberg, M. 2015. Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science, 163: 134–142.

Brodeur, R. D., Suchman, C. L., Reese, D. C., Miller, T. W., and Daly, E. A. 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Marine Biology, 154: 649–659.

Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J., *et al.* 2022. Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? Ocean & Coastal Management, 223: 106154.

Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galván, J. D., Stenseth, N. C., *et al.* 2017. Elevational range shifts in four mountain ungulate species from the S wiss A lps. Ecosphere, 8: e01761.

Cardinale, M., Casini, M., and Arrhenius, F. 2002. The influence of biotic and abiotic factors on the growth of sprat (Sprattus sprattus) in the Baltic Sea. Aquatic Living Resources, 15: 273–281.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B: Biological Sciences, 275: 1793–1801.

Casini, M., Bartolino, V., Molinero, J. C., and Kornilovs, G. 2010. Linking fisheries, trophic interactions and climate: threshold dynamics drive herring Clupea harengus growth in the central Baltic Sea. Marine Ecology Progress Series, 413: 241–252.

Chaudhary, C., Richardson, A. J., Schoeman, D. S., and Costello, M. J. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. Proceedings of the National Academy of Sciences, 118: e2015094118.

Cheung, W. W. L., Watson, R., and Pauly, D. 2013. Signature of ocean warming in global fisheries catch. Nature, 497: 365–368.

Conley, D. J., Carstensen, J., Ærtebjerg, G., Christensen, P. B., Dalsgaard, T., Hansen, J. L. S., and Josefson, A. B. 2007. LONG-TERM CHANGES AND IMPACTS OF HYPOXIA IN DANISH COASTAL WATERS. Ecological Applications, 17. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/05-0766.1 (Accessed 16 January 2025).

Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., *et al.* 2009. Hypoxia-related Processes in the Baltic Sea. Environmental Science & Technology, 43: 3412–3420.

Curtis, J., Wall, K., Albins, M., and Stallings, C. 2017. Diet shifts in a native mesopredator across a range of invasive lionfish biomass. Marine Ecology Progress Series, 573: 215–228.

Deane, D. C. 2022. Species accumulation in small–large vs large–small order: more species but not all species? Oecologia, 200: 273–284.

DeLong, E. R., DeLong, D. M., and Clarke-Pearson, D. L. 1988. Comparing the Areas under Two or More Correlated Receiver Operating Characteristic Curves: A Nonparametric Approach. Biometrics, 44: 837.

Dodson, J. J., Daigle, G., Hammer, C., Polte, P., Kotterba, P., Winkler, G., and Zimmermann, C. 2019. Environmental determinants of larval herring (Clupea harengus) abundance and distribution in the western Baltic Sea. Limnology and Oceanography, 64: 317–329.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., *et al.* 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature, 506: 216–220.

Eilola, K., Meier, H. E. M., and Almroth, E. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. Journal of Marine Systems, 75: 163–184.

Eriksson, B. K., Sieben, K., Eklöf, J., Ljunggren, L., Olsson, J., Casini, M., and Bergström, U. 2011. Effects of Altered Offshore Food Webs on Coastal Ecosystems Emphasize the Need for Cross-Ecosystem Management. AMBIO, 40: 786–797.

Fey, D. P., Hiller, A., Margonski, P., Moll, D., Nilsson, H., Pongolini, L., Stybel, N., *et al.* 2014. HERRING Impact Report Herring spawning areas - present and future challenges.

Freeman, E. A., and Moisen, G. 2008. PresenceAbsence: An R Package for Presence Absence Analysis. Journal of Statistical Software, 23. http://www.jstatsoft.org/v23/i11/ (Accessed 14 February 2024).

Frelat, R., Lindegren, M., Denker, T. S., Floeter, J., Fock, H. O., Sguotti, C., Stäbler, M., *et al.* 2017. Community ecology in 3D: Tensor decomposition reveals spatio-temporal dynamics of large ecological communities. PLOS ONE, 12: e0188205.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Froese, R., Papaioannou, E., and Scotti, M. 2022. Climate change or mismanagement? Environmental Biology of Fishes, 105: 1363–1380.

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., and Genner, M. J. 2020. Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species. Current Biology, 30: 1572-1577.e2.

Heessen, H. J. L., Daan, N., and Ellis, J. R. (Eds). 2015. Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys. Brill | Wageningen Academic. https://brill.com/view/title/68532 (Accessed 2 January 2024).

HELCOM. 2003. Baltic Sea Environment Proceedings No. 87.

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G., *et al.* 2013. Projected impacts of climate change on marine fish and fisheries. ICES Journal of Marine Science, 70: 1023–1037.

ICES. 2009. Manual for the Baltic International Acoustic Survey (BIAS).

ICES. 2017. Manual for the Baltic International Trawl Surveys (BITS). Series of ICES Survey Protocols SISP 7 - BITS: 95. ICES.

ICES. 2024a. Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Herring_i_Clupea_harengus_i_in_subdivisions_20_24_spring_spawners_Skagerrak_Kattegat_and_western_Baltic_/25019273 (Accessed 16 January 2025).

ICES. 2024b. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports. https://ices-library.figshare.com/articles/report/Baltic_Fisheries_Assessment_Working_Group_WGBFAS_/25764978 (Accessed 9 October 2024).

Illing, B., Moyano, M., Hufnagl, M., and Peck, M. A. 2016. Projected habitat loss for Atlantic herring in the Baltic Sea. Marine Environmental Research, 113: 164–173.

Jackson, S. T. 2021. Transformational ecology and climate change. Science, 373: 1085–1086.

Lang, J. M., and Benbow, M. E. 2013. Species Interactions and Competition. Nature Education Knowledge, 4: 8.

Lee-Yaw, J. A., McCune, J. L., Pironon, S., and Sheth, S. N. 2022. Species distribution models rarely predict the biology of real populations. Ecography, 2022: e05877.

Lefébure, R., Larsson, S., and Byström, P. 2014. Temperature and size-dependent attack rates of the three-spined stickleback (Gasterosteus aculeatus); are sticklebacks in the Baltic Sea resource-limited? Journal of Experimental Marine Biology and Ecology, 451: 82–90.

Legendre, P., Dallot, S., and Legendre, L. 1985. Succession of Species within a Community: Chronological Clustering, with Applications to Marine and Freshwater Zooplankton. The American Naturalist, 125: 257–288.

Lindgren, F., Rue, H., and Lindström, J. 2011. An Explicit Link between Gaussian Fields and Gaussian Markov Random Fields: The Stochastic Partial Differential Equation Approach. Journal of the Royal Statistical Society Series B: Statistical Methodology, 73: 423–498.

Liu, Y., Meier, H. E. M., and Eilola, K. 2017. Nutrient transports in the Baltic Sea – results from a 30-year physical–biogeochemical reanalysis. Biogeosciences, 14: 2113–2131.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology, 85: 784–794.

MacKenzie, B. R., Horbowy, J., and Köster, F. W. 2008. Incorporating environmental variability in stock assessment: predicting recruitment, spawner biomass,

and landings of sprat (Sprattus sprattus) in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1334–1341.

MacNeil, L., Madiraca, F., Otto, S., and Scotti, M. 2025. Spatial Change of Dominant Baltic Sea Demersal Fish Across Two Decades. Ecology and Evolution, 15: e71309.

Matthäus, W., and Schinke, H. 1999. The influence of river runoff on deep water conditions of the Baltic Sea. *In* Biological, Physical and Geochemical Features of Enclosed and Semi-enclosed Marine Systems, pp. 1–10. Ed. by E. M. Blomqvist, E. Bonsdorff, and K. Essink. Springer Netherlands, Dordrecht. http://link.springer.com/10.1007/978-94-017-0912-5_1 (Accessed 16 January 2025).

Millar, C., Large, S., Magnusson, A., and Pinto, C. 2023. icesSAG: Stock Assessment Graphs Database Web Services. https://CRAN.R-project.org/package=icesSAG.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E.: 215–235.

Morisita, M. 1962. Id-index, a measure of dispersion of individuals. Res. Popul. Ecol., 4: 1–7.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries, 20: 203–217.

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., and Bergström, U. 2022. Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback. ICES Journal of Marine Science, 79: 1419–1434.

Orio, A., Bergström, U., Casini, M., Erlandsson, M., Eschbaum, R., Hüssy, K., Lehmann, A., *et al.* 2017. Characterizing and predicting the distribution of

Baltic Sea flounder (Platichthys flesus) during the spawning season. Journal of Sea Research, 126: 46–55.

Orio, A., Bergström, U., Florin, A., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap between interacting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Ory, N. C., Gröger, J. P., Lehmann, A., Mittermayer, F., and Clemmesen, C. 2022. Early Arrival of Spring-Spawner Atlantic Herring at Their Spawning Ground in the Kiel Fjord, Western Baltic, Relates to Increasing Sea Water Temperature. SSRN Electronic Journal. https://www.ssrn.com/abstract=4164412 (Accessed 16 February 2024).

Otto, S. A., Simons, S., Stoll, J. S., and Lawson, P. 2016. Making progress on bycatch avoidance in the ocean salmon fishery using a transdisciplinary approach. ICES Journal of Marine Science, 73: 2380–2394.

Otto, S. A. 2019, January 7. How to normalize the RMSE [Blog post]. https://www.marinedatascience.co/blog/2019/01/07/normalizing-the-rmse/.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., *et al.* 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., *et al.* 2020. Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography, 43: 197–208.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308: 1912–1915.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (Sprattus sprattus) eggs and yolk sac larvae. Marine Biology, 154: 295–306.

Pie, M. R., and Caron, F. S. 2022. Geographical range overlap networks and the macroecology of species co-occurrence. PLOS ONE, 17: e0266275.

Polte, P., Gröhsler, T., Kotterba, P., Von Nordheim, L., Moll, D., Santos, J., Rodriguez-Tress, P., *et al.* 2021. Reduced Reproductive Success of Western Baltic Herring (Clupea harengus) as a Response to Warming Winters. Frontiers in Marine Science, 8: 589242.

Priya, A. K., M, M., Rajamanickam, S., Sivarethinamohan, S., Gaddam, M. K. R., Velusamy, P., R, G., *et al.* 2023. Impact of climate change and anthropogenic activities on aquatic ecosystem – A review. Environmental Research, 238: 117233.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rajasilta, M., Hänninen, J., Laaksonen, L., Laine, P., Suomela, J.-P., Vuorinen, I., and Mäkinen, K. 2019. Influence of environmental conditions, population density, and prey type on the lipid content in Baltic herring (Clupea harengus membras) from the northern Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 76: 576–585.

Rau, A., Lewin, W.-C., Zettler, M. L., Gogina, M., and Von Dorrien, C. 2019. Abiotic and biotic drivers of flatfish abundance within distinct demersal fish assemblages in a brackish ecosystem (western Baltic Sea). Estuarine, Coastal and Shelf Science, 220: 38–47.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances, 4: eaar8195.

Seifert, Tauber, and Kayser. 2001. A high resolution spherical grid topography of the Baltic Sea – 2nd edition. Baltic Sea Science Congress, Stockholm 25-29. November 2001.

Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Ryberg, M. P., Lindegren, M., Durant, J. M., *et al.* 2019. Catastrophic dynamics limit Atlantic cod recovery. Proceedings of the Royal Society B: Biological Sciences, 286: 20182877.

Sunday, J. M., Bates, A. E., and Dulvy, N. K. 2012. Thermal tolerance and the global redistribution of animals. Nature Climate Change, 2: 686–690.

The BACC Author Team. 2008. Assessment of Climate Change for the Baltic Sea Basin.

Tomczak, M. T., Müller-Karulis, B., Blenckner, T., Ehrnsten, E., Eero, M., Gustafsson, B., Norkko, A., *et al.* 2022. Reference state, structure, regime shifts, and regulatory drivers in a coastal sea over the last century: The Central Baltic Sea case. Limnology and Oceanography, 67. https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.11975 (Accessed 16 January 2025).

Verges, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Jr, K. L. H., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B: Biological Sciences, 281: 20140846.

Wang, L., Akritas, M. G., and Van Keilegom, I. 2008. An ANOVA-type nonparametric diagnostic test for heteroscedastic regression models. Journal of Nonparametric Statistics, 20: 365–382.

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., *et al.* 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Science of The Total Environment, 733: 137782.

Woillez, M., Rivoirard, J., and Petitgas, P. 2009. Notes on survey-based spatial indicators for monitoring fish populations. Aquatic Living Resources, 22: 155–164.

Zillén, L., Conley, D. J., Andrén, T., Andrén, E., and Björck, S. 2008. Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. Earth-Science Reviews, 91: 77–92.

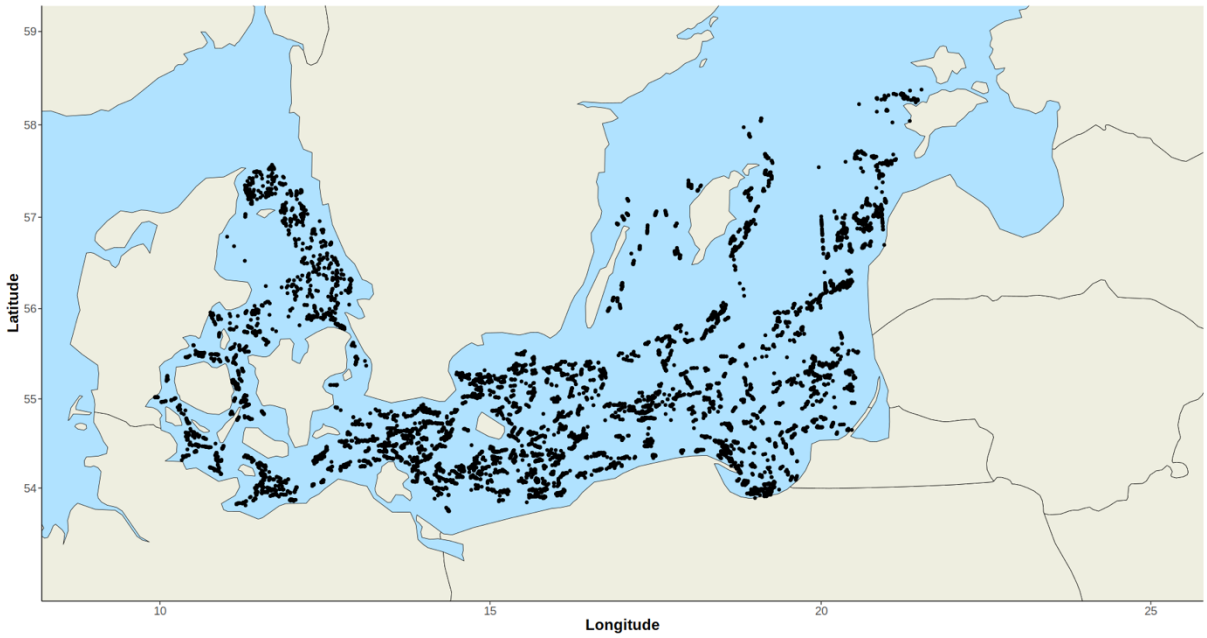
ACKNOWLEDGEMENTS

We would like to thank Hans-Harald Hinrichsen for sharing substrate data with us. Our gratitude also goes to Markus H. E. Meier and Cyril Dutheil for their advice on gathering the data and the modelling process.

SUPPLEMENTARY MATERIAL

Model input

a)



b)

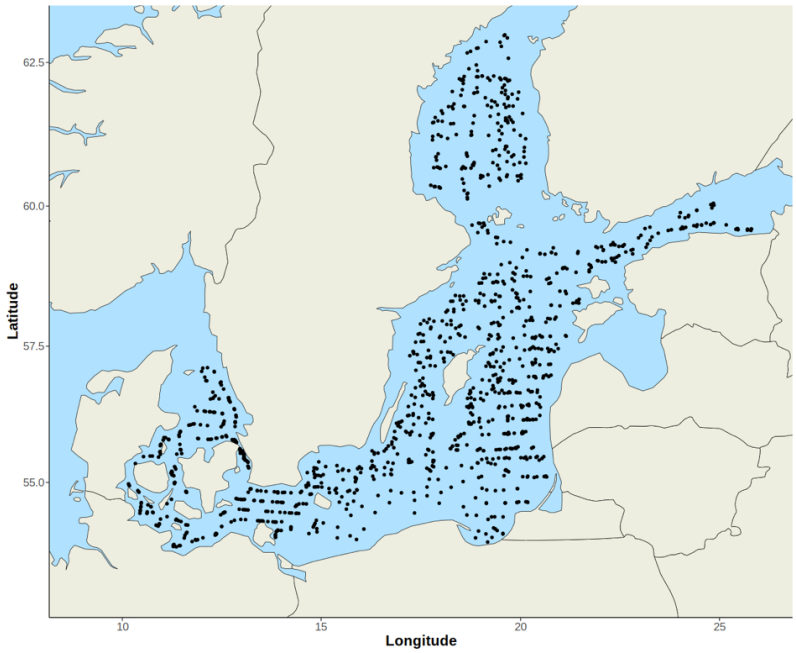


Figure S1. Samples used in the study before aggregation to grid cells: a) BITS data, and b) BIAS data.

Table S1. Overview of used landings data from ICES stock assessments.

Species/Stock	*ICES Subdivisions*	*Assessment year*
Dab	22-32	2023
Flounder	22 and 23	2022
Flounder	24 and 25	2022
Flounder	26 and 27	2022
Plaice	21-23	2023
Plaice	24-32	2023
WBS cod	22-24	2023
EBS cod	24-32	2023
Herring (spring spawners)	20-24	2022
Herring	25-29 (excluding 28.1), 32	2022
Herring	28.1	2022
Herring	30 and 31	2022
Sprat	22-32	2022

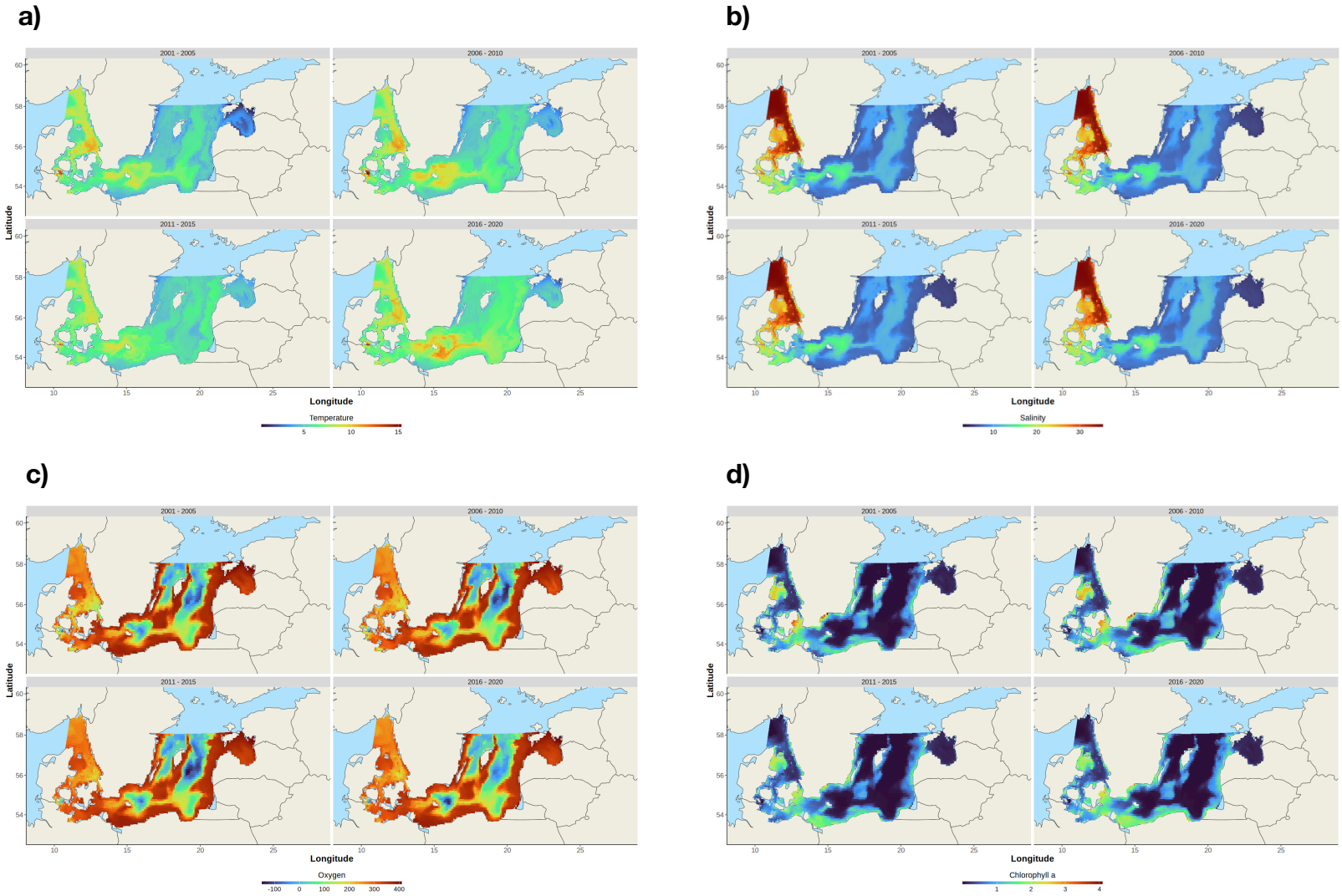


Figure S2. Dynamic covariates in the Baltic Sea at the bottom between 2001 and 2020 shown as median values over 5-year periods: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for modelling demersal and benthopelagic species.

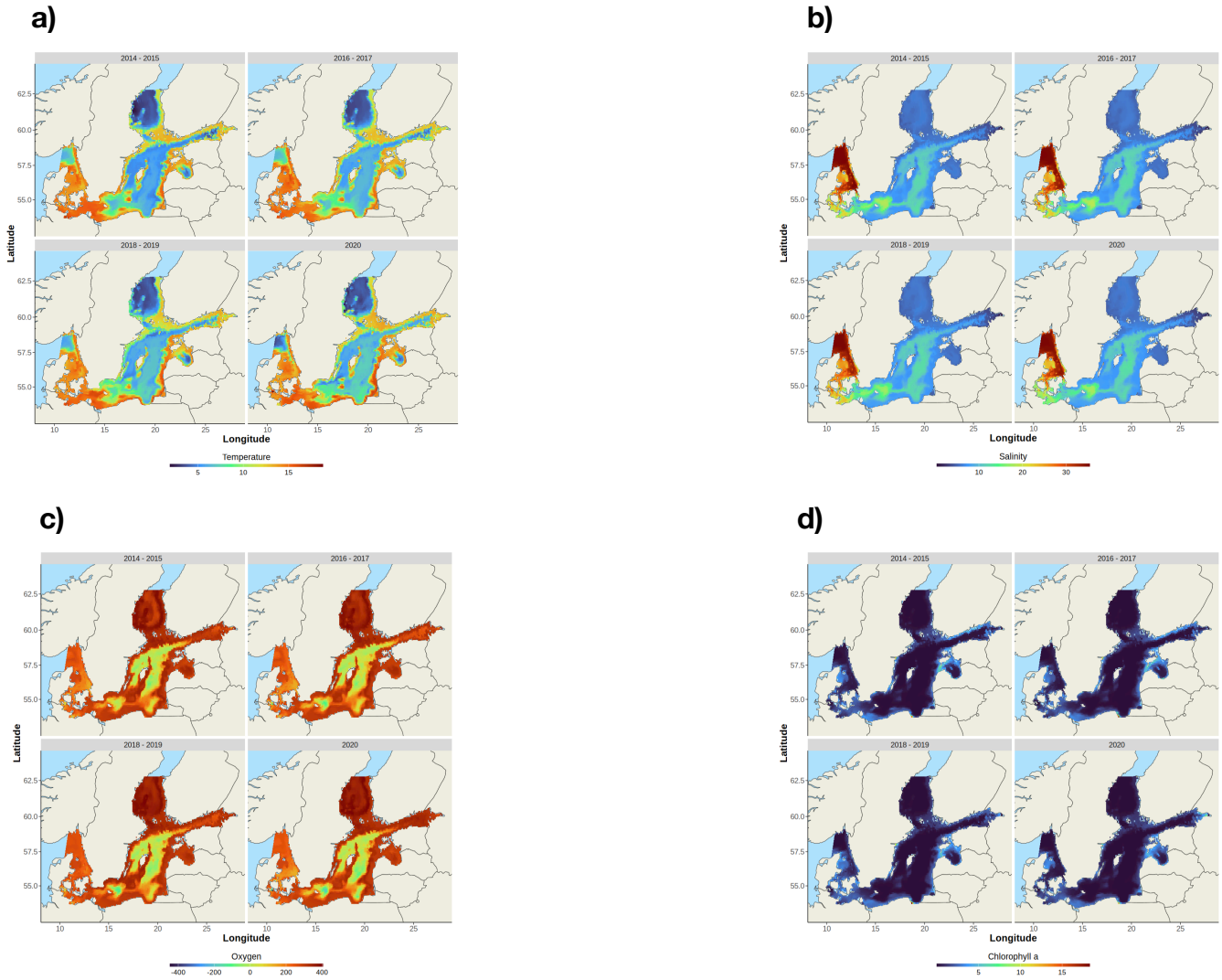


Figure S3. Dynamic covariates in the Baltic Sea at the bottom between 2014 and 2020 shown as median values over three 2-year periods and in 2020: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for modelling herring.

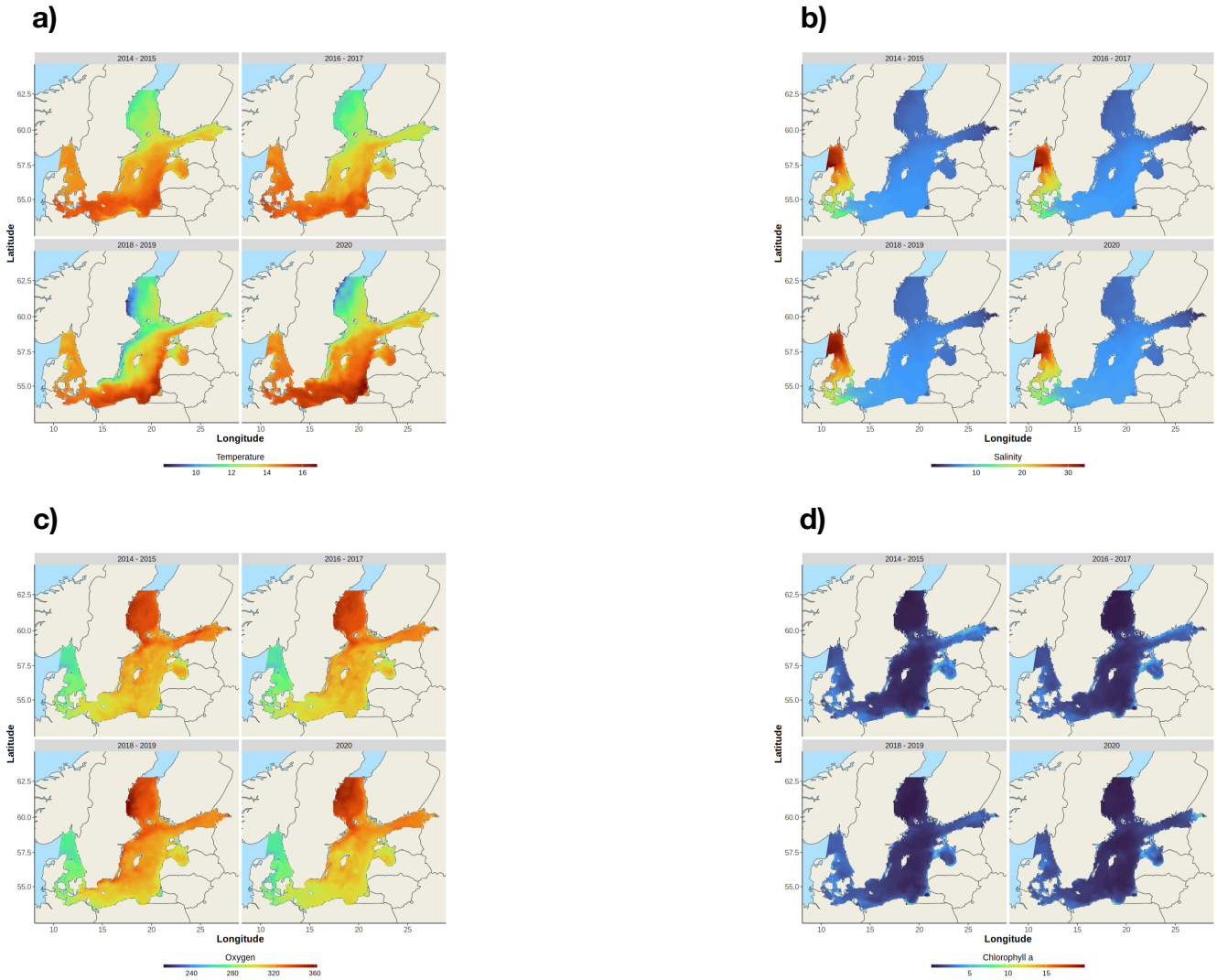


Figure S4. Dynamic covariates in the Baltic Sea at the surface between 2014 and 2020 shown as median values over three 2-year periods and in 2020: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for modelling sprat and stickleback.

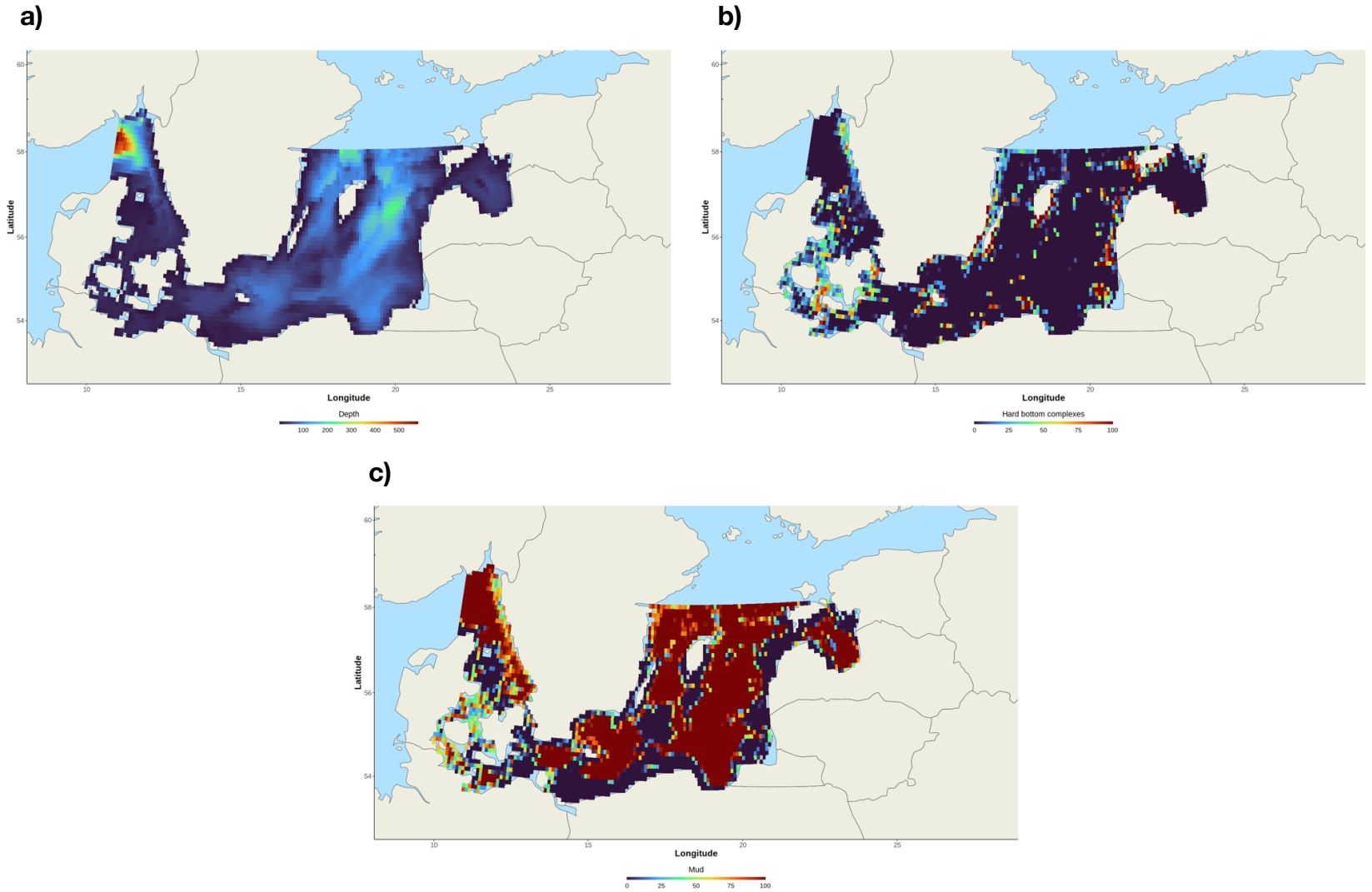


Figure S5. Static covariates in the Baltic Sea at the bottom: a) depth, b) percentage of hard bottom complexes, and c) percentage of mud. They were used for modelling BITS data; used for modelling demersal, benthopelagic species, and herring (only depth).

Model output

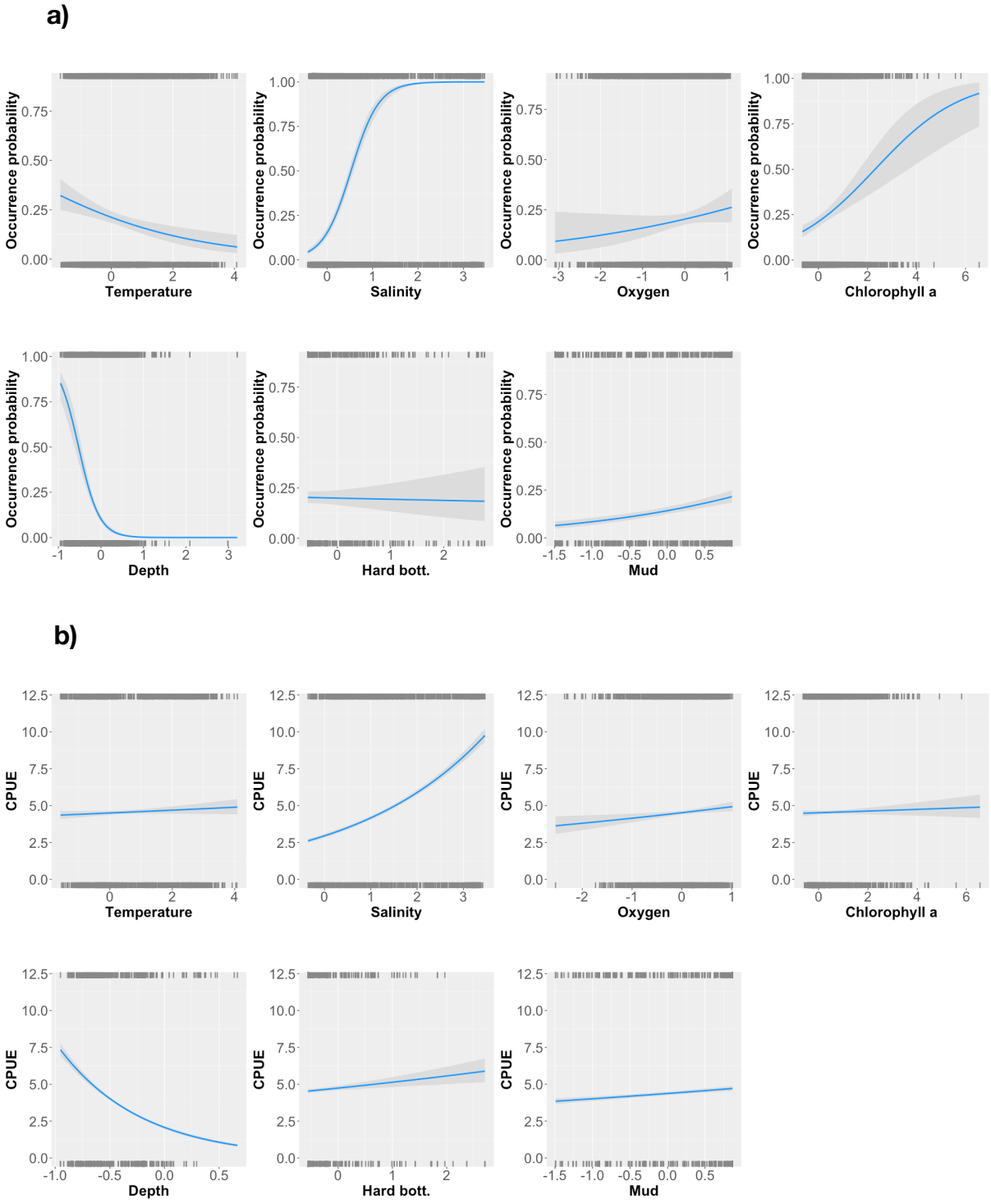


Figure S6. Response curves for the a) occurrence-based model and b) abundance-based model of the common dab.

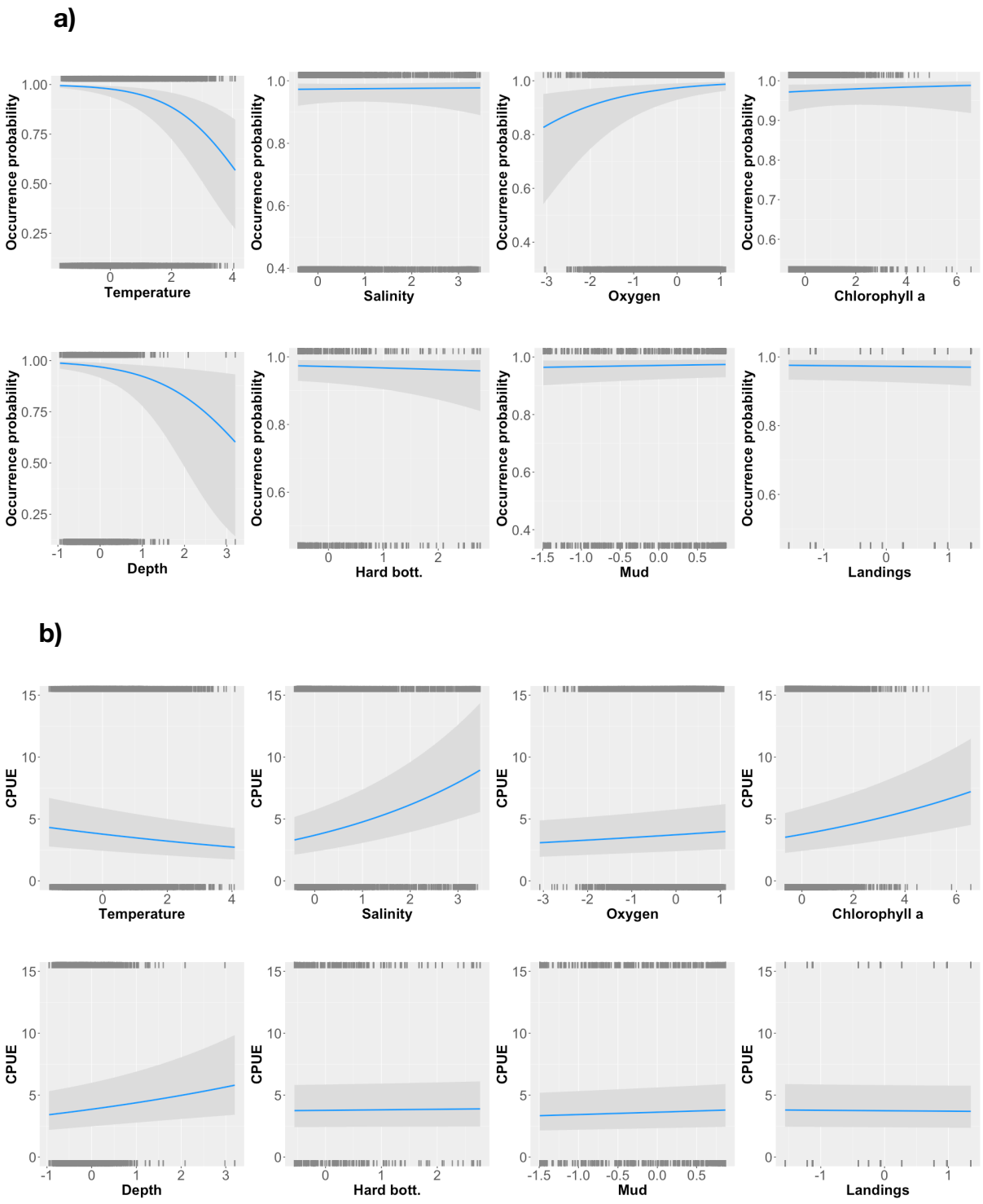


Figure S7. Response curves for the a) occurrence-based model and b) abundance-based model of the European flounder.

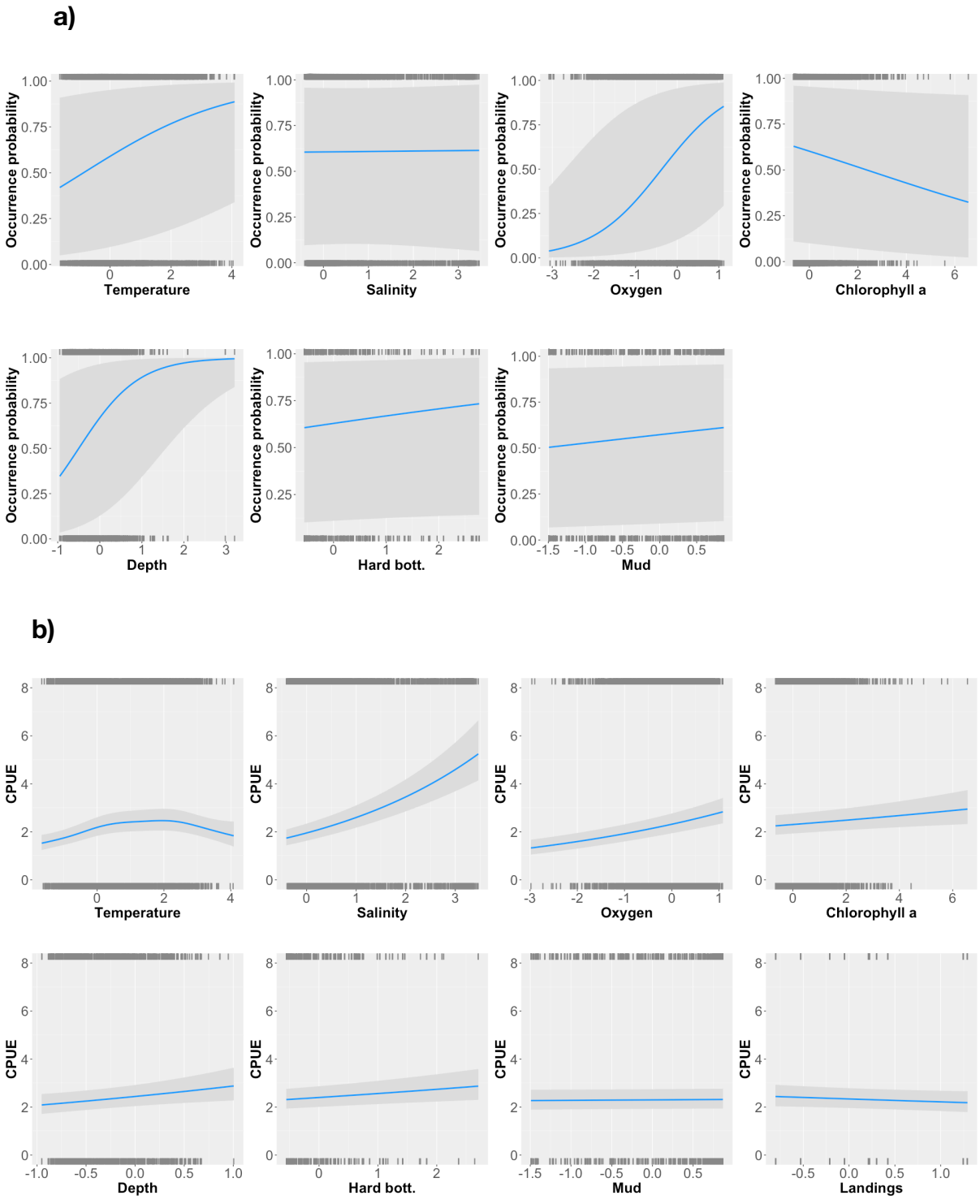


Figure S8. Response curves for the a) occurrence-based model and b) abundance-based model of the European plaice.

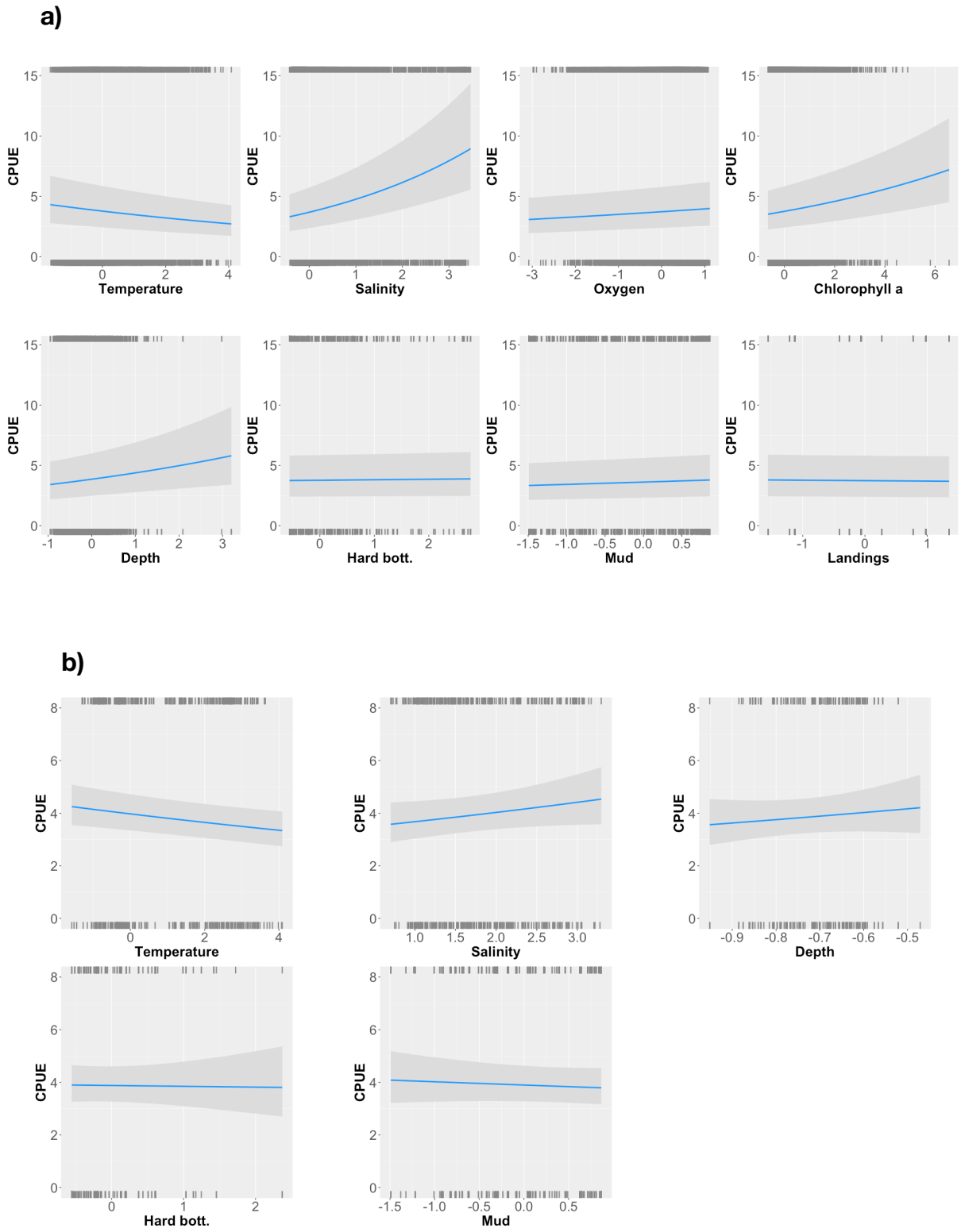


Figure S9. Response curves for the a) occurrence-based model and b) abundance-based model of the WBS cod.

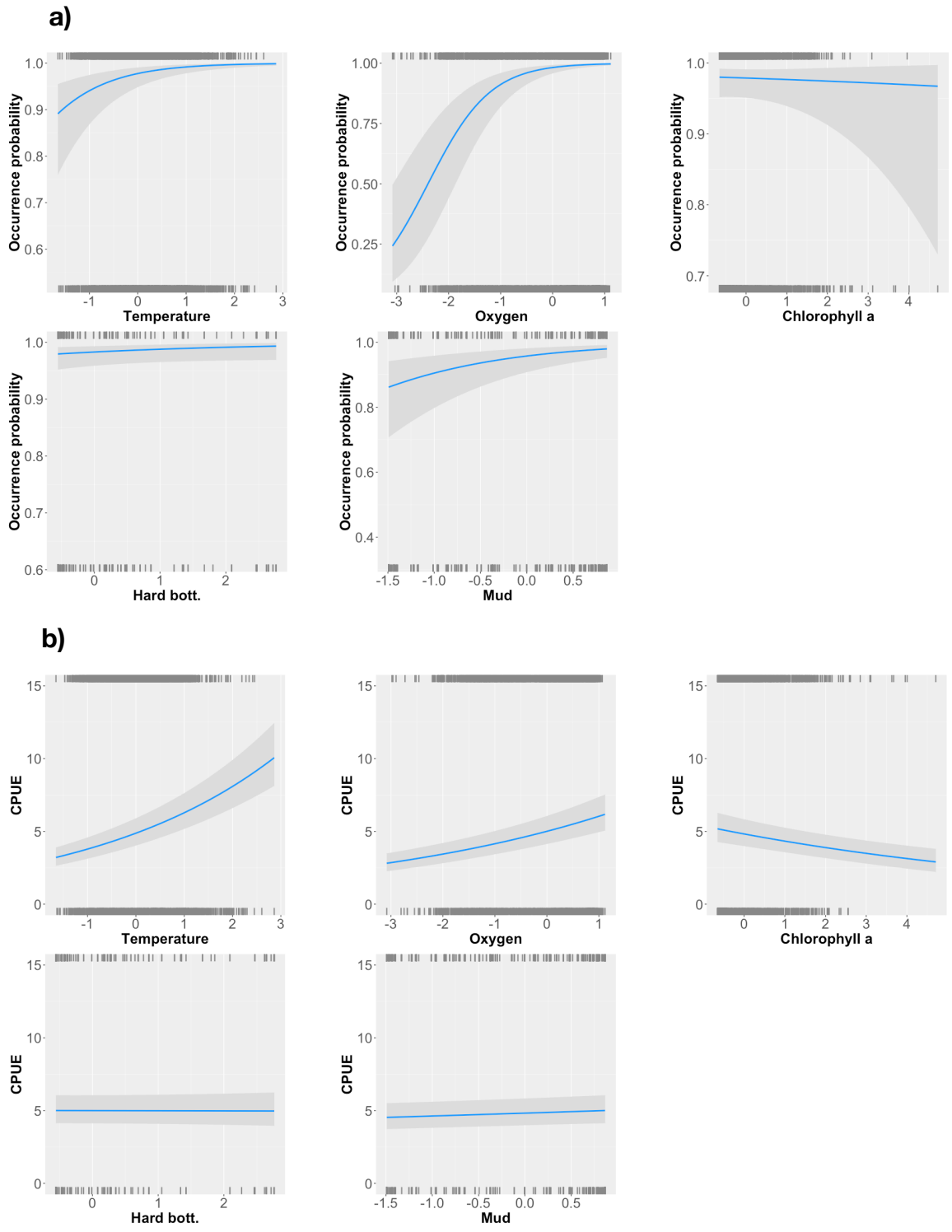


Figure S10. Response curves for the a) occurrence-based model and b) abundance-based model of the EBS cod.

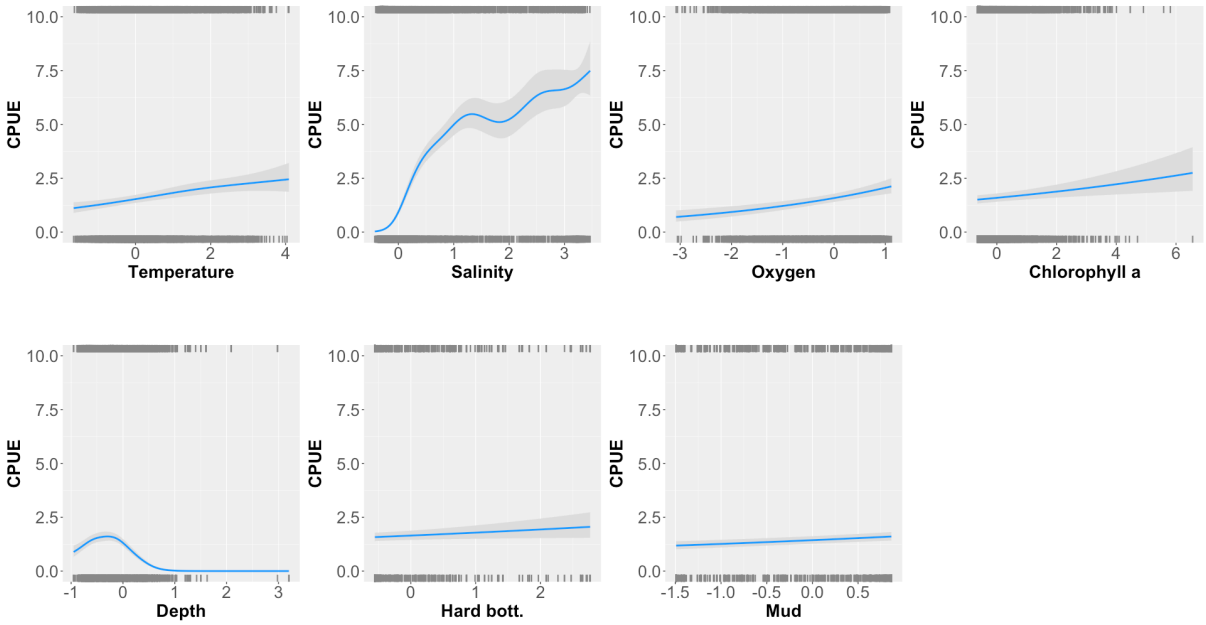


Figure S11. Response curves for the zero-inflated abundance model of the whiting.

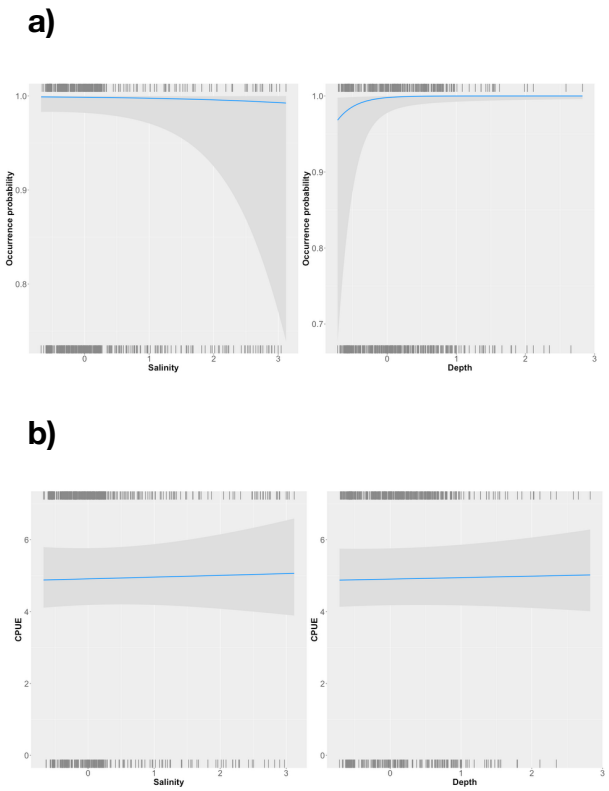
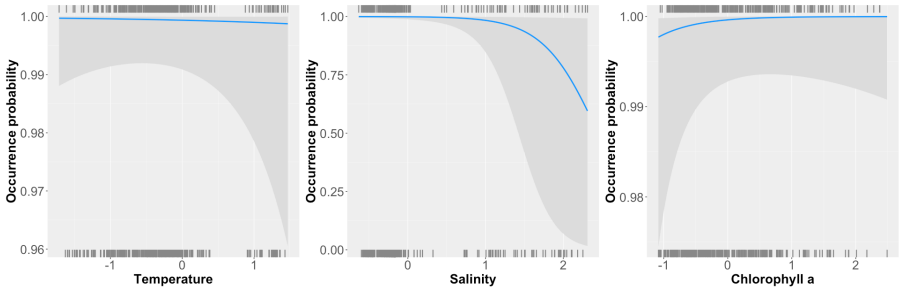


Figure S12. Response curves for the a) occurrence-based model and b) abundance-based model of the Atlantic herring.

a)



b)

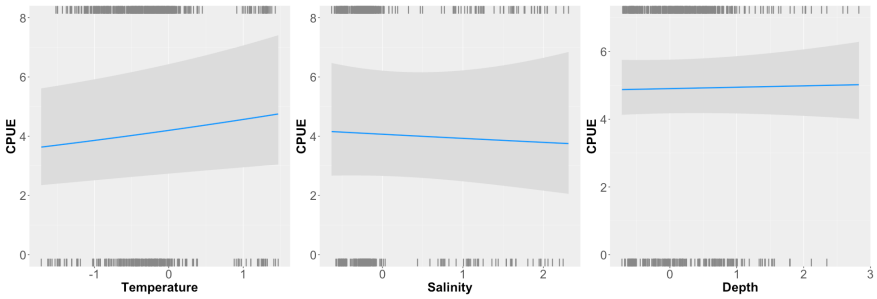
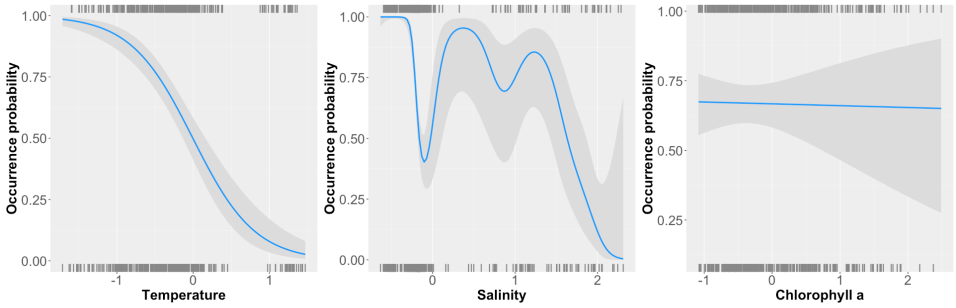


Figure S13. Response curves for the a) occurrence-based model and b) abundance-based model of the European sprat.

a)



b)

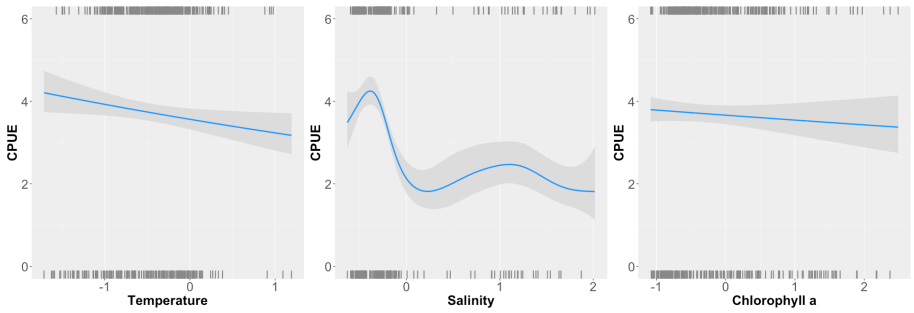


Figure S14. Response curves for the a) occurrence-based model and b) abundance-based model of the three-spined stickleback.

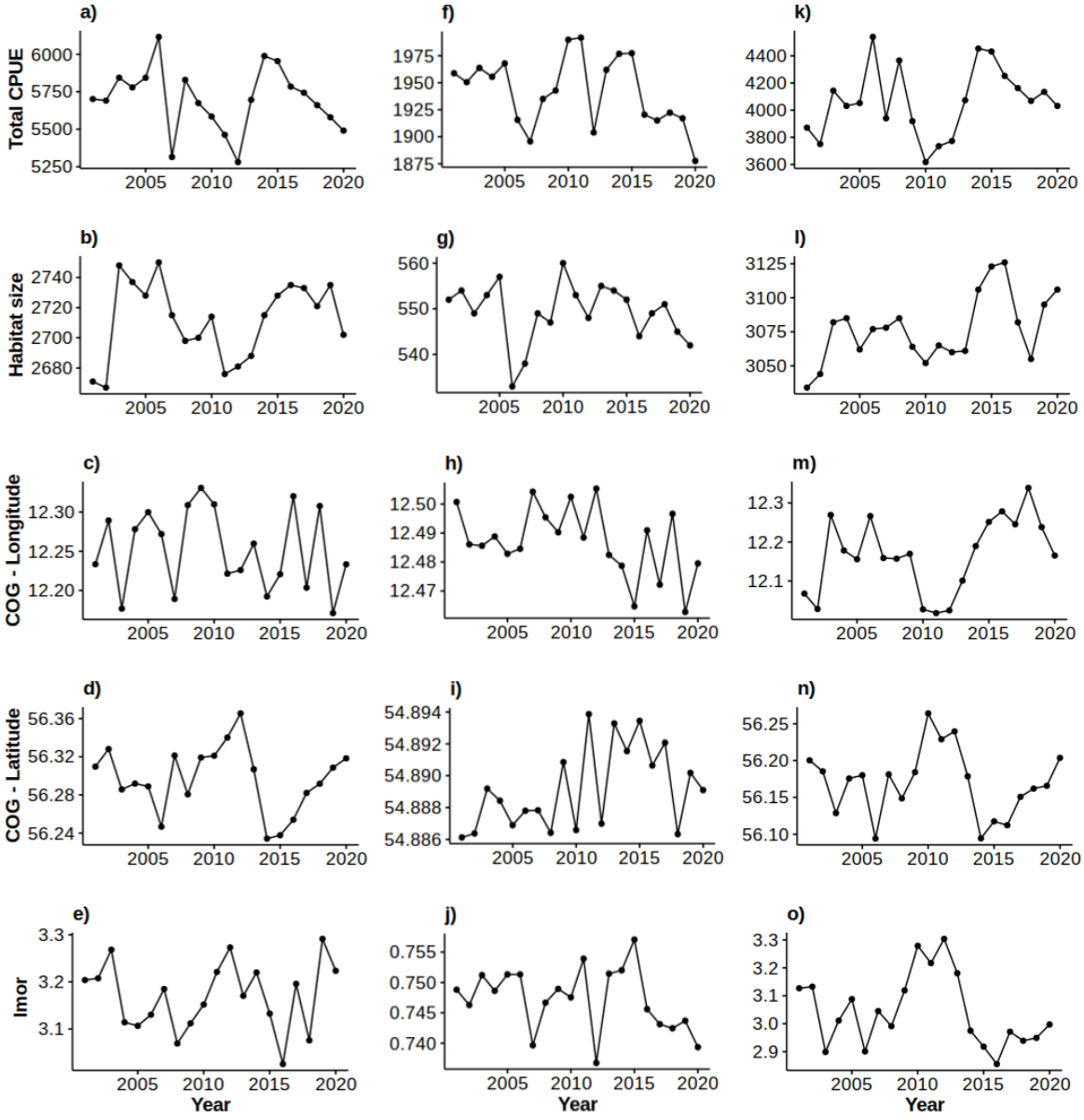


Figure S15. Indices summarizing spatiotemporal patterns in the distributions of common dab (a-e), WBS cod (f-j), and whiting (k-o) distributions.

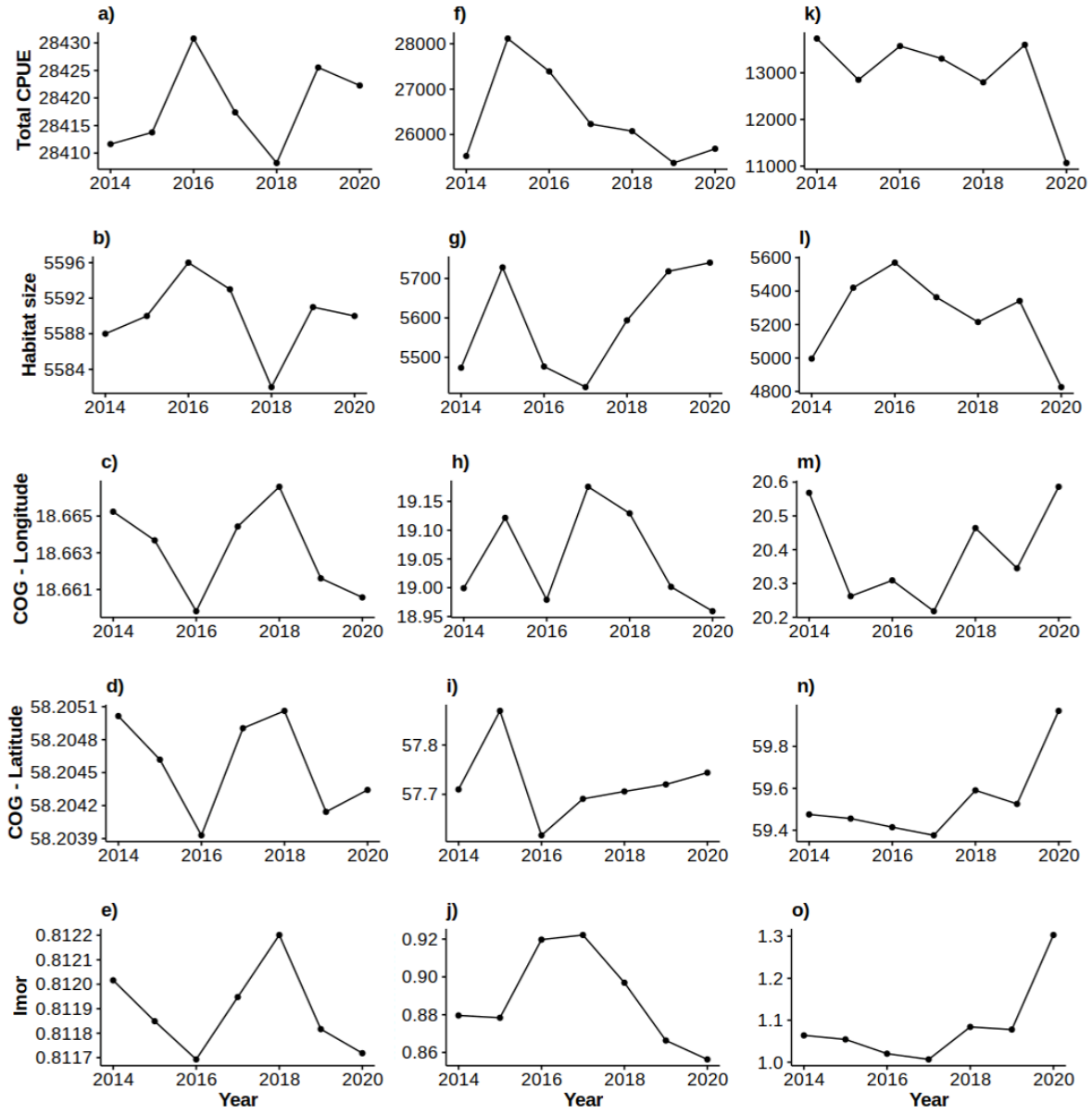


Figure S16. Indices summarizing spatiotemporal patterns in the distributions of Atlantic herring (a-e), European sprat (f-j), and three-spined stickleback (k-o) distributions.

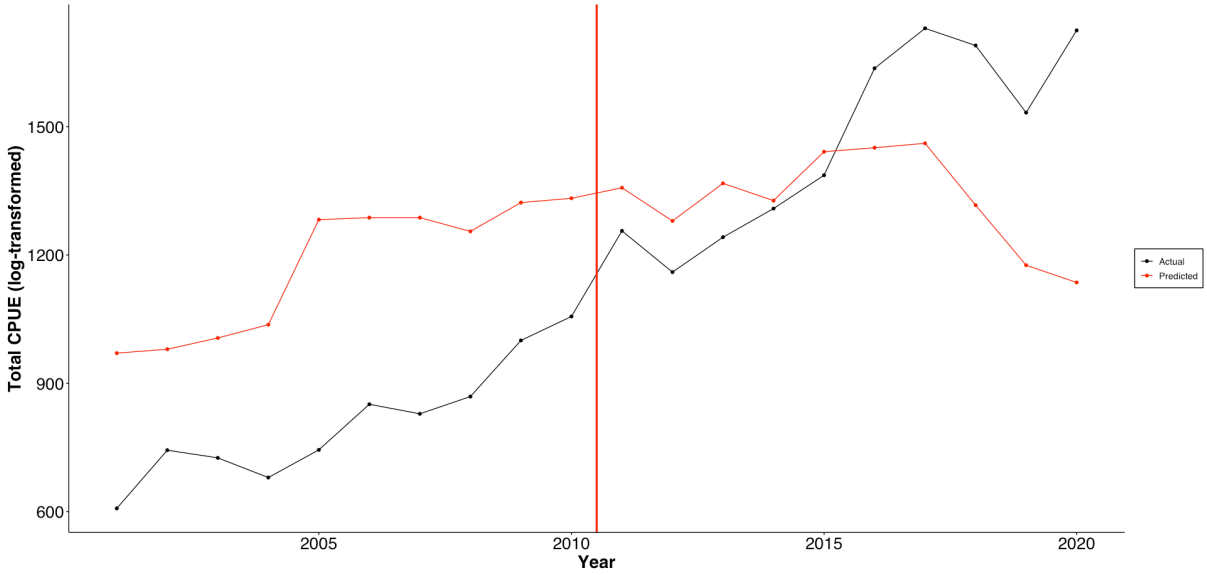


Figure S17. Yearly total CPUE of the European plaice in the Baltic Sea between 2001 and 2020. Black line with points is the actual total CPUE, red line with points is the predicted total CPUE. The vertical red line shows where the original dataset was split for training the models (2001 – 2010) and for testing their performance (2011 – 2020).

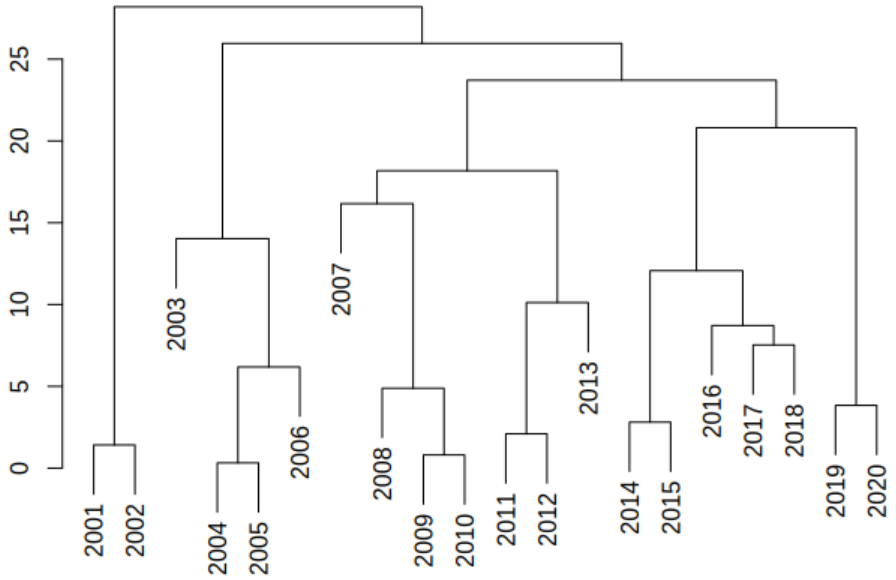


Figure S18. Constrained hierarchical cluster plot for spatial indicators of common dab.

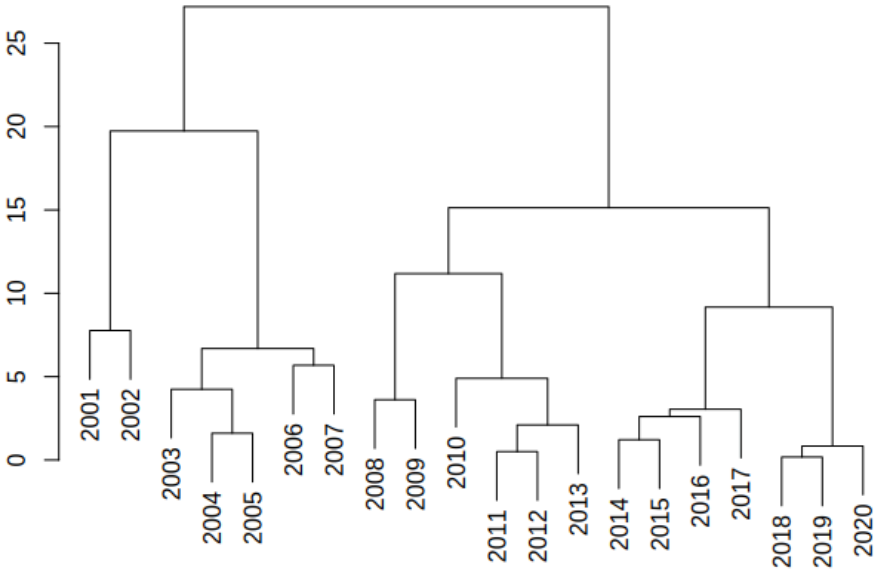


Figure S19. Constrained hierarchical cluster plot for spatial indicators of European flounder.

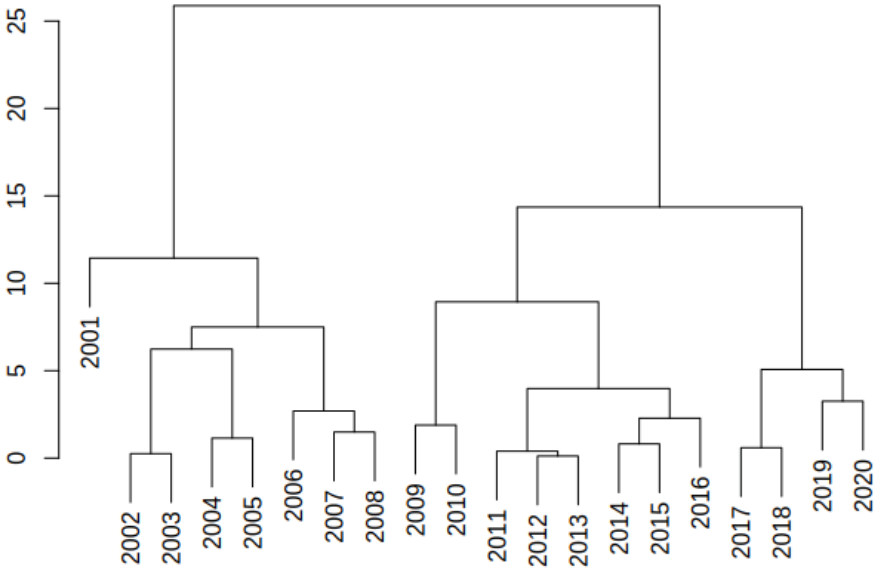


Figure S20. Constrained hierarchical cluster plot for spatial indicators of European plaice.

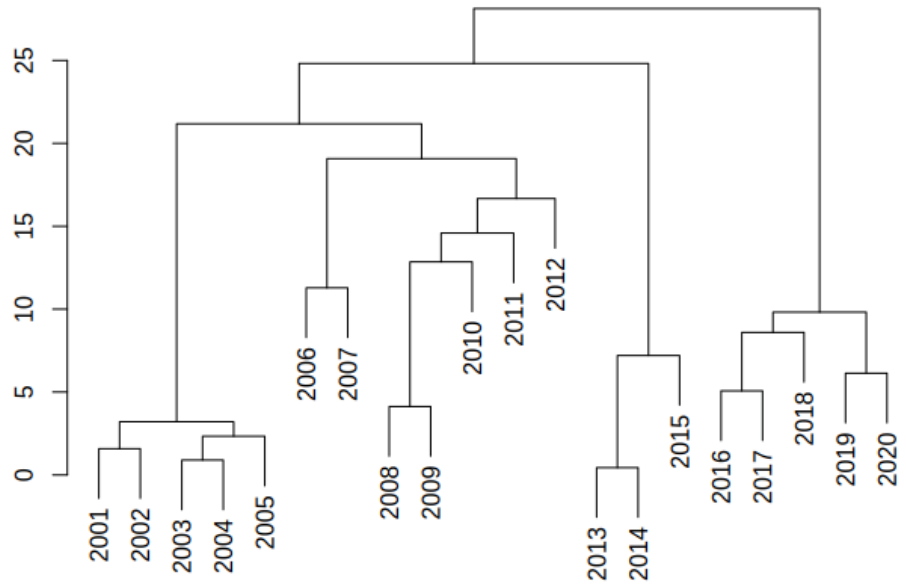


Figure S21. Constrained hierarchical cluster plot for spatial indicators of WBS cod.

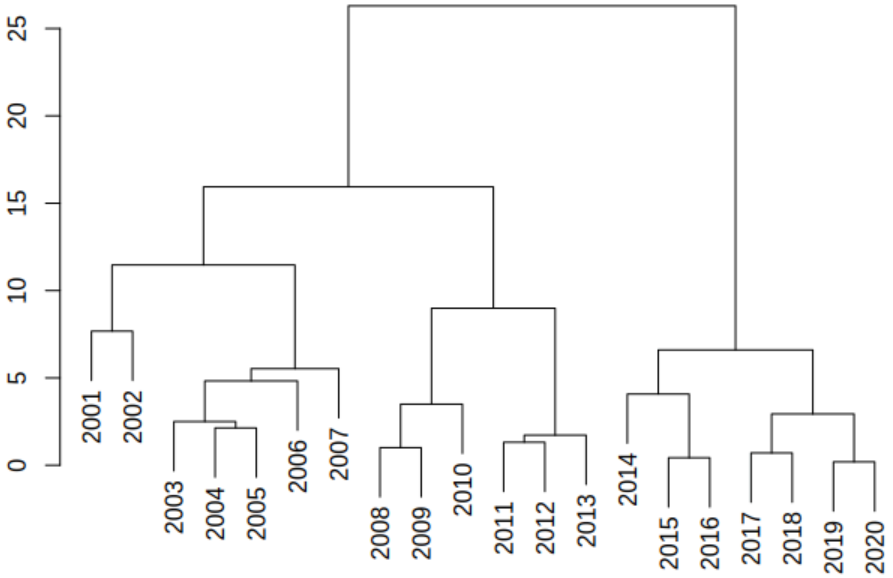


Figure S22. Constrained hierarchical cluster plot for spatial indicators of EBS cod.

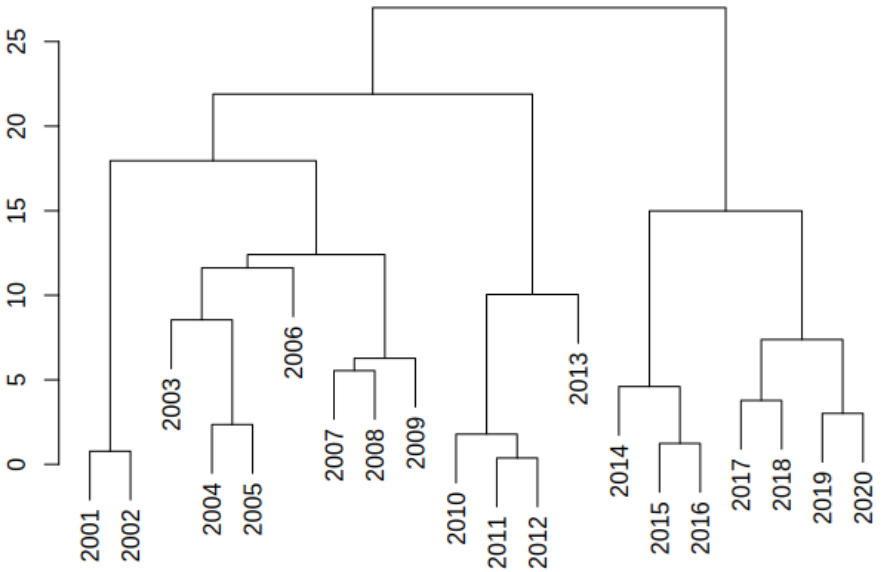


Figure S23. Constrained hierarchical cluster plot for spatial indicators of whiting.

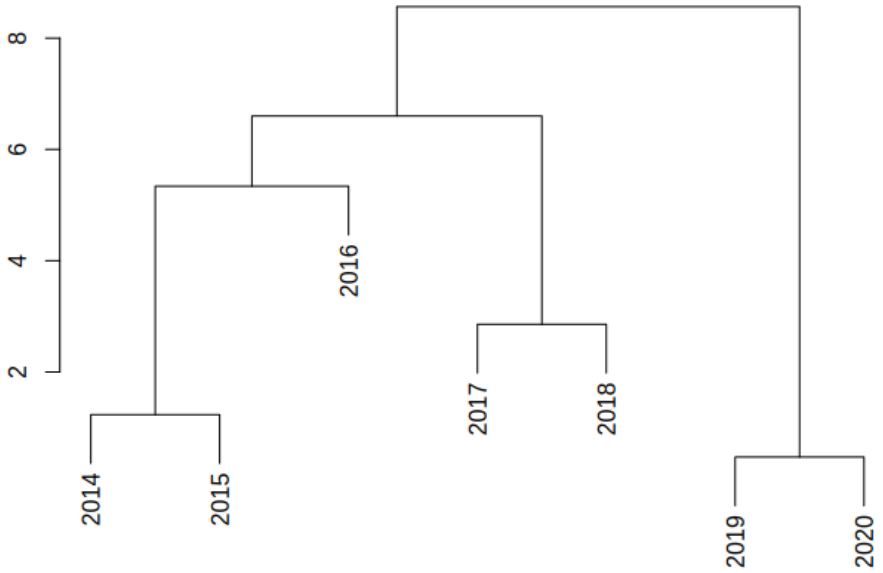


Figure S24. Constrained hierarchical cluster plot for spatial indicators of Atlantic herring.

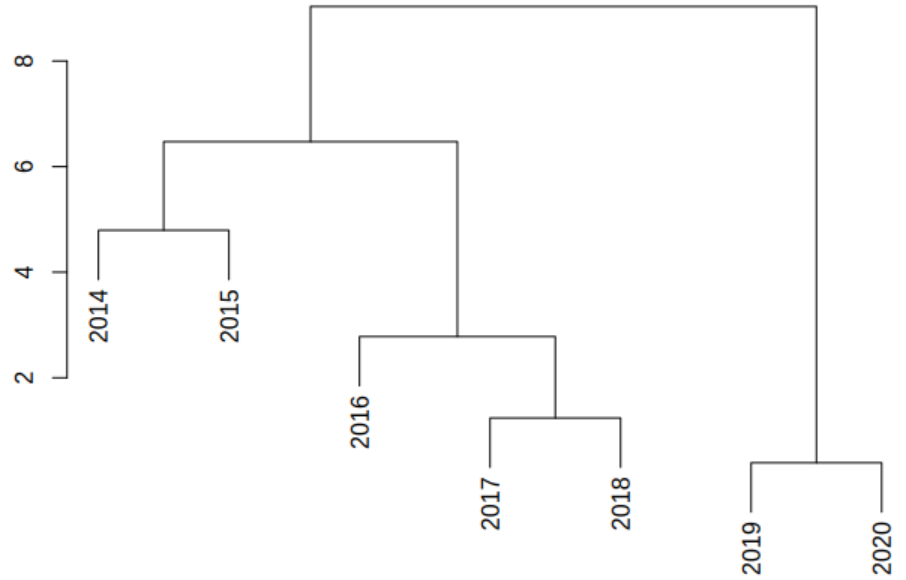


Figure S25. Constrained hierarchical cluster plot for spatial indicators of European sprat.

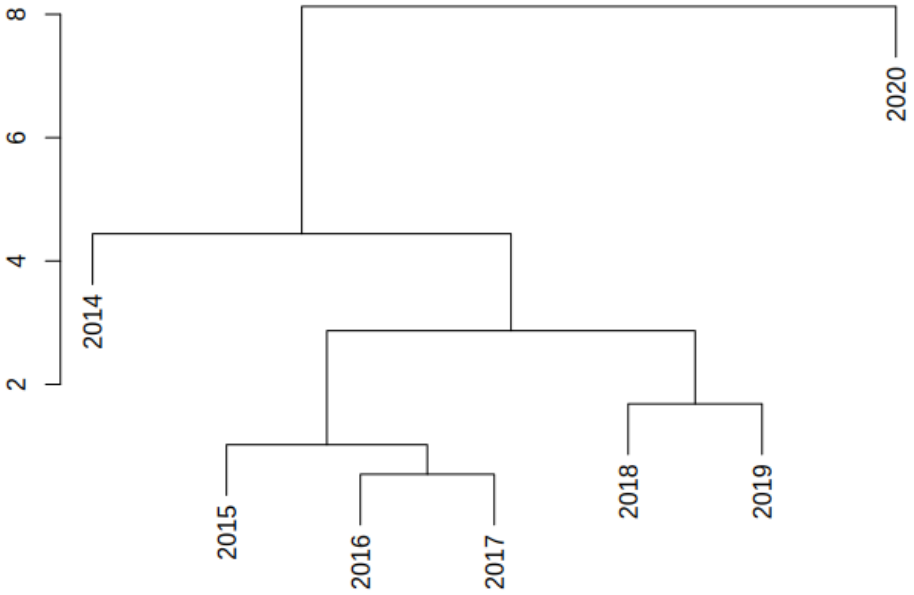


Figure S26. Constrained hierarchical cluster plot for spatial indicators of three-spined stickleback.

CHAPTER 2

Shifting distributions of Baltic Sea fish under future environmental change

Frane Madiraca[1], Liam MacNeil[2], Cyril Dutheil[3,4], H. E. Markus Meier[3], Marco Scotti[2,5], Christian Möllmann[1], and Saskia A. Otto[1]

[1] Institute of Marine Ecosystem and Fishery Science, Center for Earth System Research and Sustainability (CEN), Hamburg University, Hamburg, Germany

[2] Marine Ecology Research Division, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

[3] Department of Physical Oceanography and Instrumentation, Leibniz Institute for Baltic Sea Research Warnemünde, Rostock, Germany

[4] Institute of Research for Development (IRD), Marseille, France

[5] Institute of Biosciences and Bioresources, National Research Council of Italy, Firenze, Italy

ABSTRACT

Climate change and eutrophication are among the most pressing threats to the Baltic Sea ecosystem, with potential to rearrange the distributions and alter productivity of ecologically and commercially important fish species. Projected changes in temperature, salinity, oxygen, and primary productivity drive changes in species' habitat preferences, with cascading effects on ecosystem functioning, fisheries management, and coastal livelihoods. In this study, we applied dynamic species distribution models (SDMs) to project the responses of eight key fish species (including two cod stocks) in the Baltic Sea under four future climate–nutrient scenarios. Summarizing long-term distributional changes using multiple spatial indices, we find that across species and scenarios, changes were generally consistent in direction (e.g. expansion vs. contraction or directional shifts) but varied

in magnitude. Several species are projected to benefit from Representative Concentration Pathway (RCP) 8.5 scenarios by 2098, exhibiting primarily anexpansion of suitable habitat and, where applicable, increase in abundance. These include European plaice, Eastern Baltic cod, European sprat, and three-spined stickleback. In contrast, species such as common dab, whiting, and European flounder are expected to lose suitable habitat and become more spatially aggregated, indicating increased concentration in reduced habitat areas. Furthermore, we assessed the spatial overlap between species and stocks and found evidence for potential changes in species co-occurrence in the future which may modify predator–prey dynamics and competitive interactions. However, these results should be interpreted with caution, particularly for Eastern Baltic cod, as data limitations - especially the lack of observations from warmer seasons - may obscure potential negative impacts. Despite uncertainty in the magnitude of future projections, our findings underscore the need for precautionary and adaptive fisheries management that accounts for spatial redistribution, shifting species interactions, and scenario uncertainty under ongoing environmental change.

Keywords: Baltic Sea, climate change, eutrophication, future projections, fish redistribution, spatial overlap, fisheries management

INTRODUCTION

Predicting changes in species distributions under climate change has become a major focus in ecology and conservation (Pecl *et al.*, 2017). Many terrestrial and marine species have shifted their ranges already, in response to rising temperatures, often migrating poleward or to deeper habitats (Perry *et al.*, 2005; Chen *et al.*, 2011; Sunday *et al.*, 2011). These spatial shifts are highly species-specific and can lead to ecosystem restructuring (Nagelkerken *et al.*, 2023; Priya *et al.*, 2023). In fish populations, changes in the center of gravity of distributions are commonly used as an indicator of directional range shifts (Woillez *et al.*, 2009). Such redistribution can alter spatial aggregation patterns and the extent of occupied habitat (expansion or contraction) with potential consequences for population persistence, catchability and

exposure to fishing pressure, and ecosystem stability (Pinsky and Fogarty, 2012; Pinsky *et al.*, 2020). Similarly, changes in spatial overlap between species may lead to novel species interactions or altered competitive dynamics, particularly as species ranges shift under climate change (Blois *et al.*, 2013; Alexander *et al.*, 2016). Understanding the patterns and drivers of these distributional changes is essential for anticipating future challenges for fisheries and ecosystem management (Cheung *et al.*, 2013; Free *et al.*, 2019).

As a semi-enclosed shelf sea with strong environmental gradients and a long history of intense exploitation and eutrophication, the Baltic Sea is particularly sensitive to ongoing and projected changes in the intensity anthropogenic pressures and provides a valuable case study for species redistribution. While it covers only 0.11% of the world's ocean area, the Baltic Sea accounts for ~1.2% of global capture fisheries (Reusch *et al.*, 2018), where important target species include cod, flatfishes, sprat and herring (ICES, 2022). Sea surface warming in the Baltic has already exceeded global averages (+1.35 °C in 1982-2006) (Belkin, 2009), and dramatic ecosystem restructuring has occurred since 1974 due to overfishing, hypoxia, increasing temperatures, and nutrient loading (Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020). Local contamination from land-based industries and intense shipping further exacerbate stressors for the Baltic Sea region (Reusch *et al.*, 2018). Moreover, climate warming interacts with nutrient loads causing widespread eutrophication, hypoxia, and cyanobacterial blooms (Funkey *et al.*, 2014; Wåhlström *et al.*, 2020). Although regional action plans such as the Baltic Sea Action Plan (BSAP) aim to reduce nutrient inputs, these targets do not account for the combined effects of climate change (Meier *et al.*, 2021). To project future ecosystem states under different emission trajectories, Representative Concentration Pathways (RCPs) provide useful standardized scenarios of atmospheric greenhouse gas concentrations (Moss, 2008; Van Vuuren *et al.*, 2011). Several modelling studies have explored ecosystem responses and food-web dynamics in the Baltic Sea under climate and anthropogenic forcing scenarios (Niiranen *et al.*, 2013; Blenckner *et al.*, 2015; Otto *et al.*, 2020). However, studies focusing on spatially explicit projections for individual fish species remain limited (Bauer *et al.*, 2018, 2019). A recent climate vulnerability assessment

highlighted that many western Baltic fish stocks face increased risks of population declines under projected climate change (Moll *et al.*, 2024). Since these risks are mediated in part by shifts in species distributions and habitat availability, species-specific spatial projections are needed to anticipate where and how fish populations will be affected (Illing *et al.*, 2016; Sys *et al.*, 2024).

Indeed, distributional changes have been well documented for several key Baltic species over the past decades. Shifts in the distribution of the Eastern Baltic Sea (EBS) stock of Atlantic cod (*Gadus morhua*), European flounder (*Platichthys flesus*), and European plaice (*Pleuronectes platessa*) have been linked to changes in temperature and oxygen concentrations (Orio *et al.*, 2019; MacNeil *et al.*, 2025; **Chapter 1**). Productivity of European sprat (*Sprattus sprattus*) shows positive responses to higher temperatures and lower salinities (MacKenzie and Köster, 2004; MacKenzie *et al.*, 2008; Petereit *et al.*, 2008; Ojaveer and Kalejs, 2010; **Chapter 1**), while projected freshening (Andersson *et al.*, 2015) may negatively impact common dab (*Limanda limanda*) and whiting (*Merlangius merlangus*) (MacNeil *et al.*, 2025; **Chapter 1**). The three-spined stickleback (*Gasterosteus aculeatus*) has recently expanded dramatically across coastal areas of the Baltic Sea (Bergström *et al.*, 2015; Olin *et al.*, 2022). In addition, long-term changes in spatial overlap between cod and flounder have been shown to covary with environmental variability in the Baltic Sea (Orio *et al.*, 2019, 2020). Our recent research applied spatial overlap analyses across 27 species and stock pairs of Baltic fish, revealing both persistent co-occurrence and temporal shifts in overlap patterns in relation to environmental variability (**Chapter 1**).

In addition to directional range shifts, changes in spatial aggregation and interspecific overlap may have substantial consequences for ecosystem functioning and fisheries management. The investigated species often consume the same prey items (Heessen *et al.*, 2015; Funk *et al.*, 2021) and predation also occurs between them, for example Atlantic herring and European sprat are important prey for Atlantic cod (Sparholt, 1994). Increased spatial overlap between species may intensify competition, predation, or bycatch risk, while stronger aggregation (i.e. patchiness) could increase local vulnerability to exploitation and complicate the design of spatial closures or

quota regulations (Pinsky and Fogarty, 2012; Pinsky *et al.*, 2020). Anticipating these spatial dynamics is therefore critical to support ecosystem-based fisheries management, particularly in complex, multi-stressor regions like the Baltic Sea.

In the **chapter 1** we found evidence that distributions of European flounder, European plaice and EBS cod have clearly shifted in space and time. In addition, we examined interannual trends of spatial overlap finding cases of persistent overlap as well as separation. We also detected temporal shifts in overlap between species and stock pairs. Especially interesting was the cases where plaice is involved as they could potentially lead to less competition with dab and whiting and more competition with flounder (**Chapter 1**). Given our interest in the future of these dynamics and our goal to address the aforementioned knowledge gaps, we applied the species distribution models (SDMs) developed in **chapter 1** to eight key Baltic fish species (including two cod stocks) and simulated future distributions under four scenario combinations of greenhouse gas forcing (RCP4.5 vs. RCP8.5) and nutrient reduction (Baltic Sea Action Plan vs. business-as-usual; Meier *et al.*, 2021). Two species were additionally modelled with landings-based fishing pressure. We focused on three key research questions:

i. How do species' center of gravity shift latitudinally and longitudinally under different scenarios?
ii. How do species-specific changes occur in spatial aggregation (habitat expansion or contraction), and how might these changes affect fisheries catchability and management?
iii. How does spatial overlap between species and stock pairs change under different scenarios, and what are the potential consequences for predator-prey interactions and food-web stability?

Our findings provide insights into how interacting pressures may shape future fish community distributions and offer guidance for ecosystem-based management in the Baltic Sea.

MATERIALS AND METHODS

Data

Fish survey data

Fish species occurrence and abundance data were obtained from the bottom-focused Baltic International Trawl Survey (BITS) and the pelagic-focused Baltic International Acoustic Survey (BIAS), both coordinated by ICES and available through an open data portal (ICES, 2009, 2017) (https://www.ices.dk/ data/data-portals/pages/default.aspx). These data were used to train species distribution models (SDMs) for eight demersal, benthopelagic, and pelagic fish species representative of the Baltic Sea fish community (Table 1; for details see **Chapter 1**).

BITS data was collected in February, March, October, November, and December between 2001 and 2020 - reporting standardized catch per unit of effort (CPUE) as a proxy for species abundance (ICES, 2017). BIAS data for pelagic species were available for September and October between 2014 and 2020. To match BITS data, BIAS abundance data were standardized to 30 minutes haul duration (**Chapter 1**). Observations with haul durations less than 15 minutes or missing depth information were excluded. Standardized CPUE data for juvenile and adult fish were aggregated to median CPUE values per spatial grid cell (0.1° longitude x 0.1° latitude), month and year, grouped by species and - for Atlantic cod - by stock (western and eastern). Data were then converted to presence-absence for occurrence-based models and log-transformed for abundance-based models.

Table 1. An overview of fish populations studied including their common and scientific names, range, habitat and related data sources.

Common name	*Scientific name*	*Range*	*Habitat*	*Data source*
Common dab	*Limanda limanda*	Baltic Sea	Demersal	BITS
European flounder	*Platichthys flesus*	Baltic Sea	Demersal	BITS
European plaice	*Pleuronectes platessa*	Baltic Sea	Demersal	BITS
Atlantic cod	*Gadus morhua*	Western Baltic Sea (WBS)	Bentho-pelagic	BITS
Atlantic cod	*Gadus morhua*	Eastern Baltic Sea (EBS)	Bentho-pelagic	BITS

Whiting	*Merlangius merlangus*	Baltic Sea	Bentho-pelagic	BITS
Atlantic herring	*Clupea harengus*	Baltic Sea	Pelagic	BIAS
European sprat	*Sprattus sprattus*	Baltic Sea	Pelagic	BIAS
Three-spined stickleback	*Gasterosteus aculeatus*	Baltic Sea	Pelagic	BIAS

Environmental and landings data

We applied the same set of species-specific environmental drivers as defined in **Chapter 1** (see Table 1), where the optimal predictor variables for each species were selected based on their influence on model performance.

We used spatially resolved monthly predictions of past environmental conditions describing hydrography and primary productivity, including temperature, salinity, oxygen concentration, and chlorophyll *a* concentration. These data were obtained from a regional reanalysis covering the period 2001-2020 and downloaded from the Copernicus Marine Environmental Service (CMEMS). The reanalysis is based on the NEMO-Nordic ocean-sea ice model coupled to the Swedish Coastal and Ocean Biogeochemical (SCOBI) model (Eilola *et al.*, 2009; Liu *et al.*, 2017). The horizontal resolution was approximately 2 nautical miles with up to 56 vertical layers. Future environmental conditions were derived from a regional downscaling of the MPI-ESM-LR Earth System Model (ESM) using the coupled regional climate model Rossby Centre regional Ocean - Swedish Coastal and Ocean Biogeochemical model (RCO-SCOBI; Meier *et al.*, 2021). The RCO-SCOBI simulations have a horizontal resolution of approximately 3.2 nautical miles and up to 83 vertical layers with a vertical resolution of 3m. The full simulation period spans 1850-2098. For the future period (2008-2098), two greenhouse gas emissions scenarios (RCP4.5 and RCP8.5) and two nutrient load scenarios (nutrient reductions under the Baltic Sea Action Plan (BSAP) and reference nutrient loads (Meier *et al.*, 2021) were considered, resulting in four future simulations. For both CMEMS and RCO-SCOBI datasets, bottom and surface environmental conditions were extracted to ensure comparability. Bottom values were calculated as median values from the lowest two model layers, while surface values were calculated as medians across the upper three layers, corresponding approximately to the upper 10.6 m and the bottom 5 m, respectively.

To account for present-day biases in the RCO-SCOBI simulations, a bias correction was applied using the CMEMS reanalysis as reference. Monthly climatological deviations between RCO-SCOBI and the reanalysis were calculated for each environmental variables and grid point over the period 2001–2020. These deviations were assumed to be stationary and were from the corresponding future projections (2021-2098). This bias-corrected future simulations were then combined with the CMEMS reanalysis to produce continuous environmental time series spanning 2001–2098. Both CMEMS and RCO-SCOBI data were aggregated to monthly means per spatial grid cell (0.1° longitude x 0.1° latitude) and year. Environmental data were extracted for the same months as the corresponding fish survey observations (February, March, October, November, and December) and matched to fish data by month and year.

Additional static covariates included seabed depth extracted from the digitized topography of the Baltic Sea (Seifert *et al.*, 2001) and sediment types based on photic and non-photic mean percentages of mud, sand and hard bottom complex substrate (Al-Hamdani and Reker, 2007), provided by Hans-Harald Hinrichsen. Photic and non-photic components were summed in each grid cell to obtain total substrate percentages. Yearly landings data for European flounder and European plaice SDMs were extracted from the ICES Stock Assessment Graphs database using the *icesSAG* R package (Millar *et al.*, 2023), lagged by one year to reflect fishing pressure and population responses, and combined with the environmental data. For future scenarios, landings were fixed at 2019 levels to avoid distortions from COVID-19-related fishery disruptions.

Species distribution modelling and spatial indices

Species distribution models (SDMs) were trained using the environmental and landings data described above over two distinct periods: 2001-2020 for demersal and benthopelagic (BITS fish data) and 2014-2020 for pelagic species (BIAS data). Prior to model fitting, all training and scenario datasets were standardized to zero mean and unit variance across the combined dataset to ensure consistency of covariate values across historical and future periods and among scenarios. SDMs were fitted

separately for each species using a spatial GLMM-SPDE framework implemented in sdmTMB (Anderson *et al.*, 2022), based on species-specific environmental drivers and model structures identified in **chapter 1**.

Annual model predictions (predicted CPUE per grid cell) from 2014 to 2098 were used to calculate four spatial indices for each species and year:

1. habitat size (a modified version of the positive area index (Woillez *et al.*, 2009)) for indicating the spatial range a population occupies,
2. centre of gravity (COG) (Woillez *et al.*, 2009) for representing the mean location of a population,
3. Morisita index of intraspecific aggregation (Imor) (Morisita, 1959, 1962) for distinguishing dispersed ($0 \geq Imor \leq 1$) from aggregated distributions ($Imor > 1$), and
4. the Spatial Overlap Index (SOI) (Otto *et al.*, 2016) for assessing whether the distributions between two species or stocks are separated ($SOI < 0.8$), they overlap ($SOI > 1.2$) or if the distribution of either of the two is uniform or random ($0.8 \geq SOI \leq 1.2$).

In addition to the spatial indices, total CPUE was calculated as a proxy for overall population size. Although not a spatial metric per se, total CPUE was used to contextualize distributional changes. For example, changes in distribution area or shifts in center of gravity are interpreted in relation to concurrent changes in population size. Detailed descriptions of the spatial indices are provided in **chapter 1**. To summarize temporal patterns, index values were grouped into three multi-year periods: baseline (2014 – 2020), mid-century (2053 – 2059), and end-century (2092 – 2098). Percentage changes in all indices were calculated for each future period as relative to the baseline.

All statistical analyses were conducted in the programming environment R 4.1.2 (R Core Team, 2021). The cleaned datasets and R-scripts with details on used packages will be made upon successful publishment of this article at https://github.com/franemadiraca/.

RESULTS

Projected changes in environmental conditions

The environmental covariates used to drive the SDMs exhibit distinct scenario-dependent trajectories, thereby defining the range of environmental conditions under which species distributions are projected. Changes in temperature and salinity are primarily associated with greenhouse gas scenarios and show only negligibly sensitivity to nutrient load scenarios. In contrast, oxygen and chlorophyll *a* concentrations respond to both greenhouse gas forcing and nutrient management, resulting in different combinations of covariates across scenarios (Figure 1). At the surface, temperature - a key predictor in the SDMs - is projected to increase by 2 °C under RCP8.5 scenario and by less than 0.5 °C under RCP4.5 scenario relative to the baseline period (2014-2020) (Figure 1a). Surface salinity generally declines across scenarios, though trends diverge toward the end of the century: under RCP4.5, it recovers to baseline levels, while under RCP8.5, the decline continues (Figure 1b). However, salinity projections are remain highly uncertain and may increase or decrease under future climate conditions (Meier *et al.*, 2021). Chlorophyll *a* concentrations, which enter the SDMs as a proxy for primary productivity, decrease most strongly under BSAP scenarios (Figure 1c).

At the bottom, temperature increases are more pronounced, reaching approximately 2.5 °C under RCP8.5 and about 1 °C under RCP4.5 (Figure 1d). Bottom salinity patterns closely mirror those at the surface (Figure 1e). Bottom oxygen concentrations - another key SDM covariate - span a wider range across scenarios, with the highest values projected under RCP4.5-BSAP and the lowest under RCP8.5-REF, particularly during the second half of the century (Figure 1f).

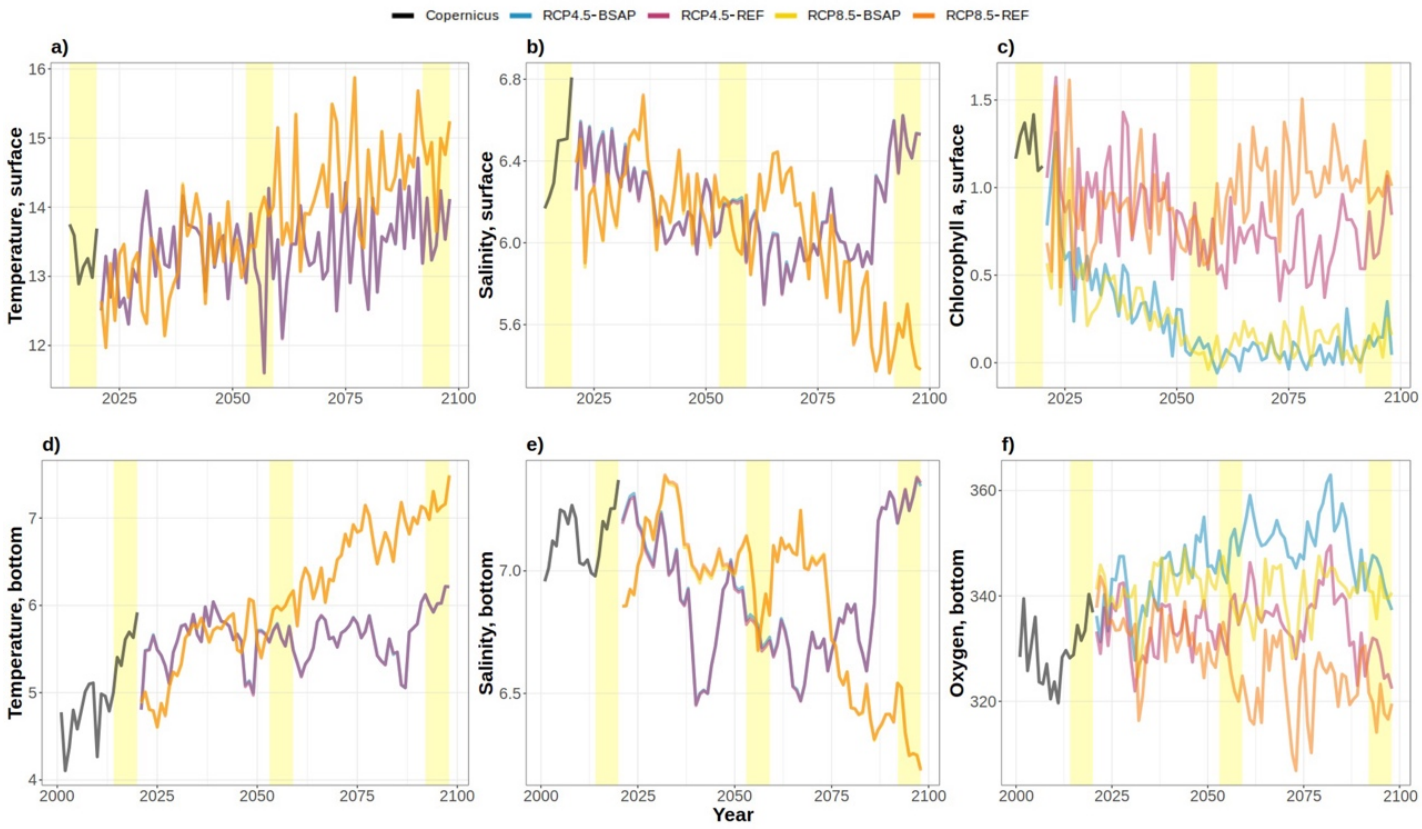


Figure 1. Median interannual values of dynamic covariates used in the species distribution models. Panels a-c show surface conditions relevant for pelagic species (BIAS sampling months): a) temperature, b) salinity, and c) chlorophyll *a*. Panels d-f show bottom conditions relevant for demersal and benthopelagic species and stocks (BITS sampling months): d) temperature, e) salinity, and f) oxygen. Grey lines represent baseline Copernicus data (2014-2020); coloured lines show projections under the four future scenarios. Light yellow rectangles indicate the periods used in percent change calculations in spatial indices.

Changes in spatial distributions of Baltic fishes

Although different environmental variables drove distributional changes across scenarios, their combined effects on spatial indices were only weakly differentiated among climate and eutrophication scenarios (Figure 2a) and between mid- and end-century periods (Figure 2b). In contrast, species- and stock-specific responses differed considerably, with European plaice showing the largest and WBS cod the smallest changes (Figure 2c). Across indices, total CPUE, habitat size and the Imor showed the highest variability, while changes in the center of gravity (COG-Longitude and COG-Latitude) were generally small.

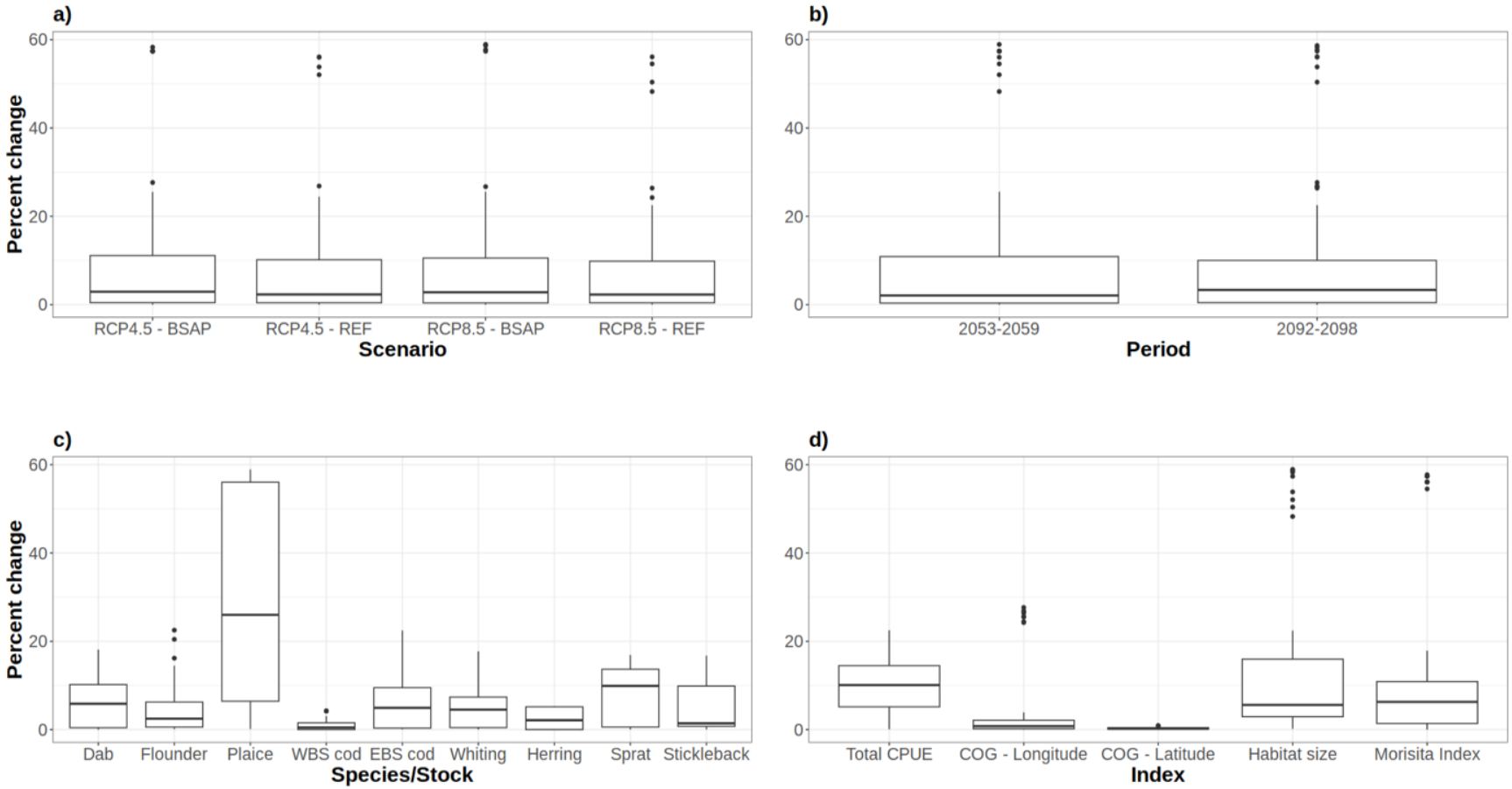


Figure 2. Absolute percent changes of spatial indices derived from SDM species and stock predictions grouped by a) scenario, b) period, c) species or stock, and d) index. Values represent percentage changes relative to the baseline period (2014-2020).

Figure 3 provides a detailed overview of species- and stock-specific percentage changes in spatial indices for the mid-century period, with end-of-century projections shown for three-spined stickleback. Based on shared response patterns that were largely consistent across scenarios, species can be grouped into three broad categories: those projected to spatially contract and aggregate, those showing limited change, and those expected to spatially expand and disperse.

Group 1- Habitat contraction under declining CPUE:

Common dab and whiting consistently show reductions in habitat size across all scenarios, with the most pronounced declines observed for dab under the REF eutrophication scenarios (~10%) (Table S1, Supplementary material). At the same time, both species become more spatially aggregated, as indicated by increasing Imor values. Aggregation is strongest for dab under BSAP scenarios (~15% increase relative to the baseline period), while for whiting the effect is most pronounced under RCP4.5-REF. Together, declining habitat size and increasing Imor values indicate a redistribution of suitable habitat into fewer, more localized patches.

European flounder also falls into this group but exhibits a partially contrasting response. Although its habitat size contracts and CPUE declines towards the end of the century across all scenarios, the species simultaneously becomes more spatially dispersed. Habitat size remains relatively stable at mid-century but decreases substantially by the end of the century, particularly under RCP8.5 (BSAP: –7%, REF: –6.8%; Table S1, Supplementary material).

Group 2 – Minimal changes in spatial distribution and CPUE:

WBS cod and Atlantic herring exhibit only minor changes in spatial indices, largely independent of scenario and period. WBS cod maintains relatively stable levels of habitat size and aggregation, with only a moderate decline in total CPUE under RCP8.5 scenarios. Herring shows even more stable patterns across all spatial indices. However, confidence in scenario-specific interpretations for herring is reduced due to the limited explanatory power of the SDM, particularly the absence

of significant dynamic covariates (Table S2 in the Supplementary Material, **Chapter 1**).

Group 3 – Habitat expansion, reduced aggregation, and diverging CPUE trends:
European plaice, EBS cod, and European sprat are characterized by increasing dispersal (decreasing Imor) and an overall expansion in habitat size under future scenarios. although their CPUE trajectories differ markedly. European plaice stands out with the largest eastward expansion (+59% in habitat size by the end of the century under RCP8.5–BSAP; Table S1, Supplementary material), and substantial dispersal (-58%), while experiencing only moderate declines in CPUE (-6%). These changes are most pronounced under scenarios combining warming with nutrient reduction (BSAP).

EBS cod also benefits under RCP8.5–BSAP, with parallel increases in habitat size (22%) and CPUE (22%) by the end of the century (Table S1, Supplementary material). In contrast, RCP4.5-REF represents the least favorable scenario for EBS cod as its habitat would increase by only 19% and total CPUE would remain close to baseline levels. European sprat shows a more moderate but consistent expansion in habitat size (up to 17%) and only small CPUE declines, particularly under RCP8.5–REF. These patterns suggests that sprat may benefit from warmer and fresher conditions and potentially from increased primary productivity (Figure 1).



Figure 3. Species- and stock-specific percent changes of spatial indices derived from distributional species and stock projections across future scenarios. All radar charts, except those for the three-spine stickleback, show changes for period 2053-2059. For the stickleback both the 2053-2059 and the 2092-2098 periods are shown. Chart scales are the same for all species and stocks except European plaice. The line indicating no precent change is the dotted line and is also denoted with a zero in bold (**0**).

A special case: the three-spined stickleback

The three-spined stickleback is unique in exhibiting directional changes in spatial indices between mid- and end-century projections. Under RCP4.5, the spatial distribution becomes more clustered, shifting from weak dispersion toward aggregation (+12% increase in the Imor), whereas under RCP8.5 it becomes increasingly dispersed by the end of the century (-16%). Similar contrasts are observed for total CPUE, which increases toward mid-century and then declines (-16%) under RCP4.5, while remaining stable and increasing toward the end of the century (+12%) under RCP8.5. Although temperature is the only significant covariate in the model - showing negative effects on both occurrence and abundance - salinity, included as a smoother (Table S2, Supplementary material), likely modulates the response. Declining salinity appears to promote occurrence but reduce abundance, possibly counteracting or amplifying the negative effect of rising temperatures depending on the scenario. Given these inconsistencies and the limited explanatory power of the model (Table S2, Supplementary Material; **Chapter 1**), scenario-specific projections for stickleback should be interpreted with caution.

Changes in species overlap

Using the SOI, we assessed spatial overlap across 27 species and stock pairs under four future scenarios, resulting in 108 individual pairwise cases. Most combinations show consistent developments in both direction and magnitude (Figure S22, Supplementary material). However, for seven species pairs, the direction of SOI change varies, depending on the scenario, including: dab - EBS cod, dab - whiting, WBS cod - whiting, WBS cod - sprat, EBS cod - whiting, EBS cod - stickleback, and herring - stickleback (Figure 4). In all but one of these pairs, climate scenarios drive directional change; only WBS cod - sprat is primarily affected by eutrophication scenarios. A delayed directional change also appears between in the WBS cod - whiting pair, but only after 2075.

Across all scenarios and periods, 13 pairs consistently show significant spatial overlap (SOI > 1.2). Many of these involve species or stocks traditionally abundant in the western Baltic, such as common dab, WBS cod, and whiting, which tend to

increase their spatial overlap over time. European flounder, which is typically dispersed throughout our study area, shows increasing overlap with these western species, while its overlap with EBS cod decline.

In contrast, European plaice, which expands eastwards in all scenarios, shows increasing overlap with European flounder and EBS cod, but decreasing overlap with common dab, WBS cod, and whiting. These dynamics suggest that benthic competitors such as dab, flounder, WBS cod, and whiting may face intensified competition, while plaice and EBS cod might experience reduced overlap with declining species, but increased interaction between themselves.

Finally, overlap between WBS cod and, its important prey species, the European sprat, is projected to decline under BSAP scenarios, and EBS cod and sprat become more separated in all scenarios.

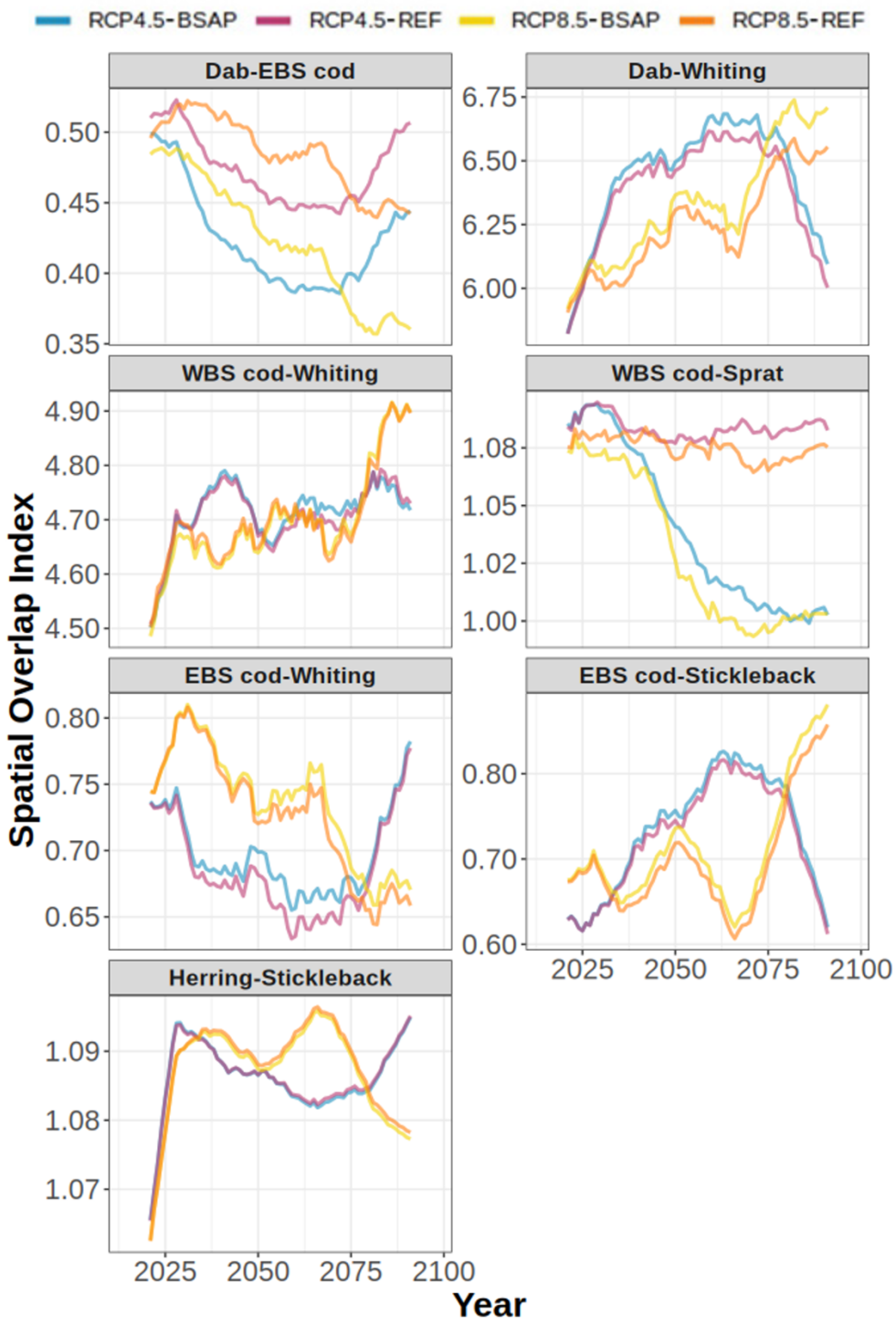


Figure 4. Overview of median interannual Spatial Overlap Index (SOI) presented as moving average (n = 15 years) across future scenarios for 7 cases where SOI trends change in direction depending on the projection scenarios.

DISCUSSION

Our study provides one of the first comprehensive projections of distributional changes in multiple key fish species in the Baltic Sea under combined climate and nutrient scenarios. Using species distribution models for eight commercially and ecologically important species and stocks, we reveal important potential changes to their distributions, spatial aggregation, and interspecific overlap. Most species showed consistent spatial responses across scenarios and time periods, with differences more often in magnitude than in the direction of change. The clear lack of longitudinal or latitudinal shifts, with the notable exception of European plaice, is in strong contrast with globally reported poleward shifts (Horta E Costa *et al.*, 2014; Vergés *et al.*, 2014; Frainer *et al.*, 2017; Pecl *et al.*, 2017; Hastings *et al.*, 2020; Pinsky *et al.*, 2020). However, such patterns are not necessarily expected in the Baltic Sea. As a semi-enclosed basin, the Baltic is bounded by coastlines that constrain large-scale redistributions, much like other enclosed seas such as the Adriatic Sea (Cavraro *et al.*, 2022). In addition, the strong horizontal salinity gradient characteristic of the Baltic plays a key role in structuring fish communities and likely limits substantial range shifts (Frelat *et al.*, 2018). The combined effects of geographical and physiological constraints likely explain the lack of pronounced directional shifts in our projections and point to a limited capacity for adaptive redistribution in response to future climate change.

We find distinct groups of potential “winners” and “losers” among species, shaped by their respective environmental niches. These findings support a wider set of distribution projections recently made for the European shelf seas (Townhill *et al.*, 2023; Sailley *et al.*, 2025). Common dab, European flounder, and whiting emerge in our study as potential “losers” under future environmental scenarios. In addition to an overall decline in total CPUE, both dab and whiting are projected to retreat into a more limited area and to become spatially more aggregated. For dab, the strongest increases in aggregation are observed under the BSAP scenarios until the end of the century where chlorophyll *a* concentration is reduced. At the end of the century the strongest aggregation occurs under the RCP8.5 scenarios, especially RCP8.5-BSAP.

These projected dynamics are consistent with the negative effects of increasing temperature, decreasing salinity and reduced nutrients (used here as proxy for prey availability) reported in previous research (Rau *et al.*, 2019; **Chapter 1**). Whiting, on the other hand, shows the highest aggregation under the RCP4.5–REF and RCP8.5-REF scenarios. However, at the end of the century, under both RCP4.5 scenarios, the species become more dispersed, contracts its habitat and declines in abundance. This indicates that, despite its general preference for warmer waters, whiting is strong constrained by its requirement for relatively high, marine salinity levels and, to a lesser extent, by oxygen availability (**Chapter 1**). As a result, any positive effects of warming may be outweighed, leading to spatial contraction and increased clustering under conditions of declining salinity and oxygen. In both species, these increases in aggregation coincide with projected habitat contractions, indicating a shift toward more fragmented and potentially vulnerable population structures. While dab and whiting respond similarly in terms of reduced habitat size, their aggregation dynamics underscore species-specific sensitivities to different combinations of climate and eutrophication drivers. European flounder follows a somewhat different spatial trajectory: its habitat size remains relatively stable until mid-century but declines by the century's end - especially under RCP8.5. This delayed response may reflect species-specific tolerance thresholds or nonlinear sensitivities to increasing temperatures and declining oxygen concentrations, key predictors for flounder in our models. In contrast, European plaice, EBS cod, and European sprat are projected to expand their habitat and become more dispersed under most scenarios, positioning them as potential "winners". European plaice exhibits the most pronounced changes, with an eastward shift, a substantial increase in habitat size, and increased dispersion - particularly under RCP8.5–BSAP, where warming is coupled with nutrient reductions and consequently oxygen increases. While total CPUE declines slightly, the spatial gains could enhance accessibility and resilience. EBS cod shows more moderate spatial expansion and higher CPUE, particularly under the same scenario. However, the modelled positive response to warming stands in contrast to established physiological constraints of cod (Bryhn *et al.*, 2022) and may reflect seasonal limitations of the BITS dataset as discussed in **chapter 1**. European sprat is expected to do best under the RCP8.5-REF scenario and worst under the RCP4.5-

BSAP scenario, mostly evident by observed declines in abundance at the end of the century. The species occurs more as salinity reduces, and its abundance is bolstered by increasing temperatures. The importance of these variables is echoed in other studies as well (Cardinale *et al.*, 2002; MacKenzie and Köster, 2004; MacKenzie *et al.*, 2008; Petereit *et al.*, 2008; Ojaveer and Kalejs, 2010).

WBS cod and Atlantic herring show comparatively little change in spatial indicators across scenarios. However, this apparent stability should not be mistaken for resilience. Both stocks have already undergone severe biomass declines (Fey *et al.*, 2014; Birgersson *et al.*, 2022; Bryhn *et al.*, 2022; ICES, 2024a) and our models do not suggest a recovery under any tested scenario. In the case of herring, the model failed to identify significant dynamic environmental drivers, which limits confidence in its future projections. Bauer *et al.* (2018) also encountered issues with herring i.e. they were less than successful in reproducing its distribution. They argue that such issues in modelling arise due to wide tolerances to environmental conditions possessed by species such as herring (Somodi *et al.*, 2017) and due to pelagic species usually having more variable distributions than demersal ones (Thorson *et al.*, 2016). However, their results show a general density increase across the investigated eutrophication scenarios despite it being less affected by nutrient loads. They consider this a result of various factors affecting its distribution simultaneously (predation by cod and seal, benthic food availability, competition with sprat for zooplankton). For WBS cod, temperature was identified as a key negative driver. Despite limited changes in habitat size and aggregation, the combination of persistent environmental pressure and lack of positive signals suggests that further declines remain possible. The three-spined stickleback represents a distinct case. It is the only species showing directional changes in spatial indices over time and between scenarios, particularly in the Imor and total CPUE. While temperature was the only significant dynamic driver, interactions with non-significant variables – especially salinity – may shape its responses. Lower salinity appears to support occurrence but may constrain abundance, possibly explaining the observed divergence across scenarios. Stickleback performed best under RCP8.5–BSAP, with stable habitat, reduced aggregation, and increased CPUE. Given its increasing role in Baltic

ecosystems (Bergström *et al.*, 2015; Olin *et al.*, 2022), this species warrants further attention regarding its ecological impacts.

Changes in in spatial overlap among species have the potential to alter predator–prey interactions and competitive relationships, thereby influencing broader food-web dynamics (Pinsky *et al.*, 2020). In our analysis, SOI changed over time for all species and stock pairs, indicating dynamic shifts in spatial co-occurrence throughout the century. However, the direction of these changes was typically consistent across the four scenario combinations, suggesting that long-term overlap trends are primarily driven by gradual warming - one of the few consistent environmental trends across all scenarios - rather than by scenario-specific differences in salinity or oxygen dynamics. These findings align with previous studies suggesting moderate but ecologically relevant shifts in co-occurrence under climate change (Jones *et al.*, 2013; Pecl *et al.*, 2017). Notably, species identified as potential "losers" in our analysis (common dab, European flounder, whiting, and to some extent WBS cod) are projected to increasingly overlap with each another, particularly under high-emission scenarios. This trend likely reflects joint habitat contraction and spatial aggregation in the western Baltic, potentially intensifying competition for benthic resources (Heessen *et al.*, 2015; Funk *et al.*, 2021). In contrast, WBS cod and one of its key prey, European sprat, are projected to spatially diverge over time, especially under nutrient reduction scenarios (BSAP), which could further constrain cod recovery (Sparholt, 1994; Receveur *et al.,* 2022). Species identified as potential "winners", such as European plaice and EBS cod, are projected to increasingly co-occur in the central and eastern Baltic, primarily driven by the pronounced eastward shift of plaice projected under all four scenarios. As their populations converge, competition between the two species may intensify, depending on resource availability and ontogenetic habitat use. In contrast, the spatial overlap between EBS cod and European flounder is expected to decline. This trend contrasts with earlier observations of growing overlap between these two species over past decades (Orio *et al.*, 2020) and may indicate a partial release from competition in the future. Our results further suggest spatial overlap between the two cod stocks will diminish under future conditions. While this could contribute to reduced inter-stock competition, it

should be interpreted with caution: our models excluded ICES Subdivision 24, a known mixing area for WBS and EBS cod (Hüssy *et al.*, 2016), from model training due to uncertainties in stock assignment. Although predictions were generated for this area, their transferability may be limited (Lee-Yaw *et al.*, 2022). As with all spatial overlap metrics, these projections reflect horizontal co-occurrence and do not account for vertical distribution, ontogenetic habitat shifts, or behavioral plasticity. In addition, a recent study indicates that the coexistence of the two stocks might be a result of depth-specific habitat use by showing that the WBS stock is more frequent in the shallower and the EBS stock in the deeper waters (Schade *et al.*, 2022). Future work combining spatial predictions with trophic data and trait-based models will be essential to fully understand the ecological implications of changing co-occurrence patterns (Sailley *et al.*, 2025).

From a management perspective, the scenario yielding the most favorable balance for Baltic fish stocks is RCP4.5-BSAP. Other studies also echo these findings given the profound effects of increasing temperature, decreasing salinity (Blenckner *et al.*, 2015) - although highly uncertain (Meier *et al.*, 2021), and heightened nutrient loads (Niiranen *et al.*, 2013). Spatial food web models developed by Bauer *et al.* (2019) also favor RCP4.5 as it results in high biodiversity and catch value in the Baltic Sea. The RCP4.5-BSAP pathway combines moderate climate mitigation with nutrient load reductions and would, according to our projections, benefit a wide range of vulnerable species including common dab, European flounder, European plaice, WBS cod, EBS cod, and whiting. It would also curb the future dominance of three-spined stickleback, whose numbers has recently increased (Bergström *et al.*, 2015; Olin *et al.*, 2022), thereby potentially limiting emergent biotic interactions, the consequences of which remain difficult to predict. At the same time, this scenario is projected to reduce the abundance of European sprat. Whether this is desirable is an open debate: the increase of sprat abundance has previously been linked to reduced herring growth (Casini *et al.*, 2010), but recent concerns about exceptionally low recruitment between 2021 and 2023 (ICES, 2024b) highlight the need for precaution. We were unable to identify a clear management scenario for Atlantic herring, as its model lacked significant dynamic predictors. Nonetheless, earlier studies suggest the

species prefers colder, more saline conditions (Illing *et al.*, 2016; Dodson *et al.*, 2019; Polte *et al.*, 2021; Ory *et al.*, 2022), which are best approximated under the RCP4.5-BSAP scenario. In this context, reducing sprat abundance could also indirectly benefit herring. By contrast, the RCP8.5–REF scenario, which reflects a business-as-usual trajectory, is the least favorable: it exacerbates the decline of most demersal species while favoring opportunistic ones. Although even more ambitious mitigation pathways such as RCP2.6 or RCP3.4 could potentially improve outcomes, their feasibility remains uncertain given current global policy trajectories.

In this study, fishing pressure was not dynamically included in most of our models and – where available - future landings were kept constant and not resolved spatially. Integrating fisheries effort in a similar way as in Bauer *et al.* (2018) where it is kept at a constant value but is spatially redistributed within the area at every time-step following the changes in spatial distributions of the targeted fish, would likely improve the created models. Still, there is ample evidence that reducing exploitation can enhance stock resilience, even when environmental conditions remain suboptimal (Sumaila and Tai, 2020). In the Northern Hemisphere, multiple cases of marine regime shifts have likely resulted from the combined effects of overfishing and environmental change (Möllmann and Diekmann, 2012). In Tasmania, for instance, overfishing of lobsters has reduced the resilience of kelp beds to climate-driven sea urchin outbreaks, increasing the risk of catastrophic shifts to sea urchin barrens (Ling *et al.*, 2009). Similarly, in the southwest Indian Ocean, overfishing and climate change are jointly increasing extinction risks for endemic sharks and rays (Pollom *et al.*, 2024). In the Baltic itself, it was found that regional management, under environmental change, would likely play a major role in its future (Niiranen *et al.*, 2013). Lowering fishing mortality on “loser” species and those already depleted, such as cod and flounder, should be a priority. Conversely, targeting abundant species like sprat may help rebalance trophic interactions, especially given its known negative effects on herring (Casini *et al.*, 2010). However, this must be approached cautiously in light of the species’ recent recruitment failure (ICES, 2024b). Other studies also indicate the importance of reducing greenhouse gas emissions and eutrophication together with ecologically focused fisheries management for maintaining a healthy and productive

Baltic ecosystem (Bauer *et al.*, 2018, 2019). Lastly, shifting species distributions might render protection measures such as Marine Protected Areas (MPAs) ineffective (Cashion *et al.*, 2020) and they largely do not incorporate common climate change adaptation principles in their design (O'Regan *et al.*, 2021). Dynamic management might be a valuable approach to mitigating such issues given that it can change in space and time, in turn helping marine ecosystems and increasing the efficiency and efficacy of fisheries management (Maxwell *et al.*, 2015; Dunn *et al.*, 2016; Gilman *et al.*, 2019; Oestreich *et al.*, 2020).

Overall, our findings underscore the need for forward-looking, precautionary management in the Baltic Sea. Limiting overfishing, enhancing adaptive capacity, and prioritizing emissions and nutrient reductions will be critical to support ecological resilience. As it stands, preserving the fish community of the Baltic Sea will be a difficult task. Our projections reveal more reasons for concern, and we argue that management should prioritize stringent conservation of the investigated species and stocks rather than risk underregulated exploitation. This is especially urgent in light of recent evidence suggesting that global stock assessments may systematically overestimate the sustainability of fisheries (Edgar *et al.*, 2024). Management efforts must focus on reducing exploitation and strengthening ecosystem resilience to ongoing and future environmental change. Doing so would support the sustainability of Baltic fisheries and enhance the adaptive capacity of the coastal communities that depend on them.

REFERENCES

Alexander, J. M., Diez, J. M., Hart, S. P., and Levine, J. M. 2016. When Climate Reshuffles Competitors: A Call for Experimental Macroecology. Trends in Ecology & Evolution, 31: 831–841.

Al-Hamdani, Z., and Reker, J. 2007. Towards marine landscapes in the Baltic Sea. BALANCE interim report #10: 116.

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. preprint. Ecology. http://biorxiv.org/lookup/doi/10.1101/2022.03.24.485545 (Accessed 2 January 2024).

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., *et al.* 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO, 44: 345–356.

Bauer, B., Meier, H. E. M., Casini, M., Hoff, A., Margoński, P., Orio, A., Saraiva, S., *et al.* 2018. Reducing eutrophication increases spatial extent of communities supporting commercial fisheries: a model case study. ICES Journal of Marine Science, 75: 1306–1317.

Bauer, B., Gustafsson, B. G., Hyytiäinen, K., Meier, H. E. M., Müller-Karulis, B., Saraiva, S., and Tomczak, M. T. 2019. Food web and fisheries in the future Baltic Sea. Ambio, 48: 1337–1349.

Belkin, I. M. 2009. Rapid warming of Large Marine Ecosystems. Progress in Oceanography, 81: 207–213.

Bergström, U., Olsson, J., Casini, M., Eriksson, B. K., Fredriksson, R., Wennhage, H., and Appelberg, M. 2015. Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science, 163: 134–142.

Birgersson, L., Söderström, S., and Belhaj, M. 2022. The Decline of Cod in the Baltic Sea - A Review of Biology, Fisheries and Management, Including Recommendations for Cod Recovery. The Fisheries Secretariat, Stockholm, Sweden.

Blenckner, T., Llope, M., Möllmann, C., Voss, R., Quaas, M. F., Casini, M., Lindegren, M., *et al.* 2015. Climate and fishing steer ecosystem regeneration to uncertain economic futures. Proceedings of the Royal Society B: Biological Sciences, 282: 20142809.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., and Finnegan, S. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. Science, 341: 499–504.

Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J., *et al.* 2022. Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? Ocean & Coastal Management, 223: 106154.

Cardinale, M., Casini, M., and Arrhenius, F. 2002. The influence of biotic and abiotic factors on the growth of sprat (Sprattus sprattus) in the Baltic Sea. Aquatic Living Resources, 15: 273–281.

Cashion, T., Nguyen, T., Ten Brink, T., Mook, A., Palacios-Abrantes, J., and Roberts, S. M. 2020. Shifting seas, shifting boundaries: Dynamic marine protected area designs for a changing climate. PLOS ONE, 15: e0241771.

Casini, M., Bartolino, V., Molinero, J. C., and Kornilovs, G. 2010. Linking fisheries, trophic interactions and climate: threshold dynamics drive herring Clupea harengus growth in the central Baltic Sea. Marine Ecology Progress Series, 413: 241–252.

Cavraro, F., Anelli Monti, M., Matić-Skoko, S., Caccin, A., and Pranovi, F. 2022. Vulnerability of the Small-Scale Fishery to Climate Changes in the Northern-Central Adriatic Sea (Mediterranean Sea). Fishes, 8: 9.

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., and Thomas, C. D. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science, 333: 1024–1026.

Cheung, W. W. L., Watson, R., and Pauly, D. 2013. Signature of ocean warming in global fisheries catch. Nature, 497: 365–368.

Dodson, J. J., Daigle, G., Hammer, C., Polte, P., Kotterba, P., Winkler, G., and Zimmermann, C. 2019. Environmental determinants of larval herring (Clupea

harengus) abundance and distribution in the western Baltic Sea. Limnology and Oceanography, 64: 317–329.

Dunn, D. C., Maxwell, S. M., Boustany, A. M., and Halpin, P. N. 2016. Dynamic ocean management increases the efficiency and efficacy of fisheries management. Proceedings of the National Academy of Sciences, 113: 668–673.

Edgar, G. J., Bates, A. E., Krueck, N. C., Baker, S. C., Stuart-Smith, R. D., and Brown, C. J. 2024. Stock assessment models overstate sustainability of the world's fisheries.

Eilola, K., Meier, H. E. M., and Almroth, E. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. Journal of Marine Systems, 75: 163–184.

Fey, D. P., Hiller, A., Margonski, P., Moll, D., Nilsson, H., Pongolini, L., Stybel, N., *et al.* 2014. HERRING Impact Report Herring spawning areas - present and future challenges.

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., and Aschan, M. M. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. Proceedings of the National Academy of Sciences, 114: 12202–12207.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. 2019. Impacts of historical warming on marine fisheries production. Science, 363: 979–983.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Funk, S., Frelat, R., Möllmann, C., Temming, A., and Krumme, U. 2021. The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod Gadus morhua in the western Baltic Sea. Journal of Fish Biology, 98: 707–722.

Funkey, C. P., Conley, D. J., Reuss, N. S., Humborg, C., Jilbert, T., and Slomp, C. P. 2014. Hypoxia Sustains Cyanobacteria Blooms in the Baltic Sea. Environmental Science & Technology, 48: 2598–2602.

Gilman, E., Kaiser, M. J., and Chaloupka, M. 2019. Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives? Ecosphere, 10: e02968.

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., and Genner, M. J. 2020. Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species. Current Biology, 30: 1572-1577.e2.

Heessen, H. J. L., Daan, N., and Ellis, J. R. (Eds). 2015. Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys. Brill | Wageningen Academic. https://brill.com/view/title/68532 (Accessed 2 January 2024).

Horta E Costa, B., Assis, J., Franco, G., Erzini, K., Henriques, M., Gonçalves, E., and Caselle, J. 2014. Tropicalization of fish assemblages in temperate biogeographic transition zones. Marine Ecology Progress Series, 504: 241–252.

Hüssy, K., Mosegaard, H., Albertsen, C. M., Nielsen, E. E., Hemmer-Hansen, J., and Eero, M. 2016. Evaluation of otolith shape as a tool for stock discrimination in marine fishes using Baltic Sea cod as a case study. Fisheries Research, 174: 210–218.

ICES. 2009. Manual for the Baltic International Acoustic Survey (BIAS).

ICES. 2017. Manual for the Baltic International Trawl Surveys (BITS). Series of ICES Survey Protocols SISP 7 - BITS: 95. ICES.

ICES. 2022. Baltic Sea ecoregion – fisheries overview. ICES Advice: Fisheries Overviews. https://ices-library.figshare.com/articles/report/Baltic_Sea_ecoregion_fisheries_overview/21646934 (Accessed 26 February 2024).

ICES. 2024a. Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Herring_i_Clupea_harengus_i_in_subdivisi

ons_20_24_spring_spawners_Skagerrak_Kattegat_and_western_Baltic_/25019273 (Accessed 16 January 2025).

ICES. 2024b. Sprat (Sprattus sprattus) in subdivisions 22–32 (Baltic Sea). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Sprat_i_Sprattus_sprattus_i_in_subdivisions_22_32_Baltic_Sea_/25019687 (Accessed 15 November 2024).

Illing, B., Moyano, M., Hufnagl, M., and Peck, M. A. 2016. Projected habitat loss for Atlantic herring in the Baltic Sea. Marine Environmental Research, 113: 164–173.

Jones, M. C., Dye, S. R., Fernandes, J. A., Frölicher, T. L., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. 2013. Predicting the Impact of Climate Change on Threatened Species in UK Waters. PLoS ONE, 8: e54216. Public Library of Science (PLoS).

Lee-Yaw, J. A., McCune, J. L., Pironon, S., and Sheth, S. N. 2022. Species distribution models rarely predict the biology of real populations. Ecography, 2022: e05877.

Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences, 106: 22341–22345.

Liu, Y., Meier, H. E. M., and Eilola, K. 2017. Nutrient transports in the Baltic Sea – results from a 30-year physical–biogeochemical reanalysis. Biogeosciences, 14: 2113–2131.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology, 85: 784–794.

MacKenzie, B. R., Horbowy, J., and Köster, F. W. 2008. Incorporating environmental variability in stock assessment: predicting recruitment, spawner biomass, and landings of sprat (Sprattus sprattus) in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1334–1341.

MacNeil, L., Madiraca, F., Otto, S., and Scotti, M. 2025. Spatial Change of Dominant Baltic Sea Demersal Fish Across Two Decades. Ecology and Evolution, 15: e71309.

Madiraca, F., MacNeil, L., Scotti, M., Möllmann, C., and Otto, S. A. in preparation. Environmentally driven shifts of Baltic fish distributions and their impact on spatiotemporal overlap between species.

Meier, H. E. M., Dieterich, C., and Gröger, M. 2021. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. Communications Earth & Environment, 2: 50.

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., *et al.* 2015. Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. Marine Policy, 58: 42–50.

Millar, C., Large, S., Magnusson, A., and Pinto, C. 2023. icesSAG: Stock Assessment Graphs Database Web Services. https://CRAN.R-project.org/package=icesSAG.

Moll, D., Asmus, H., Blöcker, A., Böttcher, U., Conradt, J., Färber, L., Funk, N., *et al.* 2024. A climate vulnerability assessment of the fish community in the Western Baltic Sea. Scientific Reports, 14: 16184.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Möllmann, C., and Diekmann, R. 2012. Marine Ecosystem Regime Shifts Induced by Climate and Overfishing. *In* Advances in Ecological Research, pp. 303–347. Elsevier. https://linkinghub.elsevier.com/retrieve/pii/B9780123983152000041 (Accessed 15 November 2024).

Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E.: 215–235.

Morisita, M. 1962. Id-index, a measure of dispersion of individuals. Res. Popul. Ecol., 4: 1–7.

Moss, R. 2008. Towards new scenarios for analysis of emissions, climate change, impacts, and response strategies: IPCC Expert Meeting report : 19-21 September, 2007, Noordwijkerhout, the Netherlands. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Nagelkerken, I., Allan, B. J. M., Booth, D. J., Donelson, J. M., Edgar, G. J., Ravasi, T., Rummer, J. L., *et al.* 2023. The effects of climate change on the ecology of fishes. PLOS Climate, 2: e0000258.

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., Müller-Karulis, B., *et al.* 2013. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. Global Change Biology, 19: 3327–3342.

Oestreich, W. K., Chapman, M. S., and Crowder, L. B. 2020. A comparative analysis of dynamic management in marine and terrestrial systems. Frontiers in Ecology and the Environment, 18: 496–504.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries, 20: 203–217.

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., and Bergström, U. 2022. Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback. ICES Journal of Marine Science, 79: 1419–1434.

O'Regan, S. M., Archer, S. K., Friesen, S. K., and Hunter, K. L. 2021. A Global Assessment of Climate Change Adaptation in Marine Protected Area Management Plans. Frontiers in Marine Science, 8: 711085.

Orio, A., Bergström, U., Florin, A., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap between interacting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Ory, N. C., Gröger, J. P., Lehmann, A., Mittermayer, F., and Clemmesen, C. 2022. Early Arrival of Spring-Spawner Atlantic Herring at Their Spawning Ground in the Kiel Fjord, Western Baltic, Relates to Increasing Sea Water Temperature. SSRN Electronic Journal. https://www.ssrn.com/abstract=4164412 (Accessed 16 February 2024).

Otto, S. A., Simons, S., Stoll, J. S., and Lawson, P. 2016. Making progress on bycatch avoidance in the ocean salmon fishery using a transdisciplinary approach. ICES Journal of Marine Science, 73: 2380–2394.

Otto, S. A., Niiranen, S., Blenckner, T., Tomczak, M. T., Müller-Karulis, B., Rubene, G., and Möllmann, C. 2020. Life Cycle Dynamics of a Key Marine Species Under Multiple Stressors. Frontiers in Marine Science, 7: 296.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., *et al.* 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., *et al.* 2020. Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography, 43: 197–208.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308: 1912–1915.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (Sprattus sprattus) eggs and yolk sac larvae. Marine Biology, 154: 295–306.

Pinsky, M. L., and Fogarty, M. 2012. Lagged social-ecological responses to climate and range shifts in fisheries. Climatic Change, 115: 883–891.

Pinsky, M. L., Selden, R. L., and Kitchel, Z. J. 2020. Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science, 12: 153–179.

Pollom, R. A., Cheok, J., Pacoureau, N., Gledhill, K. S., Kyne, P. M., Ebert, D. A., Jabado, R. W., *et al.* 2024. Overfishing and climate change elevate extinction risk of endemic sharks and rays in the southwest Indian Ocean hotspot. PLOS ONE, 19: e0306813.

Polte, P., Gröhsler, T., Kotterba, P., Von Nordheim, L., Moll, D., Santos, J., Rodriguez-Tress, P., *et al.* 2021. Reduced Reproductive Success of Western Baltic Herring (Clupea harengus) as a Response to Warming Winters. Frontiers in Marine Science, 8: 589242.

Priya, A. K., M, M., Rajamanickam, S., Sivarethinamohan, S., Gaddam, M. K. R., Velusamy, P., R, G., *et al.* 2023. Impact of climate change and anthropogenic activities on aquatic ecosystem – A review. Environmental Research, 238: 117233.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rau, A., Lewin, W.-C., Zettler, M. L., Gogina, M., and Von Dorrien, C. 2019. Abiotic and biotic drivers of flatfish abundance within distinct demersal fish assemblages in a brackish ecosystem (western Baltic Sea). Estuarine, Coastal and Shelf Science, 220: 38–47.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances, 4: eaar8195.

Sailley, S. F., Catalan, I. A., Batsleer, J., Bossier, S., Damalas, D., Hansen, C., Huret, M., *et al.* 2025. Multiple Models of European Marine Fish Stocks: Regional Winners and Losers in a Future Climate. Global Change Biology, 31. Wiley. https://onlinelibrary.wiley.com/doi/10.1111/gcb.70149 (Accessed 26 July 2025).

Schade, F. M., Weist, P., Dierking, J., and Krumme, U. 2022. Living apart together: Long-term coexistence of Baltic cod stocks associated with depth-specific habitat use. PLOS ONE, 17: e0274476.

Seifert, Tauber, and Kayser. 2001. A high resolution spherical grid topography of the Baltic Sea – 2nd edition. Baltic Sea Science Congress, Stockholm 25-29. November 2001.

Somodi, I., Lepesi, N., and Botta-Dukát, Z. 2017. Prevalence dependence in model goodness measures with special emphasis on true skill statistics. Ecology and Evolution, 7: 863–872.

Sparholt, H. 1994. Fish species interactions in the Baltic Sea. Dana, 10: 131–162.

Sumaila, U. R., and Tai, T. C. 2020. End Overfishing and Increase the Resilience of the Ocean to Climate Change. Frontiers in Marine Science, 7: 523.

Sunday, J. M., Bates, A. E., and Dulvy, N. K. 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B: Biological Sciences, 278: 1823–1830.

Sys, K., Rindorf, A., Bastardie, F., Baudron, A., Berg, C. W., Bitetto, I., Blanco, C., *et al.* 2024. SEAwise report on historic and future spatial distribution of fished stocks. Technical University of Denmark. https://data.dtu.dk/articles/online_resource/SEAwise_report_on_historic_and_future_spatial_distribution_of_fished_stocks/21694934 (Accessed 18 November 2024).

Thorson, J. T., Pinsky, M. L., and Ward, E. J. 2016. Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods in Ecology and Evolution, 7: 990–1002.

Townhill, B. L., Couce, E., Tinker, J., Kay, S., and Pinnegar, J. K. 2023. Climate change projections of commercial fish distribution and suitable habitat around north western Europe. Fish and Fisheries, 24: 848–862.

Van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., *et al.* 2011. The representative concentration pathways: an overview. Climatic Change, 109: 5–31.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B: Biological Sciences, 281: 20140846.

Wåhlström, I., Höglund, A., Almroth-Rosell, E., MacKenzie, B. R., Gröger, M., Eilola, K., Plikshs, M., *et al.* 2020. Combined climate change and nutrient load impacts on future habitats and eutrophication indicators in a eutrophic coastal sea. Limnology and Oceanography, 65: 2170–2187.

Woillez, M., Rivoirard, J., and Petitgas, P. 2009. Notes on survey-based spatial indicators for monitoring fish populations. Aquatic Living Resources, 22: 155–164.

SUPPLEMENTARY MATERIAL

Model input

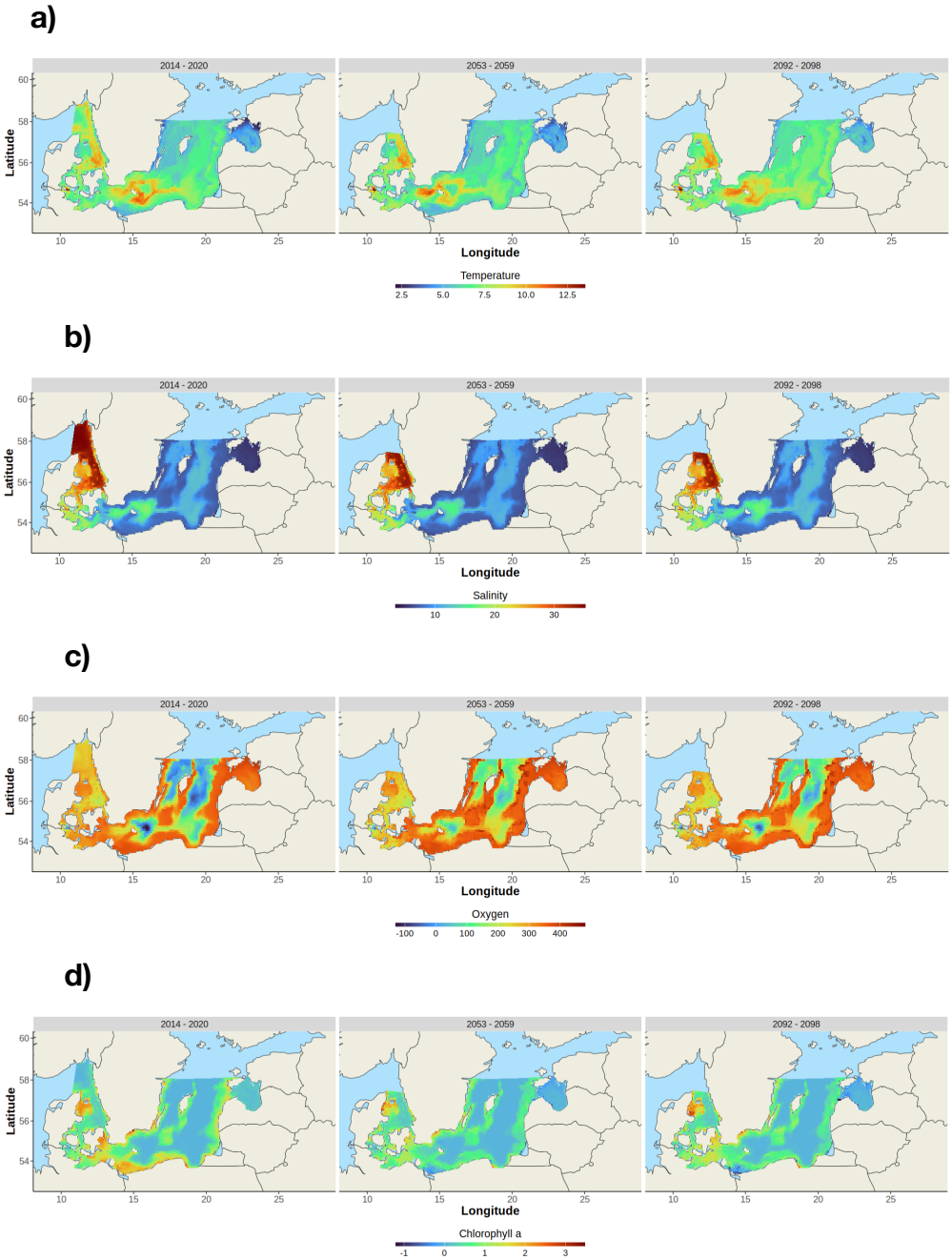


Figure S1. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for demersal and benthopelagic species analyses.

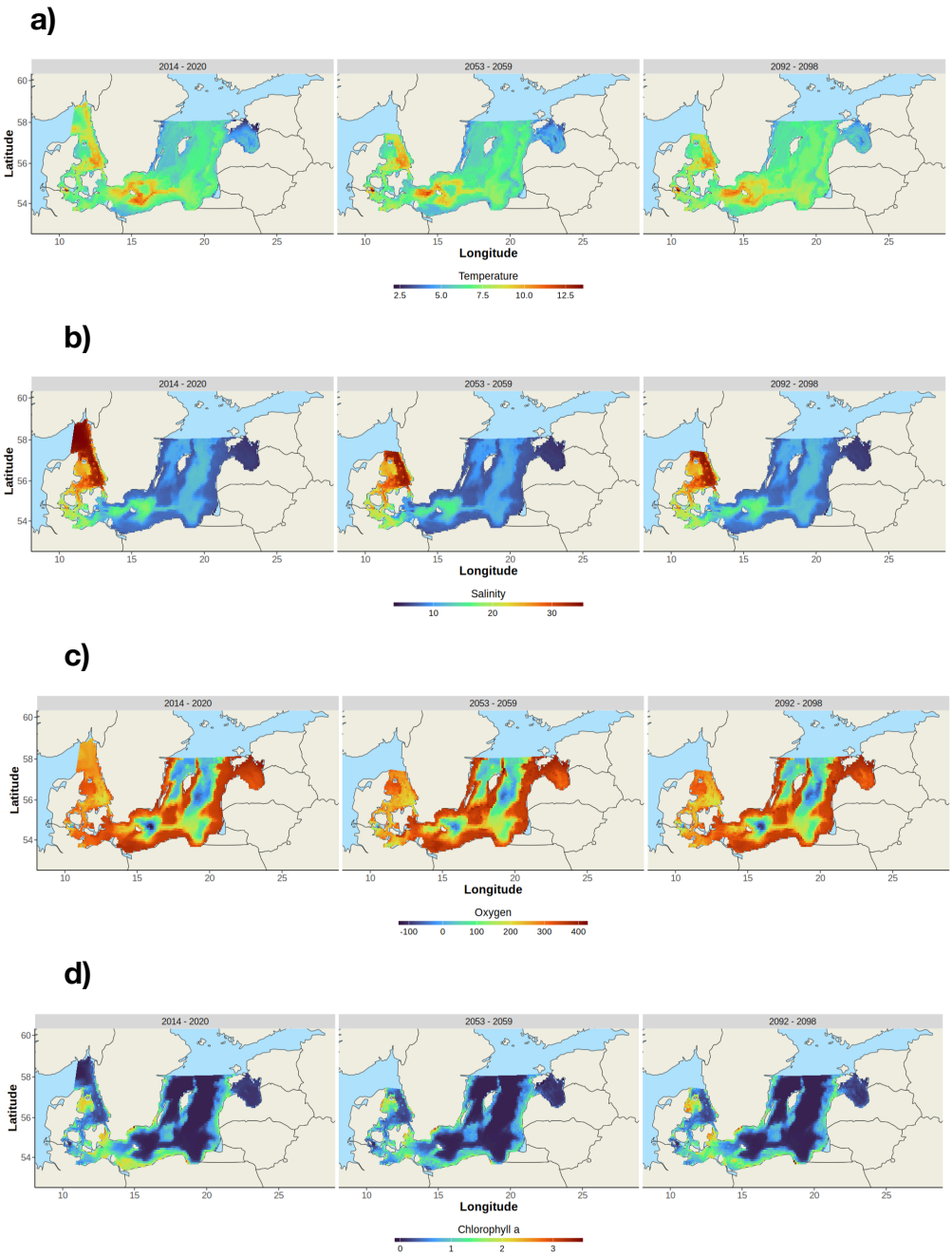


Figure S2. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for demersal and benthopelagic species analyses.

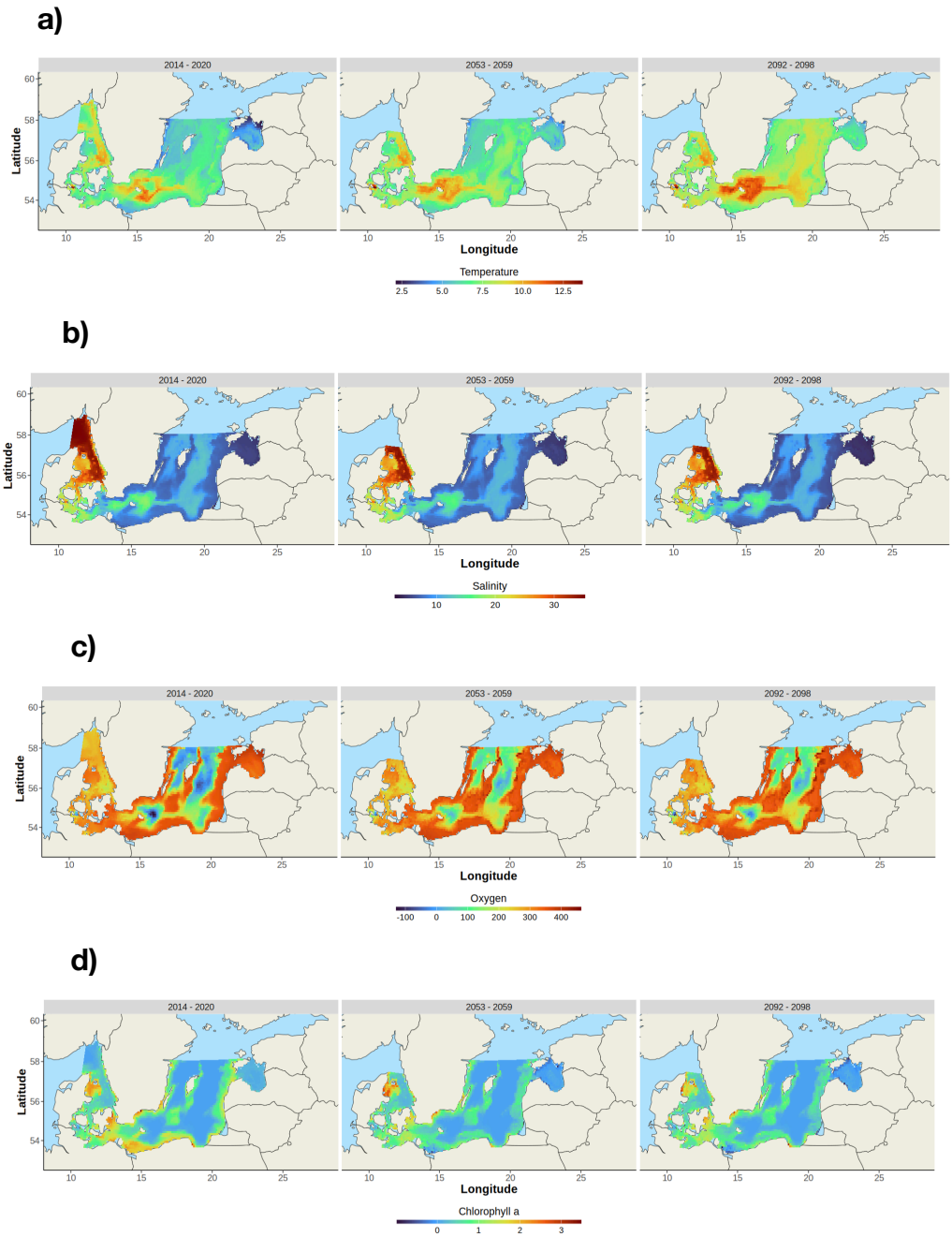


Figure S3. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for demersal and benthopelagic species analyses.

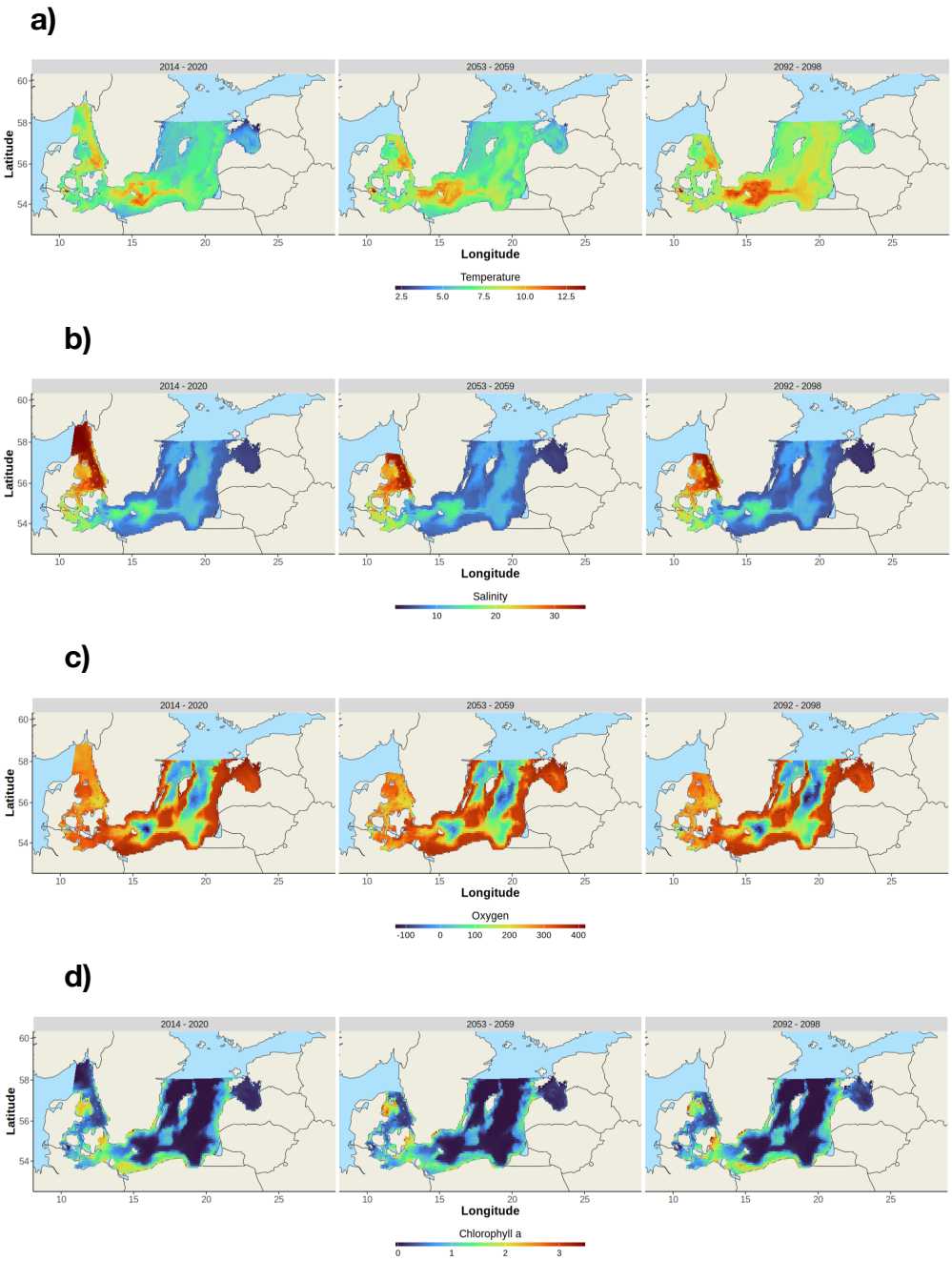


Figure S4. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for demersal and benthopelagic species analyses.

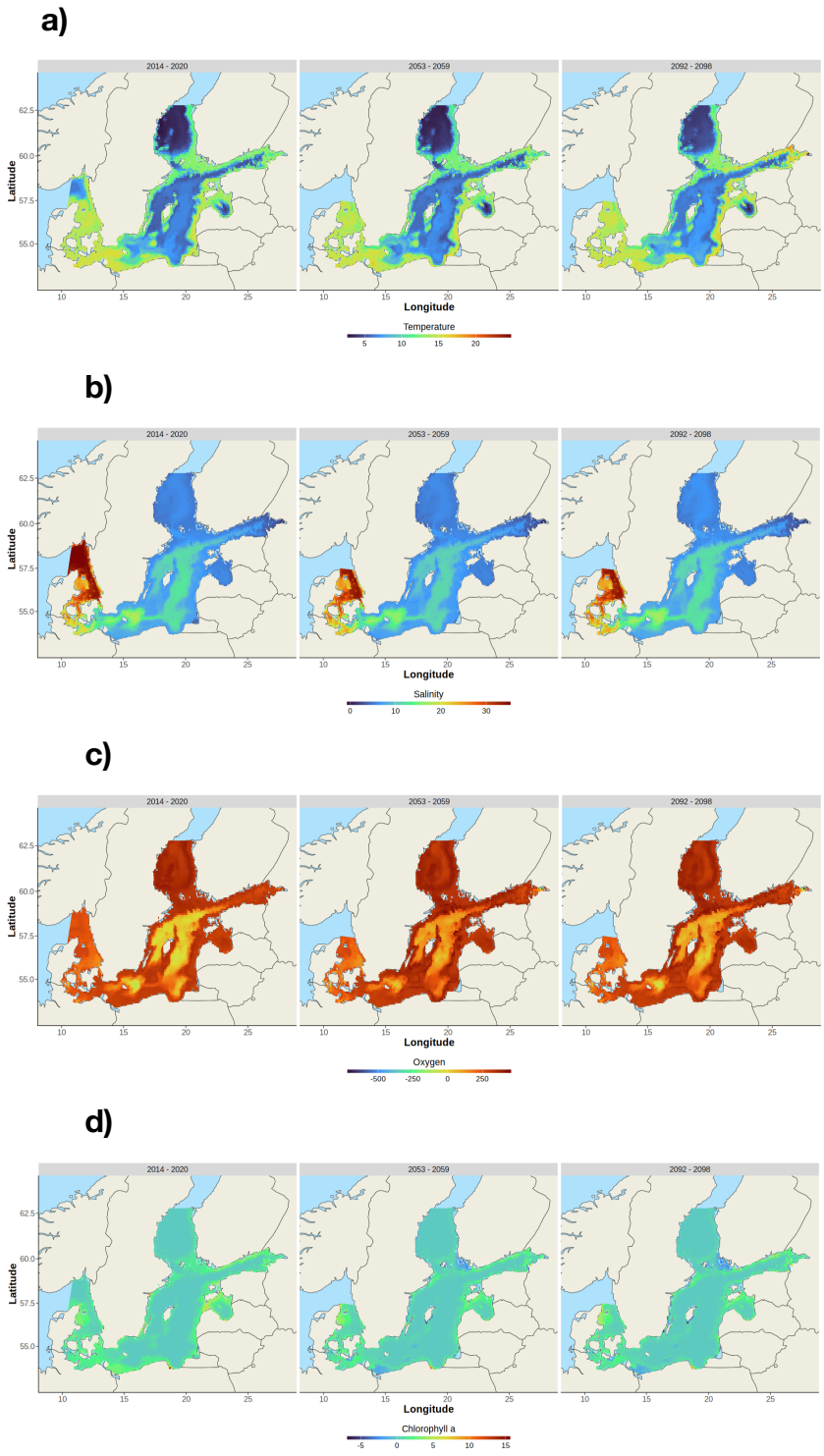


Figure S5. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for herring analyses.

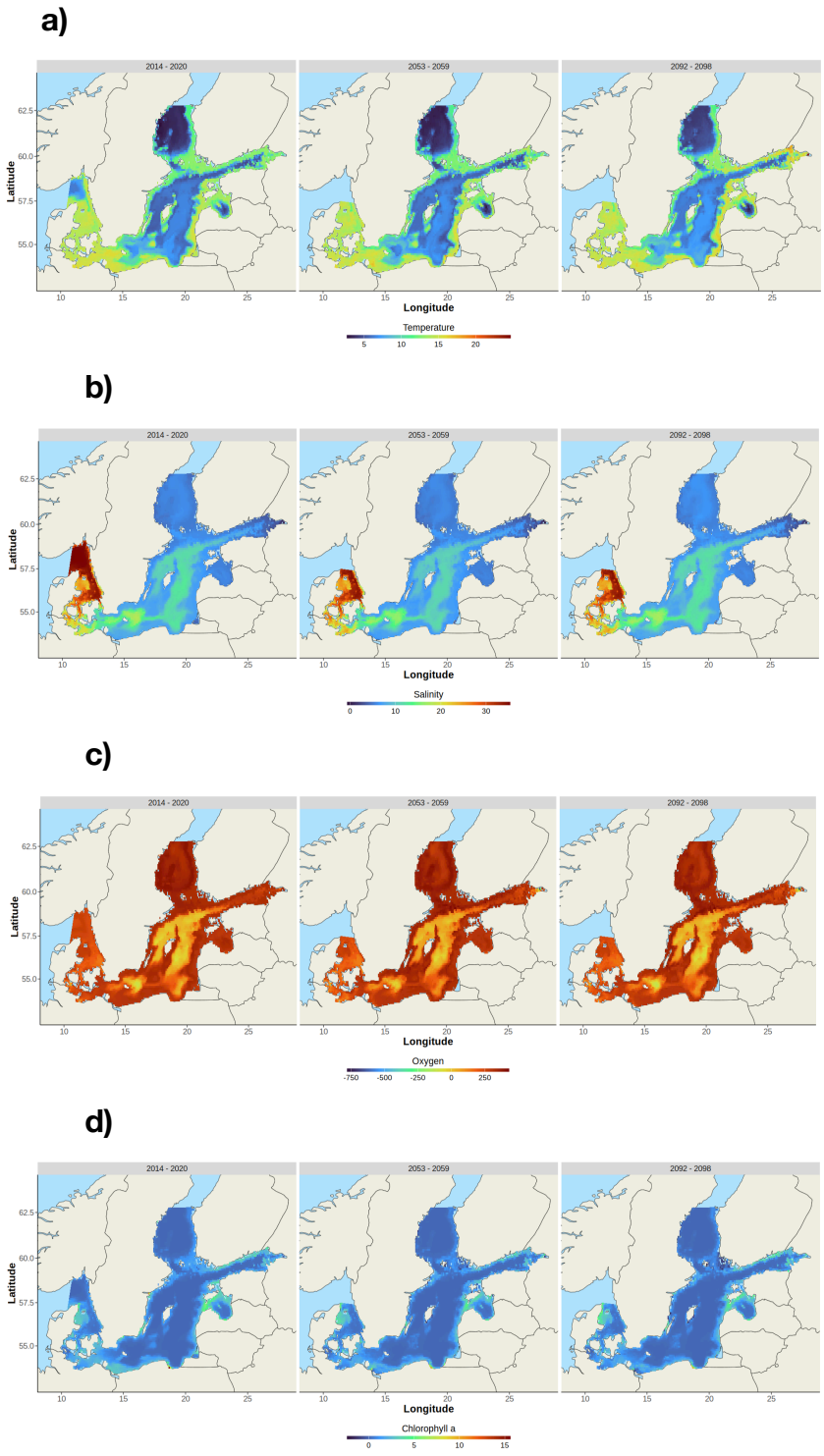


Figure S6. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for herring analyses.

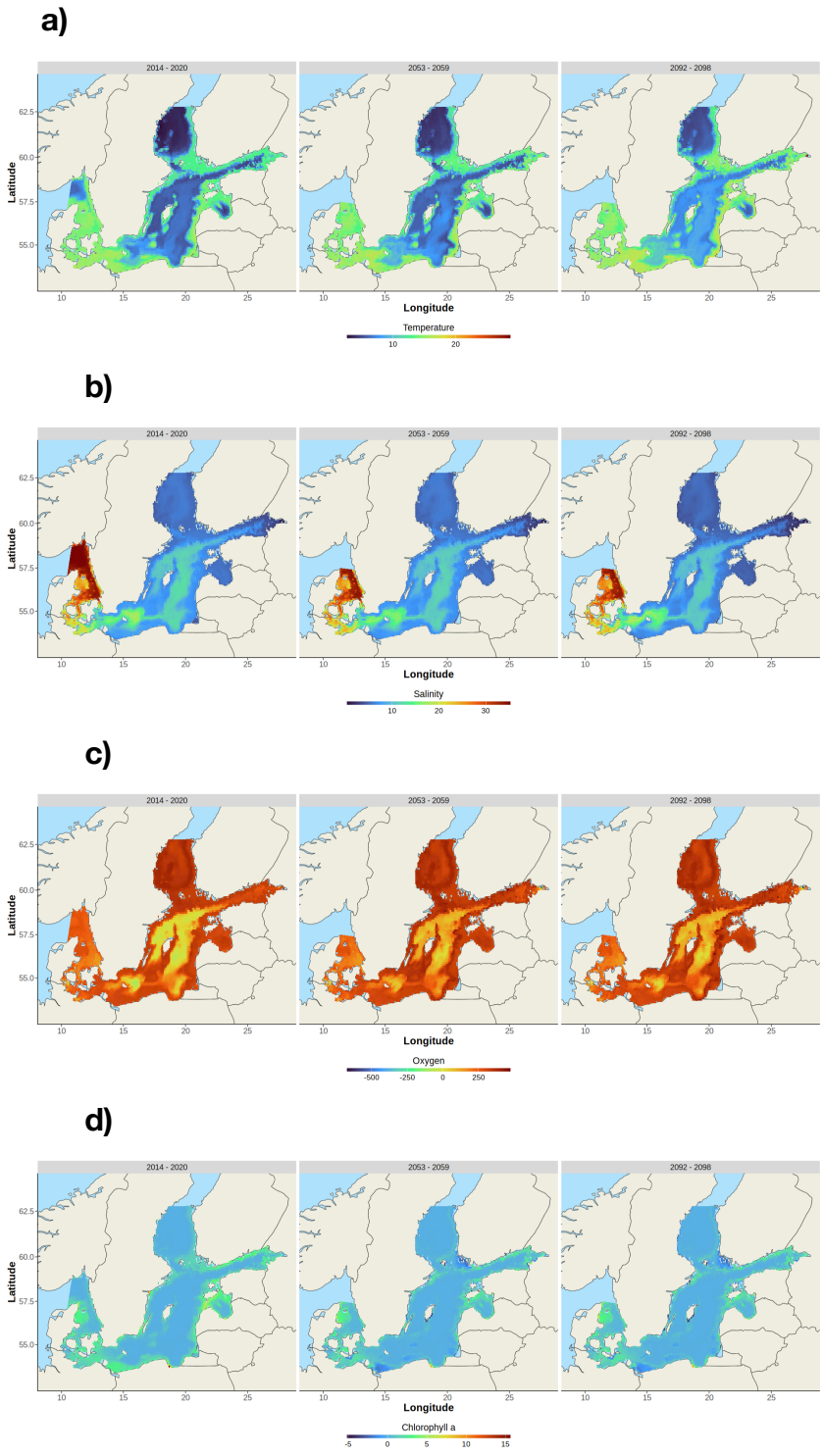


Figure S7. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for herring analyses.

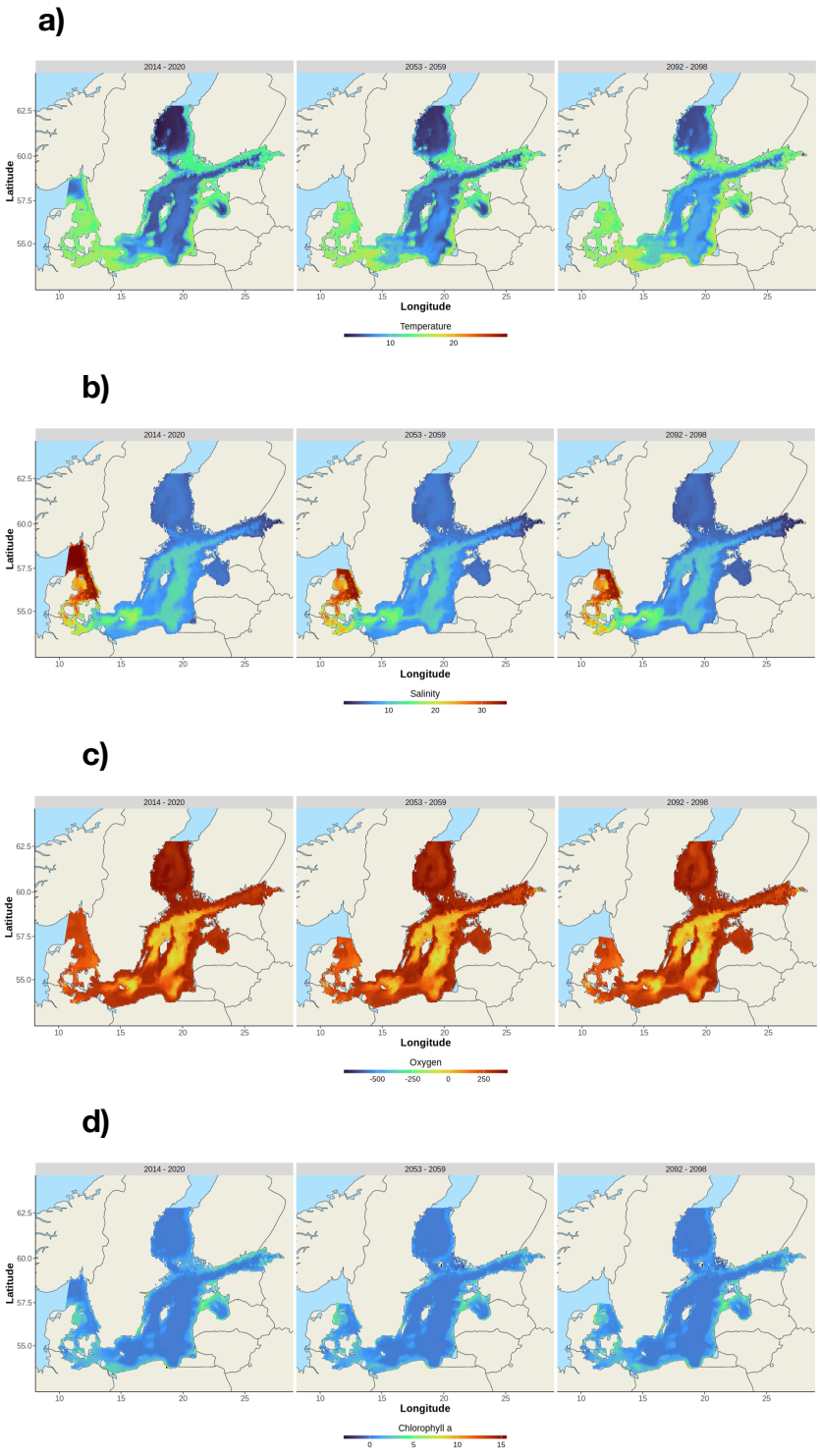


Figure S8. Dynamic covariates in the Baltic Sea at the bottom shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for herring analyses.

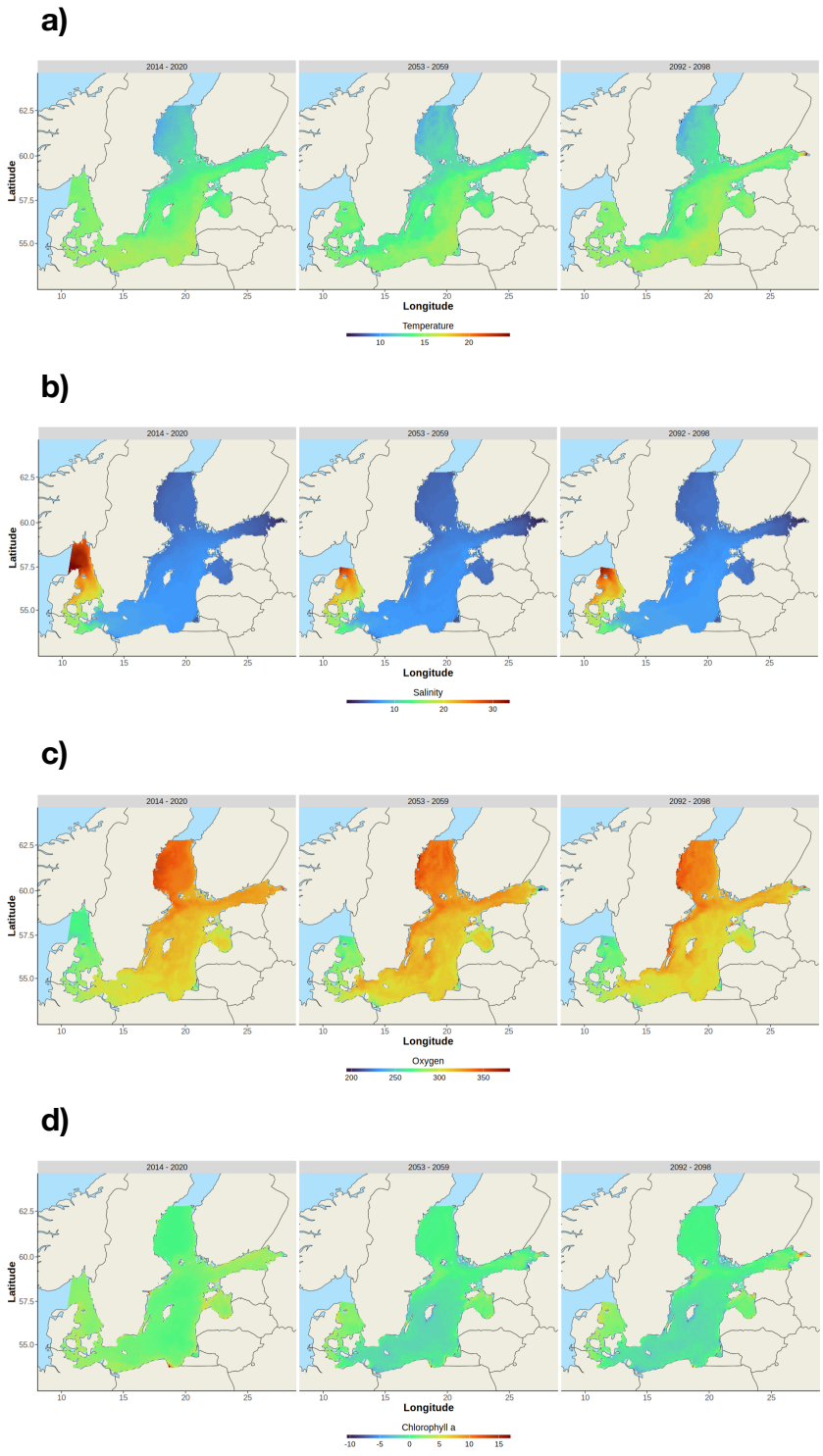


Figure S9. Dynamic covariates in the Baltic Sea at the surface shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for sprat and stickleback analyses.

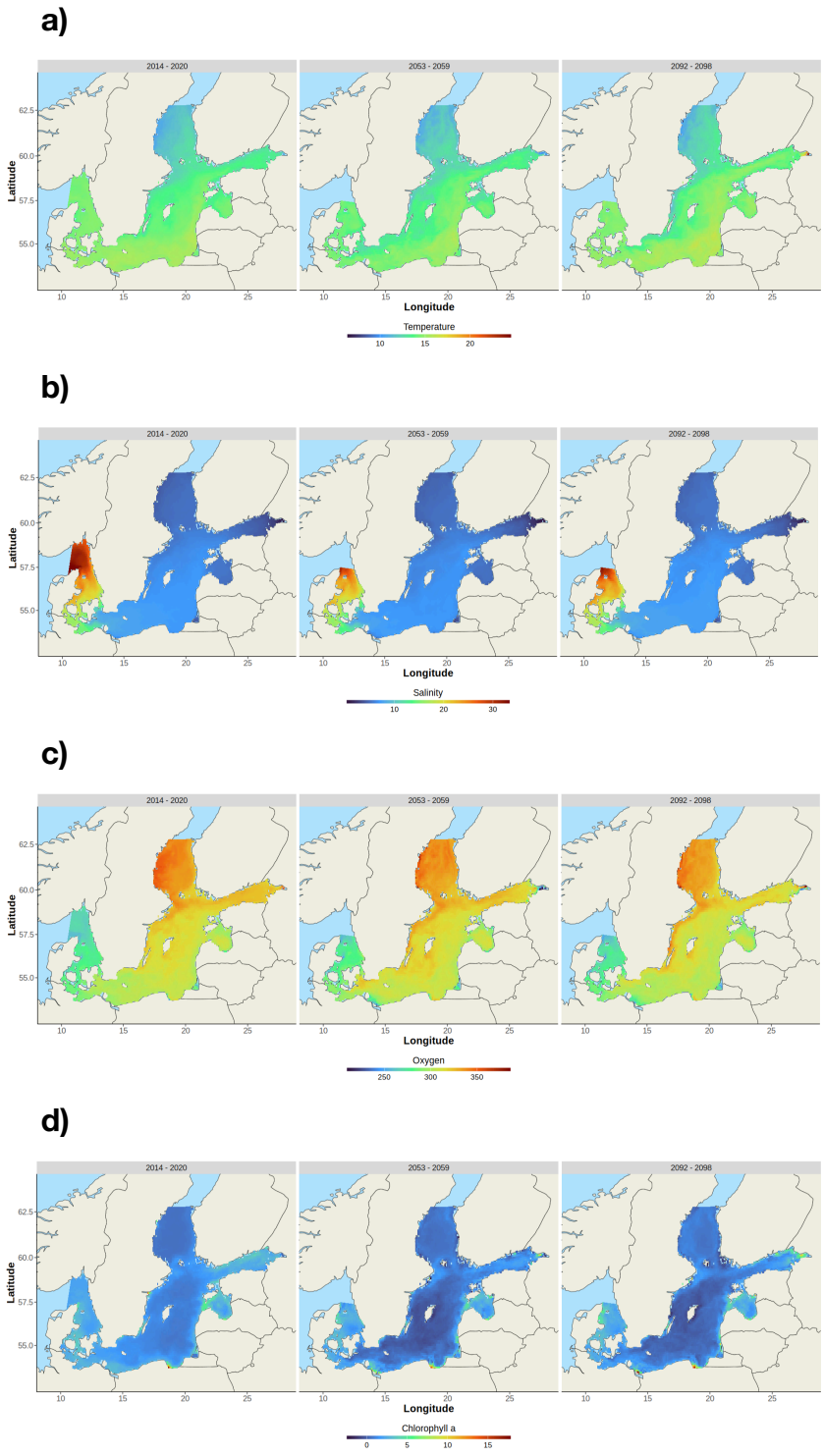


Figure S10. Dynamic covariates in the Baltic Sea at the surface shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP4.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for sprat and stickleback analyses.

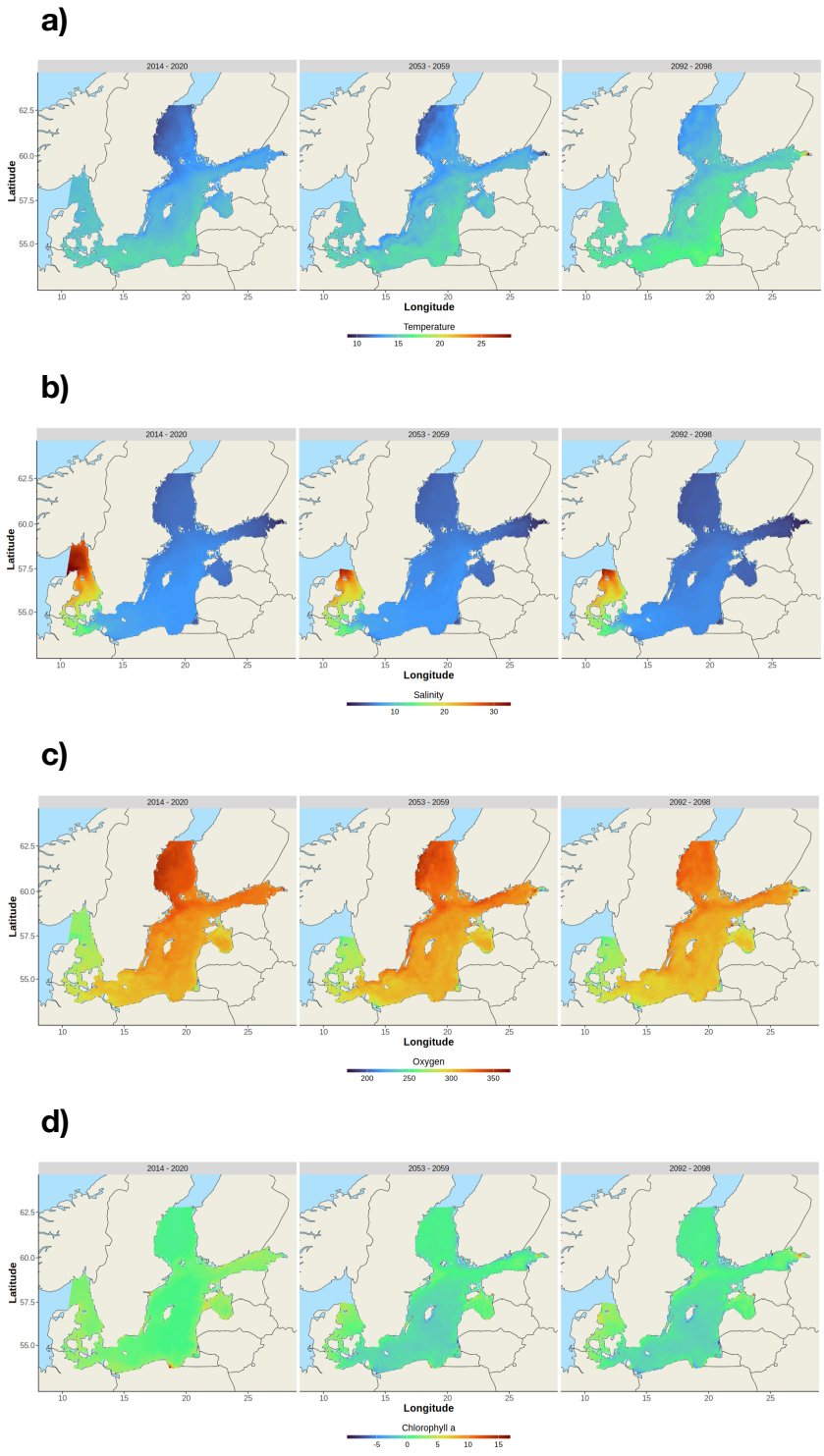


Figure S11. Dynamic covariates in the Baltic Sea at the surface shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-BSAP scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for sprat and stickleback analyses.

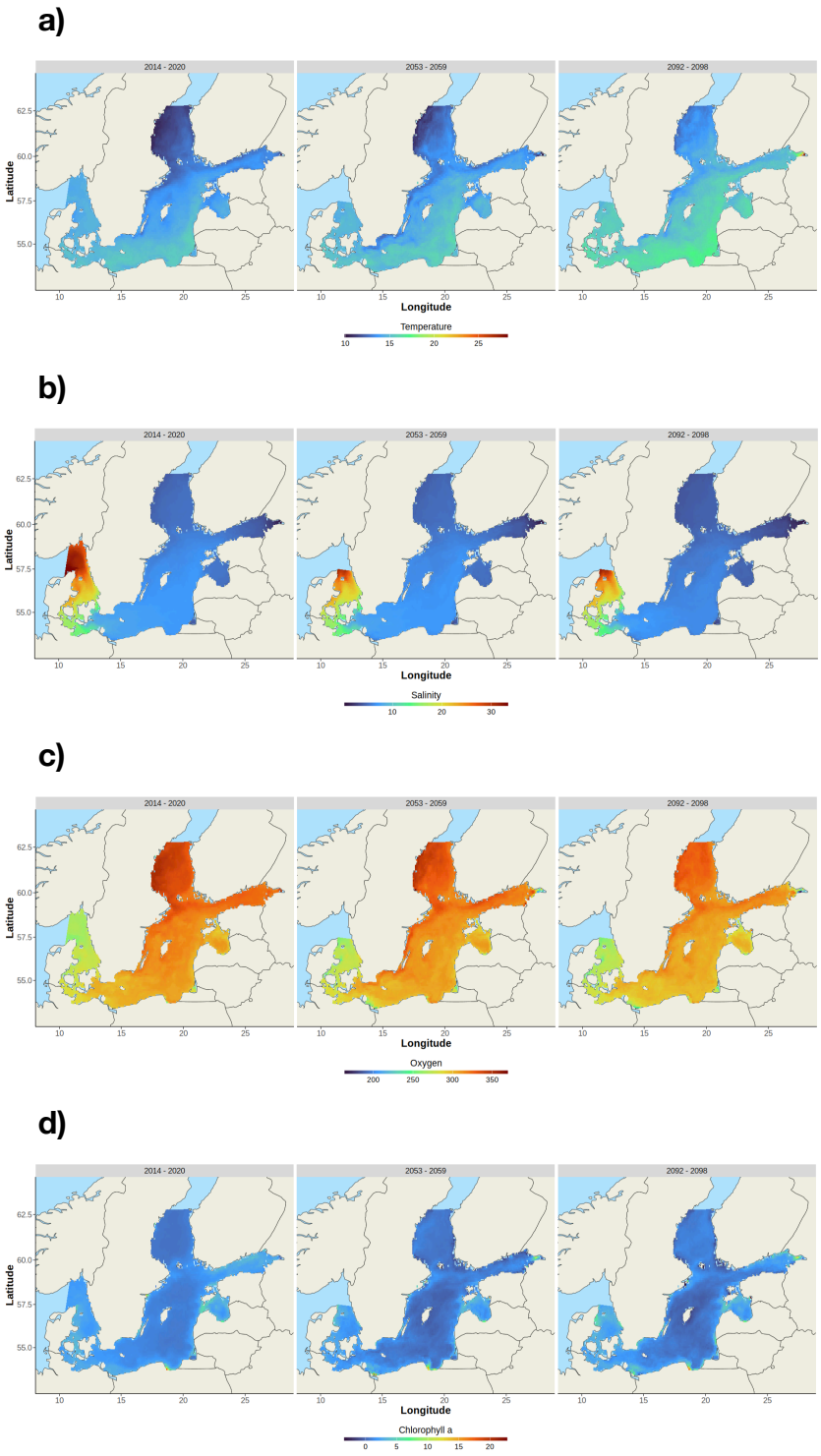


Figure S12. Dynamic covariates in the Baltic Sea at the surface shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the RCP8.5-REF scenario: a) temperature, b) salinity, c) oxygen, and d) chlorophyll *a*; used for sprat and stickleback analyses.

Model output

Table S1. Overview of percentage change of spatial indices summarizing predicted distributional changes of fish species and stocks across future periods (MOC: 2053 – 2059, EOC: 2092 – 2098) and climate change and eutrophication scenarios. Light orange and light blue colors indicate increase and decrease, respectively. Values in bold are lowest, and underlined ones are highest amongst all scenario-period combinations.

		Total CPUE		**COG - Longitude**		**Cog - Latitude**		**Habitat size**		**Morisita Index**	
		MOC	*EOC*	*MOC*	*EOC*	*MOC*	*EOC*	*MOC*	*EOC*	*MOC*	*EOC*
Common dab	*RCP4.5, BSAP*	-17.23	-13.15	**-0.89**	-0.08	-0.34	-0.41	-6.77	-4.54	11.56	6.23
	RCP4.5, REF	-14.97	-10.17	-0.01	1.02	-0.35	**-0.44**	-8.09	-5.49	7.28	**-0.44**
	RCP8.5, BSAP	-15.78	**-18.11**	-1.43	-2.52	-0.42	-0.39	-6.81	-9.08	10.28	17.85
	RCP8.5, REF	-13.80	-15.00	0.01	-0.87	-0.42	-0.42	-8.05	**-10.03**	4.83	9.89
European flounder	*RCP4.5, BSAP*	-11.75	-13.00	-1.18	-2.84	-0.20	-0.26	0.66	-2.44	**-6.03**	-2.99
	RCP4.5, REF	-13.59	-14.47	-1.40	-3.07	-0.22	-0.29	-0.97	-2.26	-5.66	-2.50
	RCP8.5, BSAP	-13.84	-20.45	-1.58	-3.56	-0.23	-0.27	-0.34	**-7.08**	-5.73	-2.22
	RCP8.5, REF	-16.18	**-22.51**	-1.88	**-3.91**	-0.26	**-0.31**	-1.13	-6.83	-5.27	-0.10
European plaice	*RCP4.5, BSAP*	-6.52	-6.68	25.52	27.65	-0.18	-0.15	57.37	58.30	-57.43	-57.38
	RCP4.5, REF	-13.07	-12.24	24.46	26.85	-0.21	-0.15	52.06	53.83	-56.03	-56.09
	RCP8.5, BSAP	-6.15	-5.63	25.57	26.71	-0.19	-0.15	58.93	58.67	-57.38	**-57.72**
	RCP8.5, REF	-13.97	**-14.53**	**24.23**	26.40	**-0.26**	-0.16	**48.26**	50.39	-54.51	-56.11
WBS cod	*RCP4.5, BSAP*	-2.67	-1.36	**-0.06**	-0.01	**0.00**	**0.00**	-1.27	-1.81	-0.87	-0.43
	RCP4.5, REF	-2.63	-1.39	**-0.06**	-0.01	**0.00**	**0.00**	-1.45	-1.81	-0.83	-0.42
	RCP8.5, BSAP	-2.48	**-4.26**	-0.03	**-0.06**	**0.00**	0.01	-0.18	**-3.08**	-0.53	**-1.22**
	RCP8.5, REF	-2.54	-4.18	-0.03	**-0.06**	**0.00**	0.01	-0.36	**-3.08**	-0.53	-1.18

EBS cod	*RCP4.5, BSAP*	8.18	9.41	0.52	0.57	0.20	0.18	21.83	20.27	-6.73	-6.61
	RCP4.5, REF	**-1.33**	-0.08	0.48	**0.37**	0.17	**0.16**	19.78	18.61	**-7.16**	-7.09
	RCP8.5, BSAP	9.76	22.46	0.48	0.69	0.20	0.23	21.57	22.42	-6.33	-4.84
	RCP8.5, REF	**-0.12**	7.52	0.42	0.47	0.17	0.18	**18.12**	20.18	-6.20	-5.04
Whiting	*RCP4.5, BSAP*	-15.66	-5.44	0.39	2.77	-0.37	**-0.47**	-5.44	-3.70	5.44	**-8.01**
	RCP4.5, REF	**-17.72**	-5.96	-0.16	2.34	-0.34	-0.45	-5.63	-3.80	9.09	-6.43
	RCP8.5, BSAP	-13.84	-14.12	1.09	-0.04	-0.42	-0.42	-5.54	-9.76	1.58	5.25
	RCP8.5, REF	-16.08	-16.72	0.58	**-0.60**	-0.41	-0.40	-5.86	**-9.85**	2.42	7.16
Atlantic herring	*RCP4.5, BSAP*	**-5.15**	-5.12	**2.12**	**2.12**	-0.01	-0.01	-5.25	**-5.27**	**0.00**	0.02
	RCP4.5, REF	**-5.15**	-5.12	**2.12**	**2.12**	-0.01	-0.01	-5.25	**-5.27**	**0.00**	0.02
	RCP8.5, BSAP	**-5.15**	**-5.15**	**2.12**	2.13	-0.01	-0.01	-5.25	-5.23	0.01	0.01
	RCP8.5, REF	**-5.15**	**-5.15**	**2.12**	2.13	-0.01	-0.01	-5.25	-5.23	0.01	**0.00**
European sprat	*RCP4.5, BSAP*	**-16.30**	-14.80	-0.04	0.18	0.70	0.77	14.59	14.19	**-12.58**	-11.89
	RCP4.5, REF	-11.81	-8.94	-0.35	-0.20	0.58	0.61	16.34	15.84	-11.43	-10.60
	RCP8.5, BSAP	-13.61	-10.00	-0.03	-0.07	0.72	0.75	**13.87**	14.95	-11.74	-10.64
	RCP8.5, REF	-9.56	-4.58	-0.45	**-0.47**	**0.57**	0.58	15.69	16.91	-10.69	-9.81
Three-spined stickleback	*RCP4.5, BSAP*	16.76	-13.51	-1.90	0.58	-0.82	0.39	0.87	-4.52	-12.10	9.79
	RCP4.5, REF	14.25	**-15.99**	**-2.02**	0.49	-0.79	0.44	0.89	**-4.86**	-12.47	10.11
	RCP8.5, BSAP	4.33	12.11	0.02	-1.39	-0.10	**-0.92**	0.38	-0.87	-2.00	-15.72
	RCP8.5, REF	1.46	8.41	0.06	-1.27	-0.03	-0.86	0.47	-0.89	-1.46	**-16.00**

Table S2. Overview of the final SDMs' structure. "Train" denotes the training and "Test" the testing dataset, "SP" denotes spatial random effects, "SPT" spatiotemporal random effects, "Temp." temperature, "Sal." salinity, "Oxy." Oxy, "Chl." Chlorophyll *a*, "Hard bott." hard bottom complexes, and "Land." denotes landings. The numbers reported in the table represent coefficient estimates obtained from the models, those noted with "*****" and in bold are deem statistically significant ($p \leq 0.05$). Response curve types are written underneath covariate coefficients: "Sc" stands for S-shaped curve, "Cv" for convex, "Cc" for concave, and "Li" for linear curve. "Sm" stands for a smoother.

Model	*Modelling framework*	*Component*	*Distribution*	*Random effects*	*Temp.*	*Sal.*	*Oxy.*	*Chl.*	*Depth*	*Hard bott.*	*Mud*	*Land.*
Common dab	1-step	Occurrence	Bernoulli	None	**-0.34*** **Cv**	**2.75*** **Sc**	0.27 Cv	**0.55*** **Sc**	**-3.35*** **Sc**	-0.04 Li	**0.59*** **Cv**	
		Density	Lognormal		0.02 Li	**0.29*** **Cv**	**0.08*** **Li**	0.01 Li	-**1.08*** Cv	**0.08*** **Li**	**0.09*** **Li**	
European flounder	1-step	Occurrence	Bernoulli	SPT-AR1	**-0.85*** **Cc**	0.04 Li	**0.59*** **Cc**	0.12 Li	**-0.76*** **Cc**	-0.14 Li	0.14 Li	-0.03 Li
		Density	Lognormal		**-0.08*** **Li**	**0.22*** **Cv**	**0.05*** **Li**	**0.10*** **Cv**	**0.10*** **Cv**	0.01 Li	**0.05*** **Li**	-0.01 Li
European plaice	2-step	Occurrence	Bernoulli	SP + SPT-AR1	**0.42*** **Cc**	0.01 Li	**1.06*** **Sc**	-0.17 Li	**1.15*** **Sc**	0.18 Li	**0.19*** **Li**	
		Density	Lognormal	SPT-AR1	0.07 Sm	**0.24*** **Cv**	**0.17*** **Cv**	**0.04*** **Li**	**0.13*** **Li**	**0.07*** **Li**	0.01 Li	-0.05 Li

WBS cod	1-step	Occurrence	Bernoulli	SP	**-0.29*** **Cc**	0.29 Cc			2.74 Cc	0.38 Cc	0.08 Li
		Density	Gamma		**-0.04*** **Li**	0.08 Li			0.28 Li	-0.01 Li	-0.03 Li
EBS cod	1-step	Occurrence	Bernoulli	SPT-AR1	**1.01*** **Cc**		**1.49*** **Sc**	-0.09 Li		0.34 Cc	**0.86*** **Cc**
		Density	Lognormal		**0.25*** **Cv**		**0.17*** **Cv**	**-0.10*** **Cv**		0.00 Li	**0.04*** **Li**
Whiting	1-step	Density	Tweedie	None	**1.56*** **Sm**	**37.73*** **Sm**	**0.23*** **Cv**	**0.08*** **Cv**	-12.14 Sm	**0.08*** **Li**	**0.13*** **Li**
Atlantic herring	1-step	Occurrence	Bernoulli	SP		-0.41 Cc			**2.38*** **Cc**		
		Density	Gamma			0.01 Li			0.01 Li		
European sprat	1-step	Occurrence	Bernoulli	SPT-AR1	-0.50 Li	**-1.90*** **Cc**		2.52 Cc			
		Density	Gamma		**0.09*** **Li**	-0.02 Li		0.03 Li			
Three-spined stickleback	1-step	Occurrence	Bernoulli	None	**-2.57*** **Sc**	-126.60 Sm		-0.04 Li			
		Density	Lognormal		**-0.10*** **Li**	3.24 Sm		-0.05 Li			

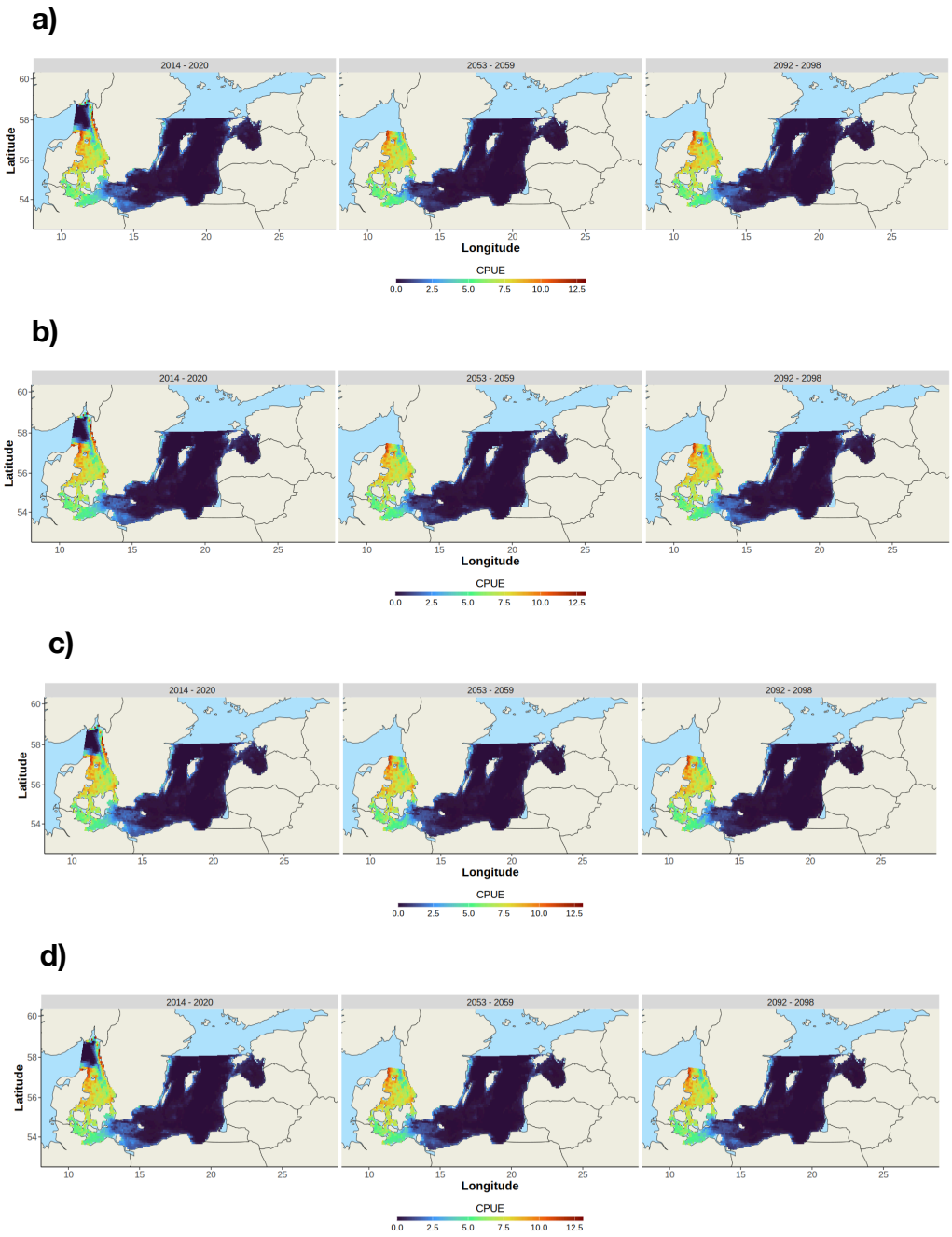


Figure S13. Predicted distribution (median CPUE) of the dab shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

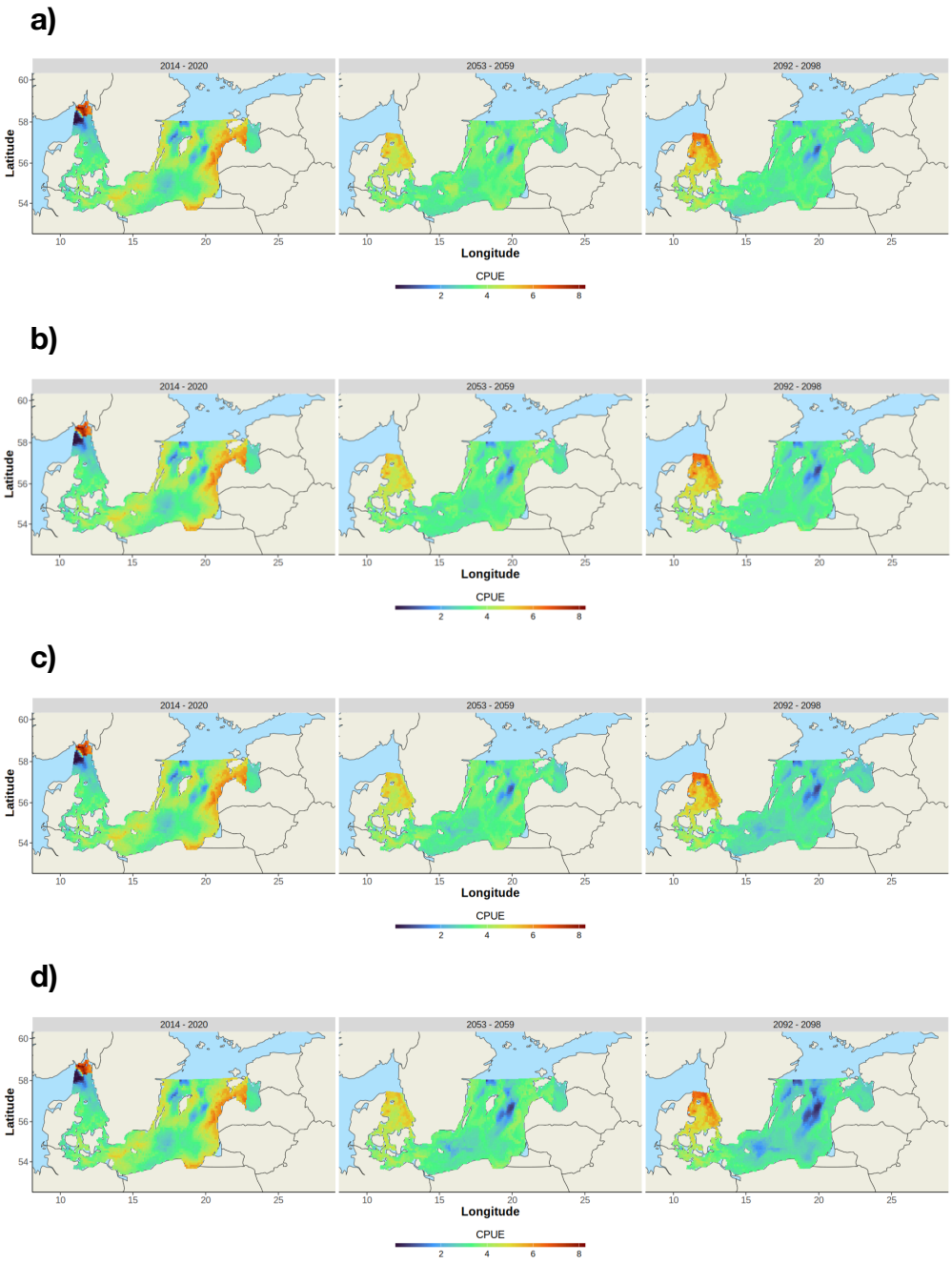


Figure S14. Predicted distribution (median CPUE) of the flounder shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

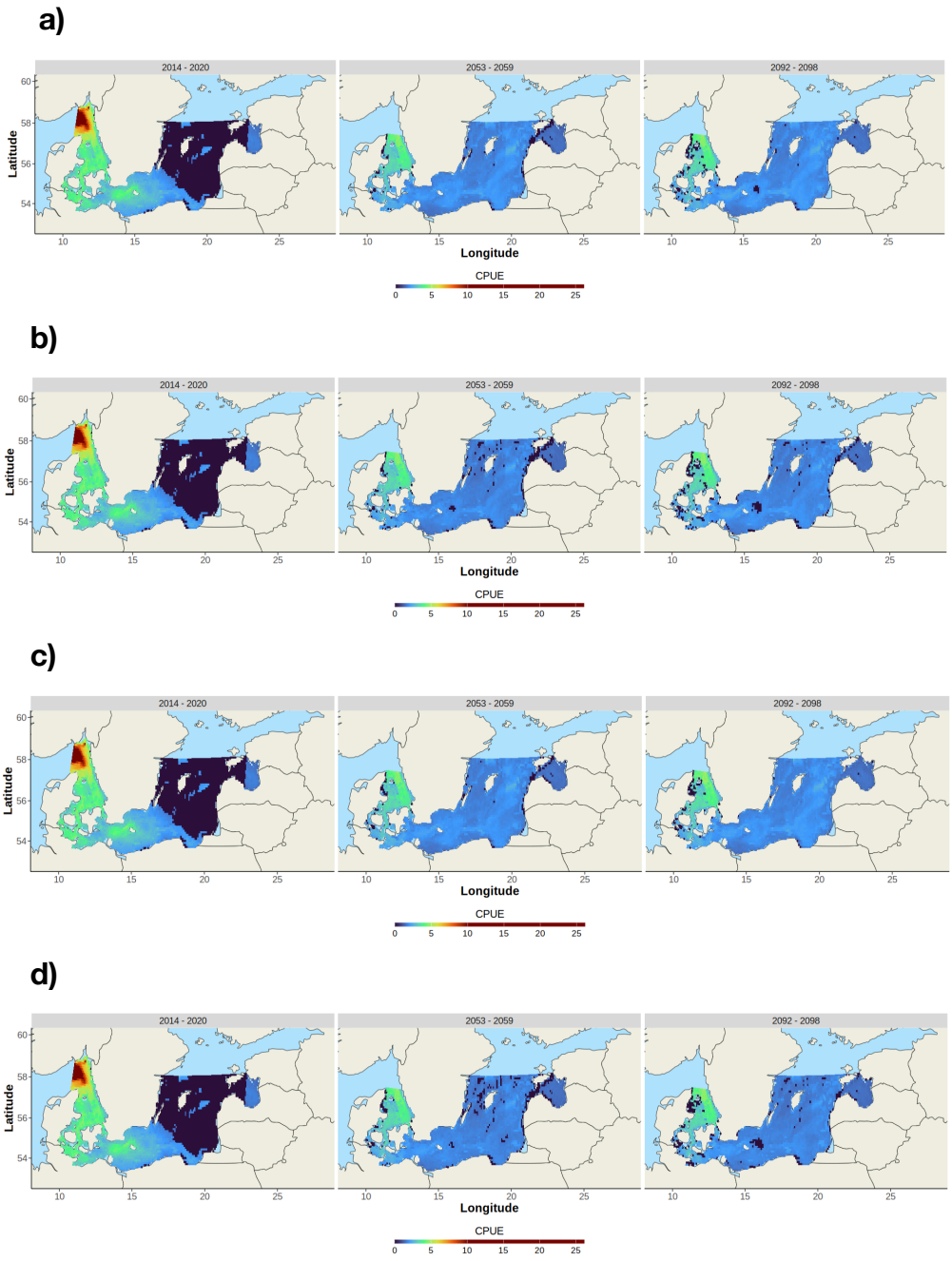


Figure S15. Predicted distribution (median CPUE) of the plaice shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios. The scale is adjusted to better highlight changes between periods.

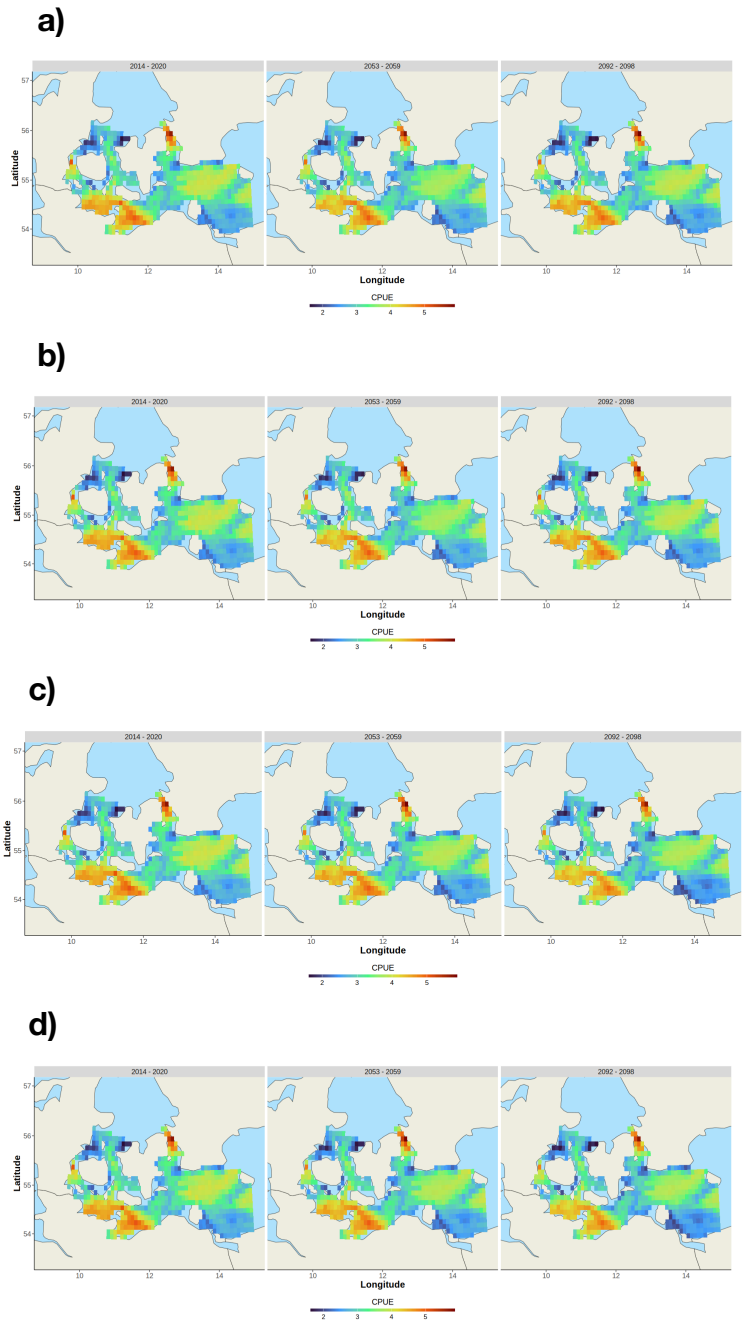


Figure S16. Predicted distribution (median CPUE) of the WBS cod shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

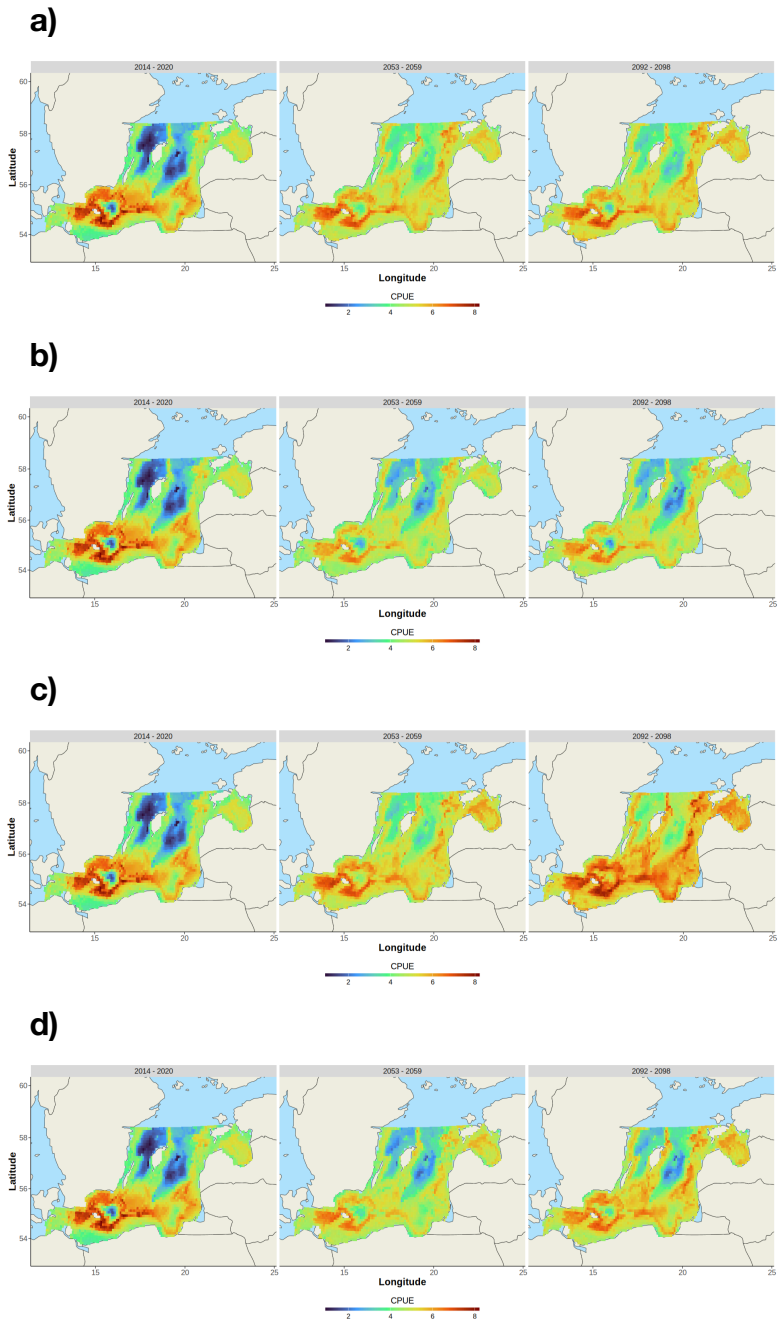


Figure S17. Predicted distribution (median CPUE) of the EBS cod shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

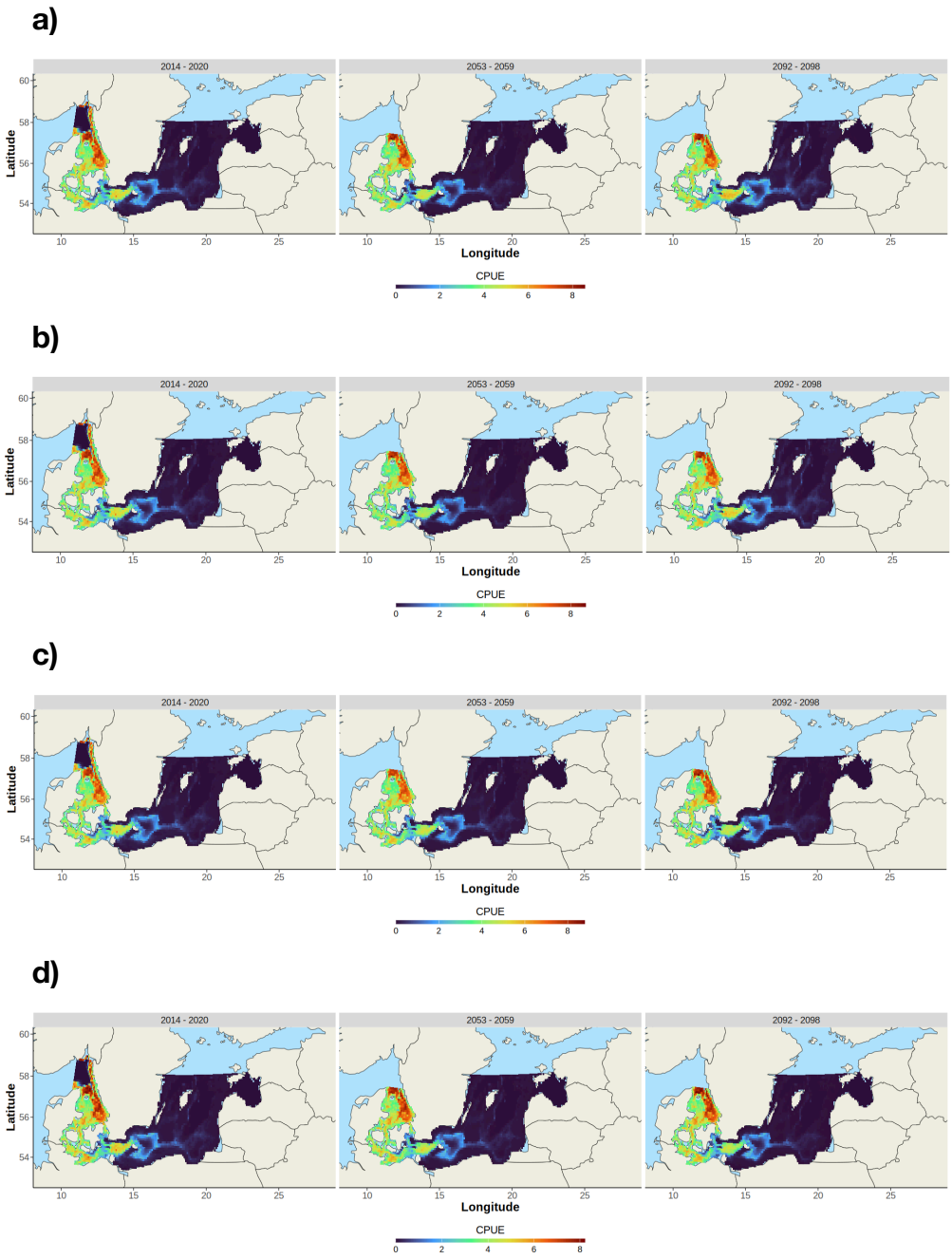


Figure S18. Predicted distribution (median CPUE) of the whiting shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

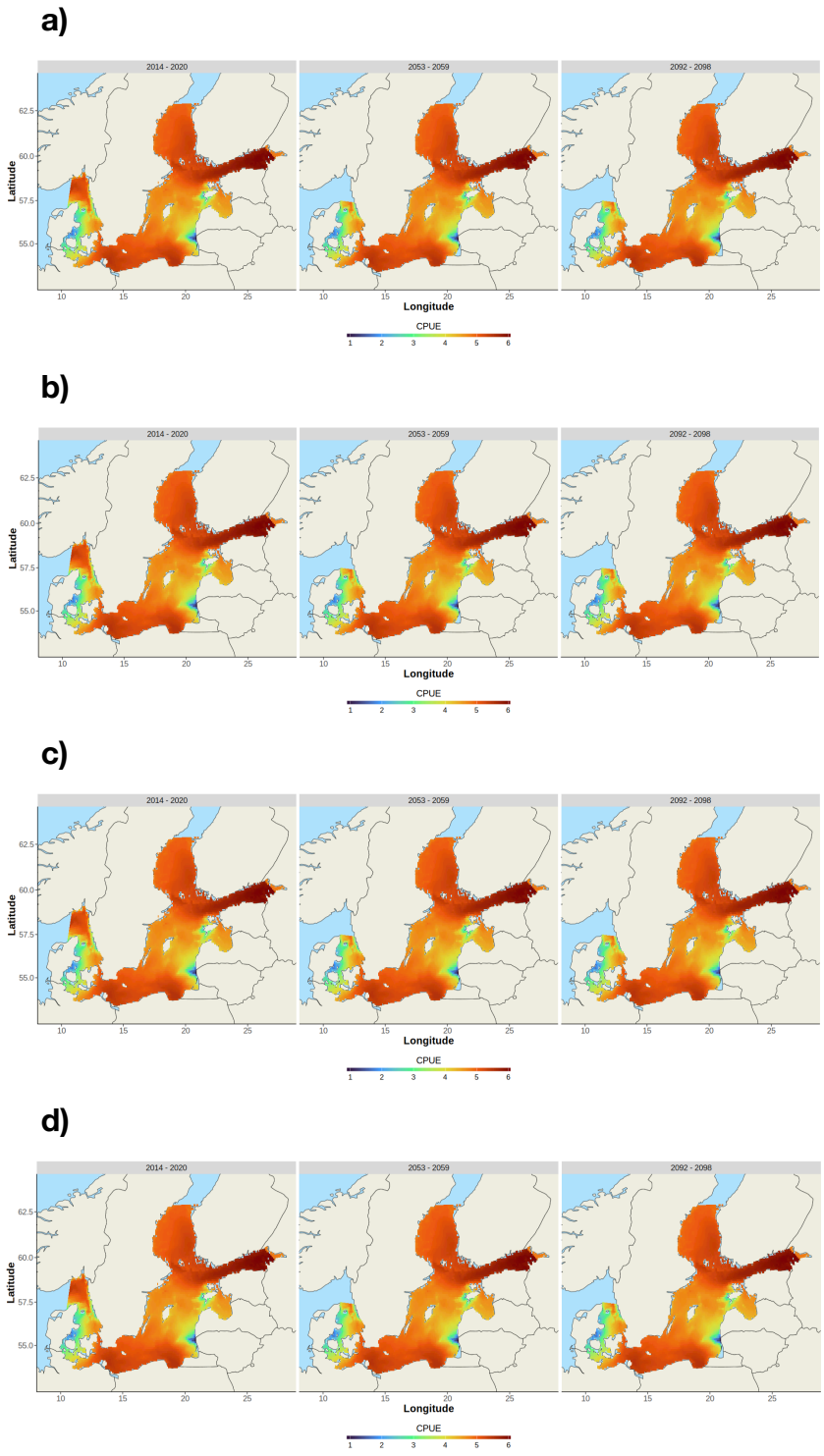


Figure S19. Predicted distribution (median CPUE) of the herring shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

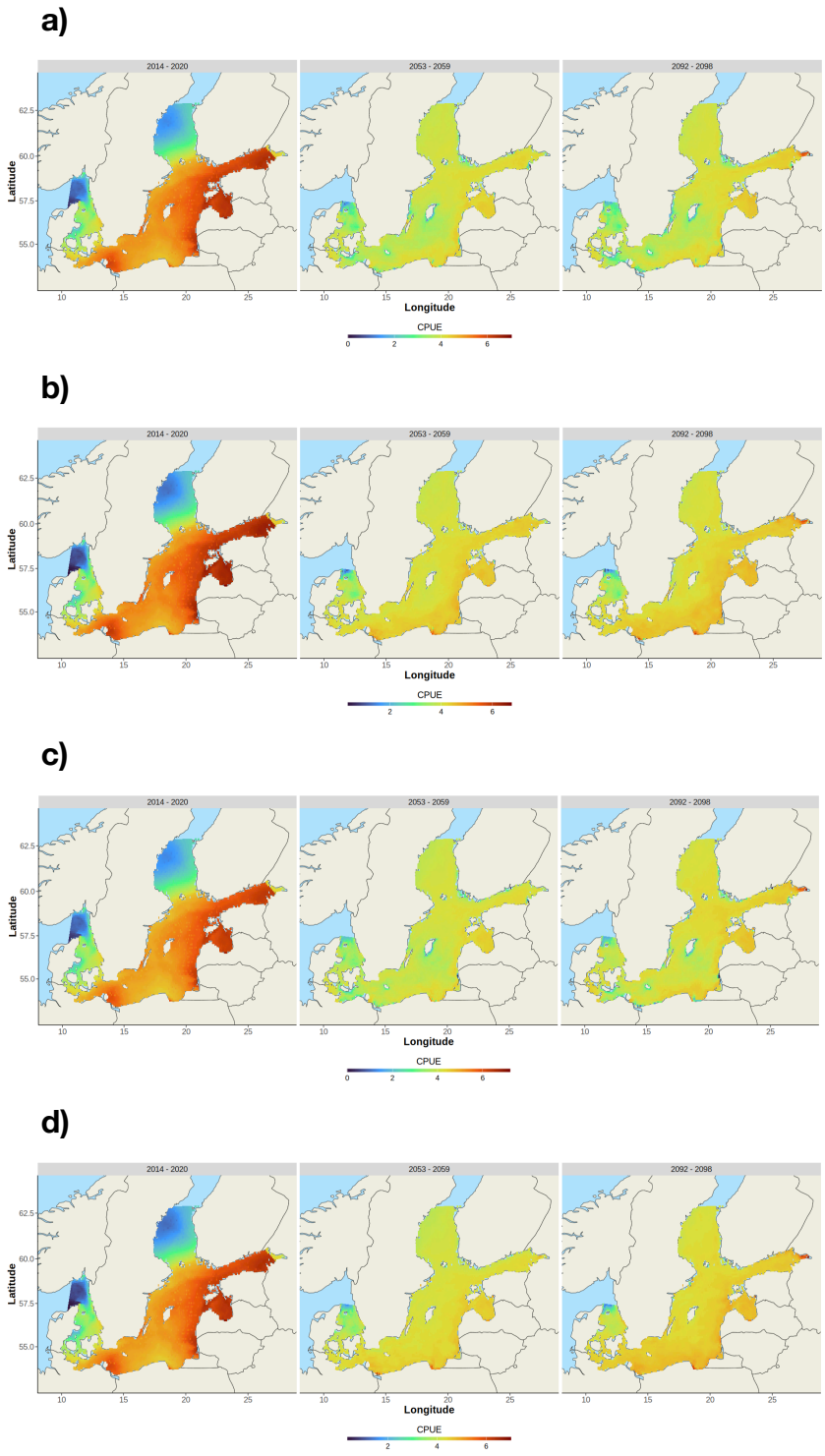


Figure S20. Predicted distribution (median CPUE) of the sprat shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios.

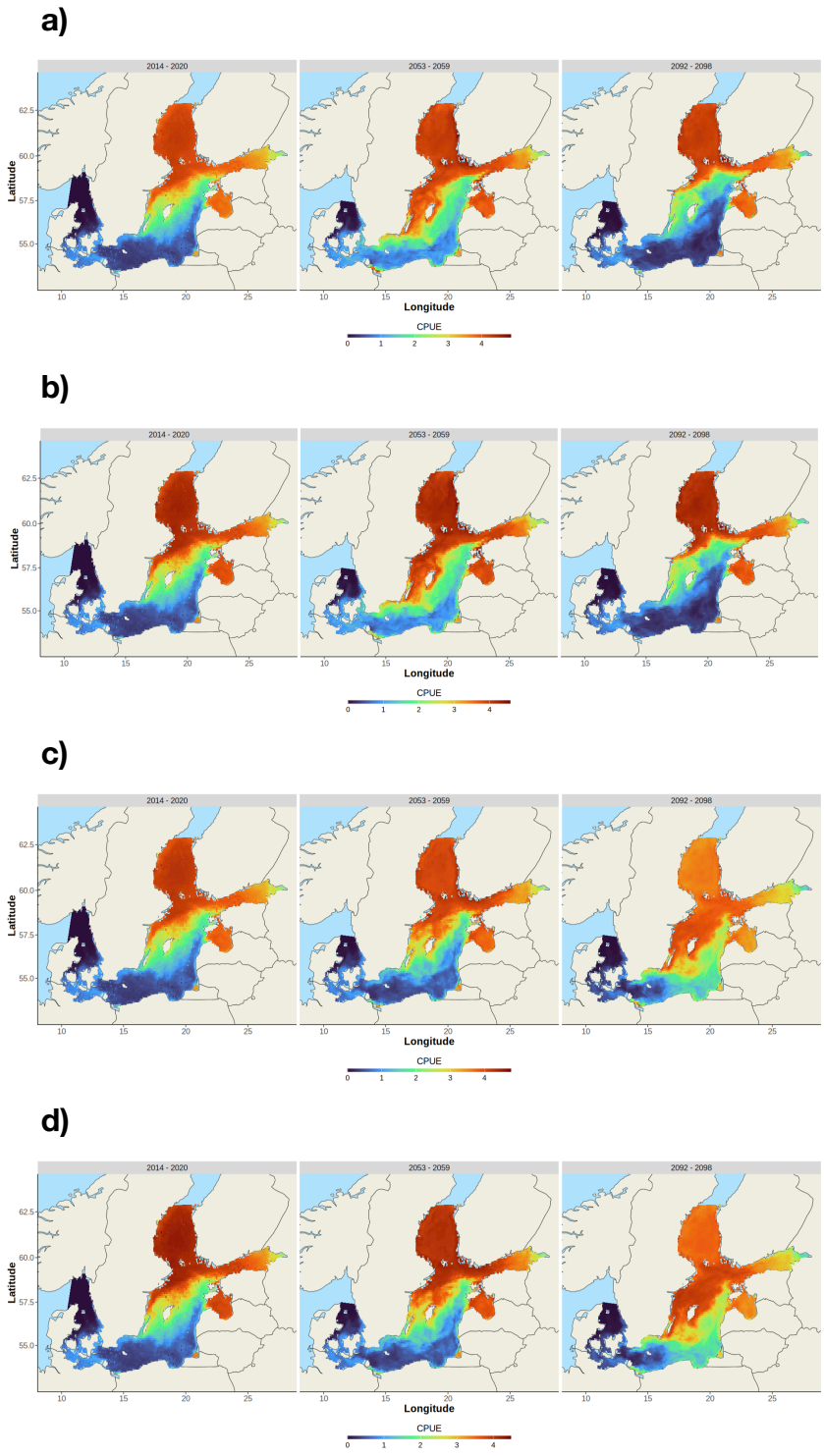


Figure S21. Predicted distribution (median CPUE) of the stickleback shown as median values in the baseline (2014-2020), middle of century (2053-2059), and end of century (2092-2098) under the: a) RCP4.5-BSAP, b), RCP4.5-REF, c) RCP8.5-BSAP, and d) RCP8.5-REF scenarios

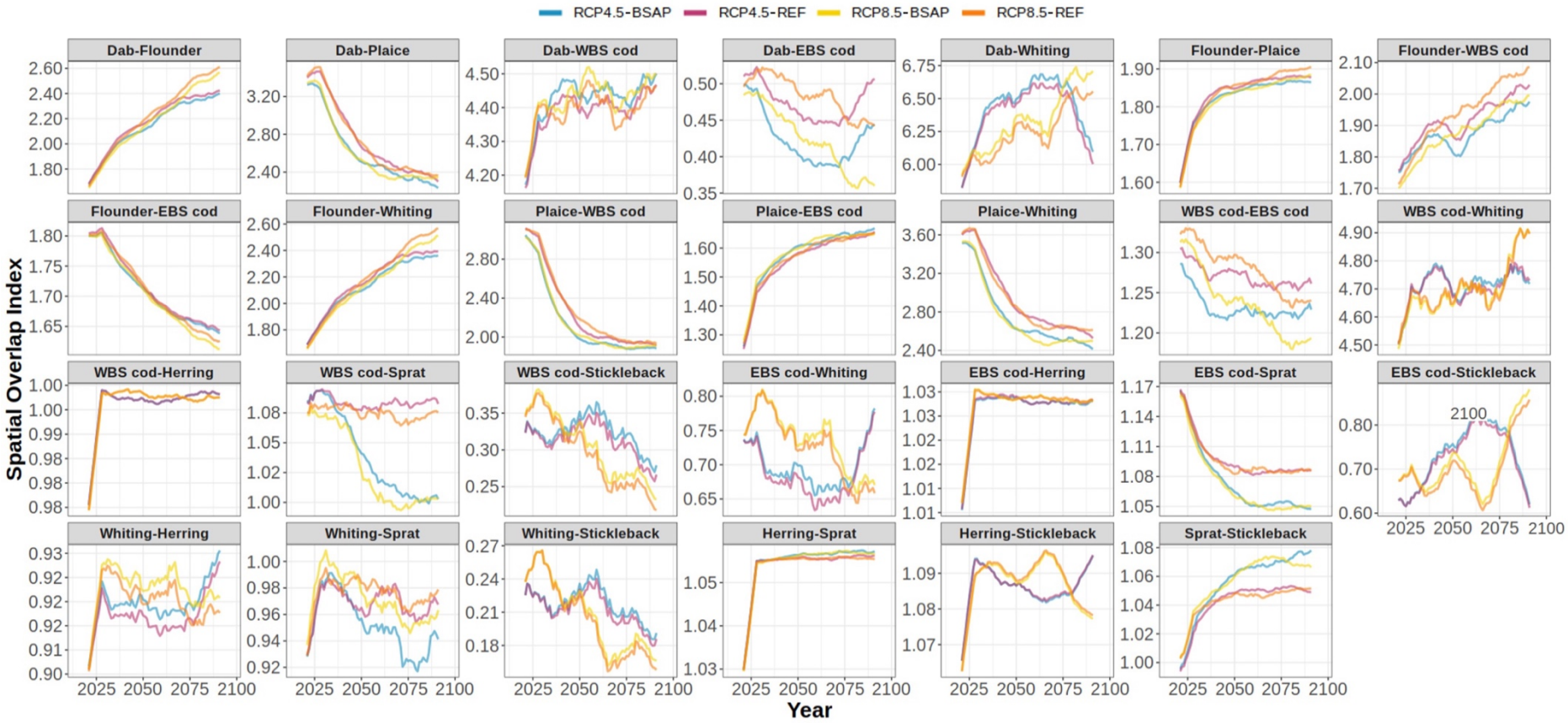


Figure S22. Overview of median interannual Spatial Overlap Index (SOI) presented as moving average (n = 15 years) across future scenarios.

CHAPTER 3

Potential mismatches between spatial protection and changing fish community structure and functioning in the Baltic Sea

Frane Madiraca[1], Christian Möllmann[1], and Saskia A. Otto[1]

[1] Institute of Marine Ecosystem and Fishery Science, Center for Earth System Research and Sustainability (CEN), Hamburg University, Hamburg, Germany

ABSTRACT

Climate change, eutrophication, and long-term exploitation have reshaped the Baltic Sea ecosystem, yet the consequences for fish community structure and functioning remain insufficiently resolved in space and time. Ecological state assessments typically rely on structural indicators and coarse spatial scales, potentially overlooking functional reorganization and fine-scale patterns that are relevant for management. In this study, we present a high-resolution spatiotemporal state assessment of the Baltic Sea fish community integrating both structural and functional indicators. Using two decades of standardized trawl survey data (2001-2020), we applied a quantitative selection framework to identify a complementary suite of six structural and four functional indicators and modelled their dynamics using spatially explicit generalized linear mixed models based on the Stochastic Partial Differential Equation (SPDE) approach. Multiple Factor Analysis (MFA) showed that structural and functional indicators contributed similarly to major axes of variation, demonstrating that both dimensions capture distinct components of community change. We mapped changes in the cumulative community state between an early (2001-2005) and a late period (2016-2020) and overlaid these patterns with existing Marine Protected Areas and current and planned offshore wind farms. Several large regions, particularly in the western and central Baltic Sea, exhibited pronounced community change yet

lacked spatial protection and are projected to undergo substantial wind-farm expansion. Our results highlight spatial mismatches between ecological change and current management footprints, underscore the value of combining structural and functional indicators at fine spatial scales, and identify priority areas where future conservation and spatial planning efforts may need to focus.

Keywords: Baltic Sea, climate change, eutrophication, fish community, ecological indicators, functional ecology, state assessment, marine protected area, wind farm

INTRODUCTION

Aquatic ecosystems worldwide are increasingly exposed to multiple stressors, most prominently climate change, overfishing, and eutrophication. These pressures drive both structural changes, such as shifts in species composition and biomass, and functional changes that affect trophic interactions and ecosystem processes (Hollowed *et al.*, 2013; Vergés *et al.*, 2014; Link and Watson, 2019; Mbaru *et al.*, 2020; Willis *et al.*, 2022; Nagelkerken *et al.*, 2023; Priya *et al.*, 2023). Understanding these dual dimensions is essential, as management frameworks such as ecosystem-based management (EBM) and maritime spatial planning (MSP) increasingly require knowledge that links ecological changes to ecosystem services, fisheries production, and conservation targets (Domínguez-Tejo, 2016; Lowerre-Barbieri *et al.*, 2019). Yet, ecological assessments still rely predominantly on structural indicators, potentially overlooking functional dynamics that are critical for ecosystem resilience and stability. In this context, the development and application of robust indicators has become a central task in marine science and policy, as they provide the link between ecological understanding and actionable management targets (Kershner *et al.*, 2011; Queirós *et al.*, 2016).

The Baltic Sea is a clear example of a system where multiple pressures and competing human interests converge in a restricted marine area, making it a central case study for EBM and MSP. Over recent decades, the region has undergone pronounced ecological shifts due to warming, eutrophication, hypoxia, and long-term

overexploitation (Conley *et al.*, 2007; Belkin, 2009; Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020). Its strong salinity gradient from southwest to northeast supports a unique mixture of marine and freshwater species (Frelat *et al.*, 2018), but also constrains their distributions. Commercially and ecologically important species such as cod and herring have collapsed or sharply declined (Fey *et al.*, 2014; Sguotti *et al.*, 2019; Bryhn *et al.*, 2022; ICES, 2024) while others, including sprat and several coastal species, have expanded. Distributional shifts and altered overlap patterns among species have been documented (Orio *et al.*, 2019, 2020; MacNeil *et al.*, 2025), with potential implications for food web dynamics. Beyond taxonomic change, functional traits of fish communities have also shifted in response to environmental change (Pecuchet *et al.*, 2020), in line with observations from other European marine ecosystems (Beukhof *et al.*, 2019b; Receveur *et al.*, 2024). Together, these concurrent structural and functional alterations highlight that community dynamics cannot be fully understood from a taxonomic perspective alone.

Recognizing both structure and function is equally critical for state assessments, which form a cornerstone of EBM and underpin policy frameworks such as the Marine Strategy Framework Directive (MSFD) (Smit *et al.*, 2021). These assessments rely on ecological indicators satisfying certain criteria to evaluate ecosystem condition and inform management decisions (Otto *et al.*, 2018; Smit *et al.*, 2021). In practice, however, most assessments have focused on structural indicators such as abundance, biomass, or taxonomic diversity, offering only indirect appraisals of ecosystem functioning (Smit *et al.*, 2021). Functional indicators, derived from species traits such as trophic level, fecundity, or maximum body size, offer complementary insights into biodiversity–ecosystem functioning relationships (Mouchet *et al.*, 2010). Although trait-based approaches are increasingly used in the Baltic (Törnroos *et al.*, 2019; Pecuchet *et al.*, 2020), studies with high spatiotemporal resolution, such as Frelat *et al.* (2018), remain rare. As a result, most existing assessments of the Baltic Sea fish community still focus on single species or aggregated biomass trends and are conducted at coarse spatial scales (Blenckner *et al.*, 2021; HELCOM, 2023). This risks masking fine-scale spatiotemporal heterogeneity within large marine ecosystems, such as the Baltic Sea, and limits our understanding of how the fish

community as a whole—beyond dominant stocks—has responded to combined pressures.

Capturing spatiotemporal dynamics at fine resolution is particularly important for spatial management, as the effectiveness of Marine Protected Areas (MPAs) (Maestro *et al.*, 2019) and fisheries closure areas (Wright *et al.*, 2015) depends on detailed knowledge of how fish communities change in space and time. Currently, 16.5% of the Baltic Sea is covered by the Baltic network of MPAs, including slightly above 13% classified as HELCOM MPAs (HELCOM, 2023). Although their designation incorporates multiple ecological criteria, they primarily reflect structural biodiversity features and do not explicitly incorporate functional aspects of fish communities (HELCOM, n.d.). At the same time, offshore wind farm development is accelerating across European waters to support decarbonization targets (European Environment Agency, 2024). While turbines may create reef-like structures that can locally benefit certain demersal species, their broader ecosystem effects remain poorly understood and may interact with other human uses such as shipping and fishing (Knorrn *et al.*, 2024). These developments create a pressing need for assessments that explicitly link ecological change with spatial management instruments. Earlier analyses indicate that several dominant fish species in the Baltic Sea have already undergone significant distributional shifts, resulting in altered spatial overlap (**Chapter 1**), and that further changes are expected under future climate and nutrient scenarios (**Chapter 2**).

Building on these findings, we here extend the focus from selected key species to the entire fish community. Using two decades of standardized trawl survey data (2001-2020), we first establish a suite of ecological indicators that jointly capture structural and functional aspects of the Baltic Sea fish community based on a quantitative selection framework and ecological theory (Otto *et al.*, 2018). We then use these indicators to investigate spatiotemporal community dynamics and link emerging patterns to management by comparing them with the location of HELCOM Marine Protected Areas (MPAs), Baltic Sea fisheries closure areas, and planned offshore wind farms. Specifically, we aim to i) compare the performance of structural and

functional indicators and establish a final suite that is complementary and representative of both aspects of the fish community, ii) analyze how this suite of indicators has changed over the past two decades at high spatiotemporal resolution, including a quantification of the relative contributions of structural vs. functional indicators, and iii) evaluate whether areas of major community change overlap with the mentioned protected areas or planned wind farms, thereby assessing the adequacy of current spatial protection measures and highlighting needs for adaptive management. Our work thus provides a framework for integrating structural and functional perspectives into community assessments, delivering insights that are directly relevant for spatial management in the Baltic Sea and transferable to other marine ecosystems.

MATERIALS AND METHODS

Data and data processing

Trawl survey data

We used data from the Baltic International Trawl Survey (BITS), a multi-decadal program coordinated by the International Council for the Exploration of the Sea (ICES) (ICES, 2017). Since 2001, BITS has followed a harmonized sampling design and gear protocol, providing standardized information on the distribution and abundance of demersal and benthopelagic fish in the Baltic Sea. Sampling is conducted twice per year, in quarter 1 (15 February - 31 March) and quarter 4 (primarily November, with additional samplings in October and December, and occasional sampling in September). Hauls were performed with standardized demersal otter trawl gears (TVL 930 meshes, TVS 520 meshes) at an average speed of 3 knots and with a mean duration of 30 minutes.

We used data from 2001-2020 and excluded hauls with durations shorter than 15 minutes, missing depth information, and those carried out in September due to inconsistent sampling. The final dataset comprised 10,489 valid hauls, corresponding to an average of 524 hauls per year, and covering ICES subdivisions 21 (Kattegat) to 29 (northern Baltic Proper). Standardized catch per unit of effort (CPUE) was pooled

across juvenile and adult individuals and aggregated by species. The dataset was accessed through the ICES Database on Trawl Surveys (DATRAS) (https://datras.ices.dk; accessed 02 June 2023).

Trait data

To calculate functional indicators, we compiled species trait information for 87 fish species recorded in the survey. Trait data were primarily obtained from a published dataset (Beukhof *et al.*, 2019a) and FishBase (Froese and Pauly, 2024). Since trait data from the Baltic Sea was largely limited in scope compared to that from North Sea populations of the same species, we decided to use the latter. This decision was made due to the proximity of the two ecosystems and the same 87 species being present in both. We initially collected 18 traits (Table S1, Supplementary material), including morphological, reproductive, and ecological characteristics. Missing values for eye diameter were inferred by visual analysis of photographs sourced from FishBase (Froese and Pauly, 2025; Table S2, Supplementary material) in the Affinity Photo 2 software (Serif, 2023). Following collinearity screening (Pearson's $R > 0.7$) and to ensure a balanced representation of different facets of fish biology and ecology, we retained nine traits: mouth position, trophic level, habitat, growth coefficient, spawning type, fecundity, fin shape, aspect of ratio of caudal fin and maximum length.

Environmental and landings data

We included several environmental and anthropogenic variables with known or potential effects on fish community structure and functioning. Hydrographic variables (temperature, salinity, and oxygen concentration) and chlorophyll *a* (as a proxy for primary productivity and prey availability) were extracted from the Copernicus Marine Environmental Service (CMEMS). These products are derived from the coupled NEMO-Nordic ice-ocean and Swedish Coastal and Ocean Biogeochemical (SCOBI) models (Eilola *et al.*, 2009; Liu *et al.*, 2017) and provided as monthly means with a horizontal resolution of 1 nautical mile and 56 vertical layers. For our analysis, we calculated the median values for the bottom 5 meters. All variables were aggregated to the same 0.1° x 0.1° spatial grid used for the indicator data. To account for fisheries

exploitation, we used annual, spatially non-resolved landings data for the Baltic Sea ecoregion extracted from the ICES fisheries overview report (ICES, 2022), lagged by one year to capture delayed community responses.

Prior to analysis, all variables were normalized to a mean of zero and a standard deviation of one. Collinearity among candidate covariates was evaluated, and variables with strong correlations (Pearson's $R > 0.7$) or variance-inflation factors (VIF) > 10 were excluded.

Indicator calculation

We calculated 32 ecological indicators describing structural and functional aspects of the fish community (Table 1). Structural indicators comprised abundance-, diversity-, and length-based metrics (e.g. species richness, Shannon's diversity, Large Fish Index), while functional indicators were derived from trait-based measures of functional diversity and community-weighted mean traits (e.g. trophic level, fecundity). Indicators were calculated using CPUE data of the same species across both indicator types to ensure consistency. All indicators were aggregated to monthly medians values per per $0.1° \times 0.1°$ grid cell and year.

Table 1. Overview of considered indicators with relevant information including including their full name, abbreviation, indicator type, and meaning. CPUE stands for Catch Per Unit of Effort - a proxy measurement of abundance. CWM stands for community-weighted mean. Indicators in bold are the ones that were chosen following the selection process.

Indicator	*Abbreviation*	*Type*	*Subgroup*	*Meaning*
Mean CPUE	mCPUE	Structural	Abundance	Mean CPUE of all fish.
Pleuronectiformes CPUE	**Pleuro**	**Structural**	**Abundance**	**Median CPUE of pleuronectiformes.**
Gadiformes CPUE	**Gadi**	**Structural**	**Abundance**	**Median CPUE of gadiformes.**
Clupeiformes CPUE	**Clupei**	**Structural**	**Abundance**	**Median CPUE of clupeiformes.**
Dab CPUE	Dab	Structural	Abundance	Median CPUE of common dab.
Flounder CPUE	Flounder	Structural	Abundance	Median CPUE of European flounder.
Plaice CPUE	Plaice	Structural	Abundance	Median CPUE of European plaice.
Cod CPUE	Cod	Structural	Abundance	Median CPUE of Atlantic cod.
Whiting CPUE	Whiting	Structural	Abundance	Median CPUE of whiting.
Herring CPUE	Herring	Structural	Abundance	Median CPUE of Atlantic herring.
Sprat CPUE	Sprat	Structural	Abundance	Median CPUE of European sprat.

Species richness	SRic	Structural	Diversity	Number of species.
Shannon's diversity	**Shannon**	**Structural**	**Diversity**	**Measurement of species diversity in a community (sample in this study) (Shannon, 1948; Magurran, 2003).**
Pielou's evenness	**Pielou**	**Structural**	**Diversity**	**Measurement of how evenly species are distributed in a community (sample in this study) (Pielou, 1966; Magurran, 2003).**
Average length	avgL	Structural	Length	Average length of all fish.
Large Fish Index of all fish over 30 cm	**LFI 30**	**Structural**	**Length**	**Proportion of fish over 30 cm (Oesterwind *et al.*, 2013) for the whole community.**
Large Fish Index of only cod over 30 cm	LFI 30 – COD	Structural	Length	Proportion of fish over 30 cm (Oesterwind *et al.*, 2013) only for cod.
Large Fish Index of all fish except cod over 30 cm	LFI 30 - NOCOD	Structural	Length	Proportion of fish over 30 cm (Oesterwind *et al.*, 2013) for the whole community with cod excluded.
Functional richness	**Fric**	**Functional**	**Diversity**	**Amount of functional space filled by the community (Villéger *et al.*, 2008).**
Functional evenness	**FEve**	**Functional**	**Diversity**	**Evenness of abundance distribution in a functional trait space (Mason *et al.*, 2005).**
Functional divergence	**FDiv**	**Functional**	**Diversity**	**Relates to how abundance is distributed within the volume of functional trait space occupied by species (Villéger *et al.*, 2008).**
Functional dispersion	FDis	Functional	Diversity	Represents the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species (Laliberte and Legendre, 2010).
Rao's quadratic entropy	RaoQ	Functional	Diversity	A measure of functional diversity based on multiple traits (Botta-Dukát, 2005).
Functional redundancy	Fred	Functional	Diversity	Represents the ability of the community to maintain ecological processes via species performing similar functions (Ricotta *et al.*, 2016).
Functional imbalance	FImb	Functional	Diversity	Alternative to FEve; indicator of the strength of interaction between species abundances and their functional dissimilarities (Ricotta, 2022).
Functional group 1 abundance	FG1a	Functional	Abundance	CPUE of species in functional group 1.
Functional group 2 abundance	FG2a	Functional	Abundance	CPUE of species in functional group 2.

CWM trophic level	CWM – TL	Functional	Individual trait	Community weighted mean of the trophic level trait in the fish community.
CWM growth coefficient	CWM – GC	Functional	Individual trait	Community weighted mean of the growth coefficient trait in the fish community.
CWM fecundity	CWM – Fec	Functional	Individual trait	Community weighted mean of fecundity in the fish community.
Caudal fin aspect ratio	CWM – AR	Functional	Individual trait	Community weighted mean of the caudal fin aspect ratio trait in the fish community.
CWM maximum length	**CWM - MaxL**	**Functional**	**Individual trait**	**Community weighted mean of the maximum length trait in the fish community.**

Data analysis and modelling approach

To link ecological dynamics with management needs, we designed a multi-step analytical framework that combined indicator selection, spatiotemporal modelling, multivariate integration, and spatial overlay with management measures (Figure 1).

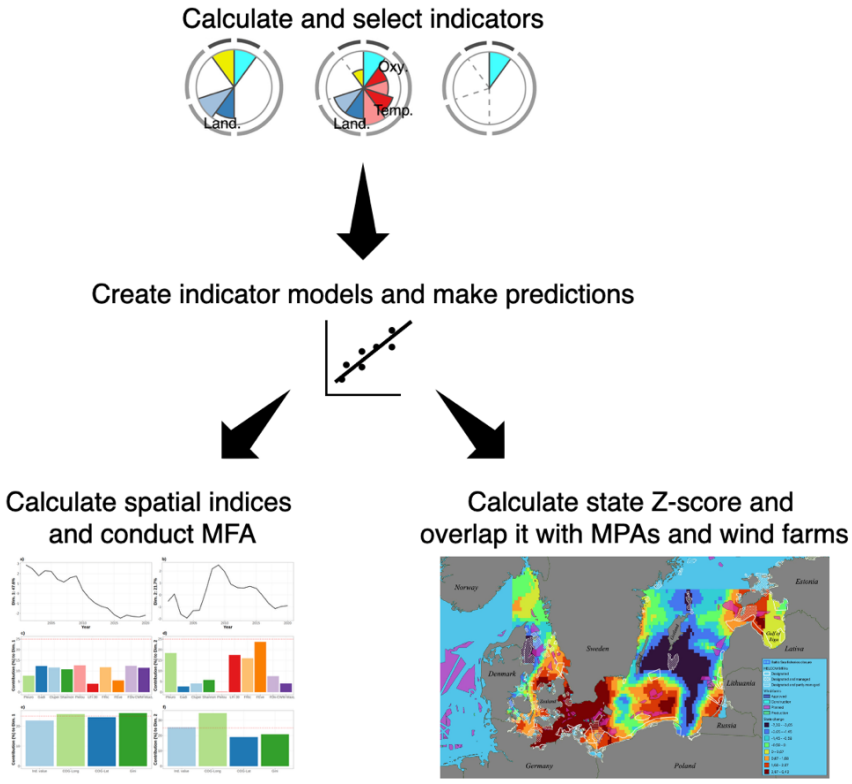


Figure 1. Overview of the study approach which includes calculation and selection of indicators, creation of spatiotemporal models used for further inference and predictions, calculation of spatial indices time series and their analysis via Multiple

Factor Analysis (MFA), and calculation of a Z-score based spatiotemporal state assessment and its overlap with marine protected areas (MPAs) and wind farms.

Indicator performance evaluation and selection

Indicators were evaluated using the protocol by Otto *et al.* (2018) implemented via the *INDperfrom* R package, which scores indicators based on sensitivity to pressures, responsiveness to trends, robustness, and management relevance. Because the protocol is designed for time series, indicators were aggregated to annual mean values prior to evaluation. Several indicators were transformed to improve distributional properties (Supplementary material – Indicator transformation). To avoid redundancy and ensure complementary ecological information, comparisons of indicator performance were conducted within the two main types (structural vs. functional) and their respective subgroups as defined in Table 1. Functional group abundances were treated as structural indicators due to their taxonomic basis. In addition to protocol scores, ecological relevance and management interpretability were considered when establishing the final indicator suite.

Dynamic Spatiotemporal Models

Selected indicators were modeled using Generalized Linear Mixed Effects Models (GLMMs) with spatial spatiotemporal random fields, implemented in the R package *sdmTMB* (Anderson *et al.*, 2022). This framework accounts for dependencies that arise from missing covariates or inherent spatial and temporal structures The model setup closely followed **chapter 1** and **chapter 2**. Models were trained on data from 2001-2017 and evaluated on out-of-sample test data from 2018-2020. Covariate selection and the final model structure (with or without random fields) were based on predictive performance, measured by the Normalized Root Mean Squared Error (NRMSE) of the testing set. Model convergence was checked using diagnostic functions provided in *sdmTMB*. Non-convergent models were refitted using smoother terms to capture non-linear effects. Models that remained unstable were excluded from further analysis.

Model outputs and integration

To investigate the joint dynamics of the fish community, we summarized the spatiotemporal model predictions of each indicator, aggregated to mean monthly values per year and grid cell, into four spatial indices: the mean estimated value (Ind. value), the center of gravity in latitude and longitude (COG - Long and COG - Lat) (Woillez *et al.*, 2009), and the Gini index of aggregation (Gini) (Gini, 1912), which we use to summarize the aggregation of the calculated ecological indicators, with a value of zero representing perfect distributional equality and a value of one representing maximum inequality. All indices were normalized to zero mean and unit variance prior to the analysis. We conducted a single Multiple Factor Analysis (MFA; Abdi *et al.*, 2013) based on the four spatial indices derived for each final indicator. The MFA was used to identify the indicators that most strongly contributed to the spatiotemporal changes and to assess whether indicators clustered according to the type of spatial change they captured (e.g. shifts in center of gravity vs. changes in aggregation). By calculating the contributions of structural against functional indicators as groups, we further assessed whether our framework appropriately captured both structural and functional aspects of fish community.

To evaluate how cumulative community change aligns with spatial management, we first transformed spatiotemporal predictions of each indicator to Z-scores and summed them to derive a cumulative community state score resolved in space and time. Mean state scores were calculated for an early (2001-2005) and a late period (2016-2020), and their differences were mapped across the study area. These patterns of community state change were then overlaid with spatial layers of HELCOM-designated MPAs (HELCOM, 2023) [Date accessed: 28.04.2025], Baltic Sea fisheries closure areas (HELCOM, 2008), and current and planned offshore wind farms (EMODnet, 2024) [Date accessed: 28.04.2025]. Cod fisheries closure areas were excluded because they apply to a single species only. This procedure allowed us to identify areas where fish community change may not be adequately addressed by current or proposed spatial management.

All data analysis and modelling was performed in R Programming Language (R Core Team, 2023, version 4.3.1). The cleaned datasets and R-scripts with details on used packages will be made available upon successful publishment of this article at https://github.com/franemadiraca/.

RESULTS

Final indicator suite and key drivers

From the 32 calculated indicators, we selected 10 that best captured complementary aspects of the Baltic Sea fish community (Table 1; Figure S1, Supplementary material). The final suite contained six structural and four functional indicators, representing both taxonomic composition and trait-based functioning. All selected indicators showed clear long-term trends, confirming their suitability for tracking persistent changes in the fish community.

The selected structural indicators capture abundance and composition across dominant taxonomic groups (Pleuro, Gadi, and Clupei), as well as diversity and size structure. Shannon diversity and Pielou showed high sensitivity and low redundancy, while order-level CPUE proved more robust to community-wide change than single-species metrics. LFI 30 was the only retained indicator from the length-based subgroup. It provides more comprehensive information than the alternative LFI metrics, as it encompasses all species in the community above the threshold size. Compared with the avgL indicator, it was preferred because the LFI indicator is specifically designed for use in HELCOM assessments (Casini and Larson, 2013) and therefore offers both ecological interpretability and direct management relevance. The functional indicators comprised FRic, FEve and FDiv - the three complementary dimensions of functional diversity (Villéger *et al.*, 2008) - together with the CWM - MaxL, a trait (maximum length) that integrates life-history strategies and is intuitively interpretable.

By combining two complementary approaches, we were able to disentangle the drivers of long-term interannual dynamics from those shaping spatial patterns. The

INDperform analysis, based on spatially aggregated time series, highlighted pressures most likely responsible for persistent temporal trends. In contrast, the spatiotemporal models (*sdmTMB*) identified the environmental gradients structuring spatial dynamics of community indicators over time. The temporal analysis indicated that fishing pressure (landings) and primary productivity (chlorophyll *a*) were more consistently linked to long-term dynamics than hydrographic conditions. Landings influenced four of the final indicators, while chlorophyll *a* affected three (Table 2). In contrast, temperature and oxygen explained trends in only two indicators each, suggesting that hydrography played a more limited role at the aggregated temporal scale. For Gadi, Clupei, and FDiv, however, no clear temporal driver could be identified, underlining that parts of the observed community change remain unexplained.

The spatiotemporal models consistently identified temperature, oxygen, and chlorophyll *a* as the most important drivers structuring spatial changes over time. Temperature was significant in seven of the ten models, oxygen and chlorophyll *a* in five each, and salinity in three (Table 2). Landings were never identified as significant spatial drivers, which is not unexpected given that the variable entered the models only as a spatially aggregated time series rather than with local variation. Chlorophyll *a* was particularly influential for Clupei and several functional indicators, while salinity structured distributions of Pleuro and FDiv. Pielou showed no significant covariates, yet the model still performed well, suggesting that spatiotemporal random effects effectively captured unobserved drivers. Overall, the final models showed strong predictive performance with high accuracy (Table S3, Supplementary Material). All included either AR1 or IID spatiotemporal random fields, and the LFI 30 included both spatial and spatiotemporal AR1 fields. A small fraction of negative predictions occurred in four models (Pleuro, Gadi, Shannon, and FRic), but these accounted for ≤ 3.2% of values and were truncated to zero to avoid biologically implausible outputs.

Table 2. Overview of the final models' structure. "Temp." denotes temperature, "Sal." salinity, "Oxy." Oxy, "Chl." Chlorophyll *a*, and "Land." denotes landings. The numbers reported in the table represent coefficient estimates obtained from the models, those noted with "*" and in bold are deem statistically significant ($p \leq 0.05$).

Indicator	*Covariates determining temporal indicator dynamics (INDperform)*	*Covariates in spatiotemporal models*				
		Temp.	*Sal.*	*Oxy.*	*Chl.*	*Land.*
Pleuro	**Temp.**, Land.	**0.14***	**0.61***	-2.45		
Gadi		**0.21***	-0.17	**29.40***		
Clupei		**0.09***		**0.20***	**-0.07***	
Shannon	Land.	**0.04***	**0.13***	**0.05***	0.01	
Pielou	Chl.				-0.00	0.00
LFI 30	Oxy.	**-0.05***		0.01	**-0.04***	
FRic	**Temp.**, Oxy., Land.	**0.00***	**-0.18***	0.00	**0.01***	
FEve		**-0.02***		**-0.03***		
FDiv	**Chl.**		-0.00	**0.02***	**-0.01***	0.00
CWM - MaxL	**Chl.**, Land.			0.01	**0.02***	

Changes in indicator patterns

Overall spatial indices of used indicators show highly varied development over time. Indicator value rises for Pleuro, Clupei, Shannon, FRic and decreases for other. COG - Long values indicate eastward movement for Clupei, Shannon, Pielou, and FRic and westward for others. COG - Lat show northward movement only for Pielou, FEve, and CWM - MaxL. Gini increases for Pleuro, Gadi, Pielou, and LFI 30 and decreases for others (Figure S3, Supplementary material). After analyzing the spatial indices of selected indicators with MFA, we found that the first two dimension explained 69.27% of the variance. The first dimensions accounts for 47.62% and the second for 21.65%. If we examine their trends, we can see a relatively consistent and steep decline over time of the first one (Figure 2a). A more complex trend is evident for the second one where we initially see a slight decline, followed by a large and steep increase, and, afterwards, a large and steep decrease (Figure 2b). If we examine the contributions of the indicators to each dimension, we can see that most of the indicators (except Pleuro, LFI 30, and FEve) contribute at relatively similar levels (Figure 2c). In the case of the second dimension, the picture is considerably different with only four indicators (Pleuro, LFI 30cm, FRic, and FEve) contributing much more than the rest. If we sum up the contributions by type (Figure 2d), we can see that

structural indicators contribute more to the first dimension with 59% in total. Functional indicators contribute more to the second dimension 51.3% in total. All spatial indices show similar contribution levels to the first dimension with COG - Long and Gini contributing more than 25% (Figure 2e) while, to the second dimension, COG - Long contributes the most passing 30% followed by Ind. Value which barely passes 25% (Figure 2f).

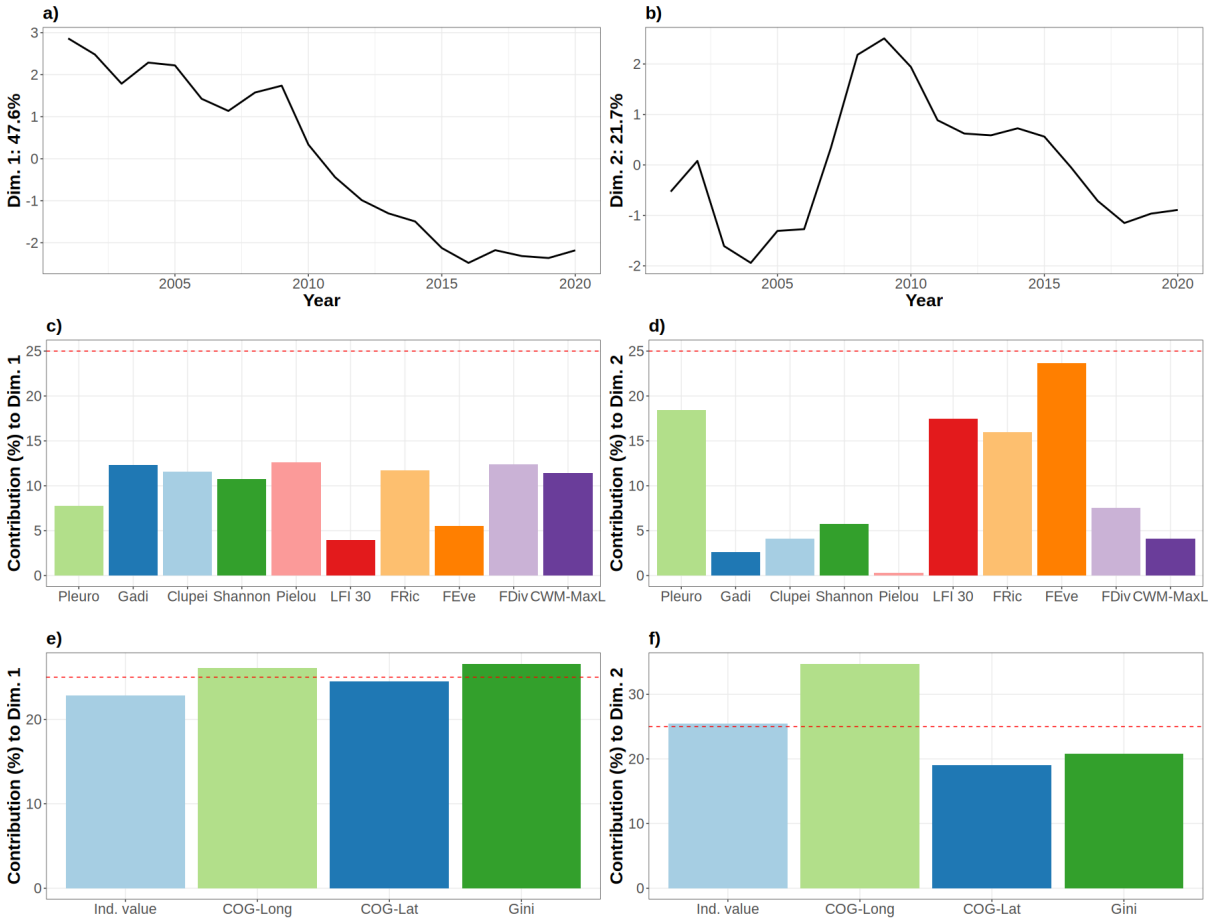


Figure 2. Results of the MFA: a) trend of dimension 1 which explains 47.6% of the variance, b) trend of dimension 2 which explains 21.7% of the variance, c) contributions of individual indicators to dimension 1, d) contributions of individual indicators to dimension 2, e) contributions of individual spatial indices to dimension 1, and f) contributions of individual spatial indices to dimension 2. “Dim.” denotes dimension.

Spatial state changes and overlap with management areas

The state of the fish community changed noticeably between the early (2001-2005) and the late (2016-2020) periods (Figure 3). Negative Z-scores indicate that indicators were lower in the late period compared to the early period, while positive scores indicate an increase. Because not all indicators can be interpreted as inherently "good" when high or "bad" when low, the cumulative community state score should be understood as a measure of overall change rather than absolute status.

Areas of substantial decrease were concentrated in two relatively small regions - the northeast tip of Denmark and north of the Swedish island Gotland- both largely covered by designated and managed HELCOM MPAs. In contrast, a much more extensive area of decline spanned between the islands Gotland and Öland and along the coasts of Latvia, Lithuania, Russia, and Poland. Although an MPA exists within this region, its extent is much smaller than the area of community decline. The largest decrease, however, occurred in the Western Baltic Sea between Denmark, Germany, and Sweden. While this region hosts several small MPAs and a fisheries closure area, the majority of the decline zone remains outside existing protections. This area is also subject to substantial overlap with current wind farms, with further large-scale expansion planned. Increases in community state were more localized, occurring in smaller hotspots north of Zealand, north of the Polish coast, along the coasts of Russia and Lithuania, and in the Gulf of Riga. Among these, the hotspot north of Poland overlaps with planned wind farm development, suggesting potential future interactions between ecological change and new uses of the marine space.

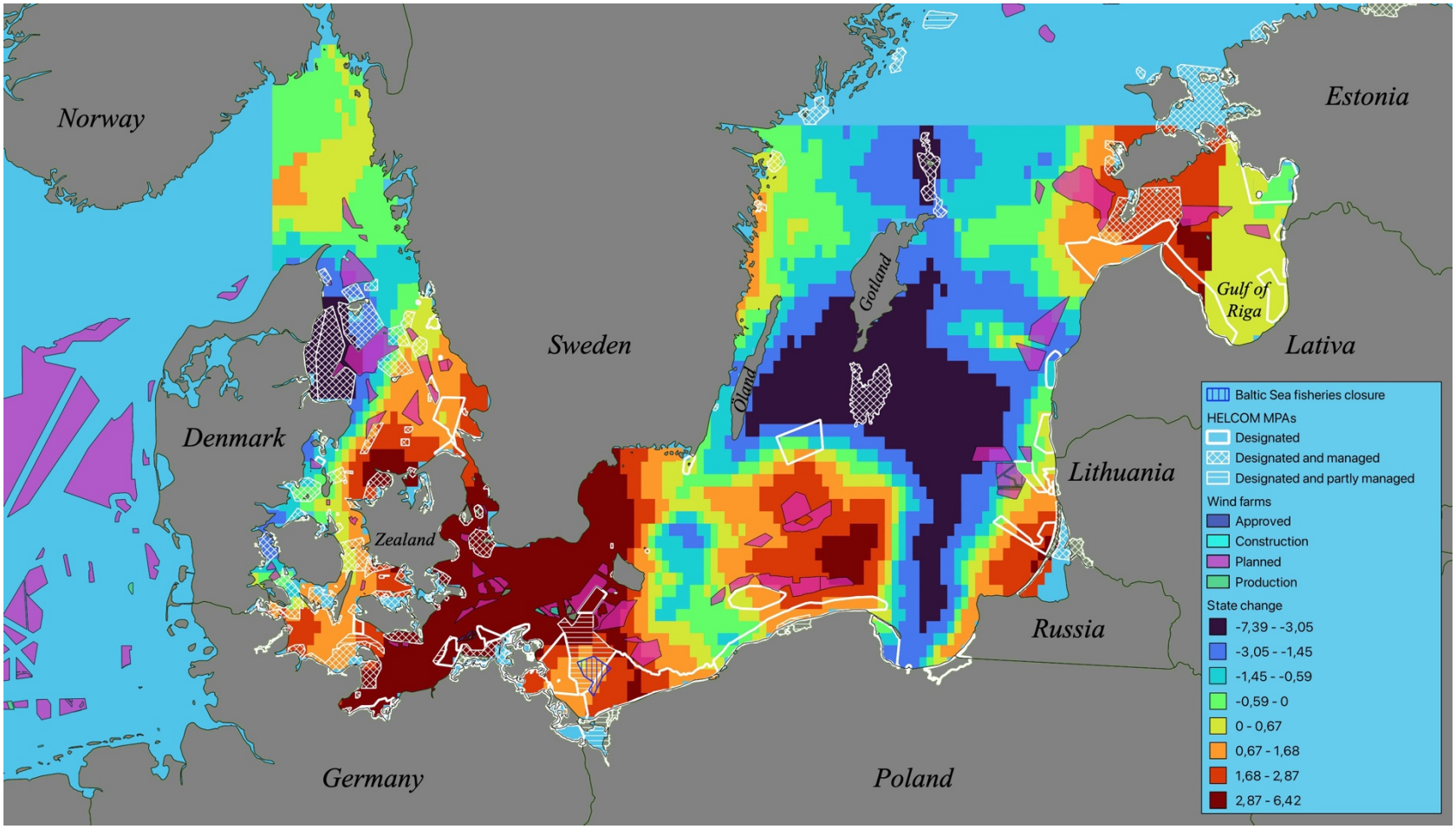


Figure 3. The change in fish community state Z-score between the early (2001-2005) and late (2016-2020) periods with Baltic Sea fisheries closure area, HELCOM MPAs, and wind farms overlaid.

DISCUSSION

Our study provides a comprehensive assessment of recent changes in the Baltic fish community by combining high spatiotemporal resolution with an integrated indicator framework. We identified key environmental variables that drive the spatiotemporal dynamics of the selected indicators and mapped areas where the state of the fish community has changed most strongly. These patterns suggest that current spatial protection may not fully cover regions of pronounced community change and that future wind farm expansion is likely to interact with these dynamics. Our findings are consistent with earlier work indicating that climate change and eutrophication have altered the structure and functioning of the Baltic Sea ecosystem (Conley *et al.*, 2009; Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020) and with studies documenting distributional shifts and changing spatial overlap of fish species under these pressures (Orio *et al.*, 2019, 2020; MacNeil *et al.*, 2025; **Chapter 1**; **Chapter 2**). Within our study period, temperature showed the strongest change and was the most frequent significant covariate across spatiotemporal models, with oxygen, chlorophyll *a*, and salinity also often important. This is consistent with long-standing evidence that these variables shape growth, survival and distribution limits of Baltic fish species (Köster *et al.*, 2005; Ojaveer and Kalejs, 2005; Mackenzie *et al.*, 2007). Declining oxygen and altered salinity stratification, in particular, have repeatedly been linked to recruitment failure in cod and broader community restructuring. Because all of these variables are expected to continue changing under ongoing climate and anthropogenic forcing (Andersson *et al.*, 2015), further consequences for the fish community are likely, in line with global patterns of climate-driven marine reorganization (Vergés *et al.*, 2014; Pecl *et al.*, 2017; McLean *et al.*, 2019; Zhao *et al.*, 2022; Souza *et al.*, 2023). It should also be noted that BITS data are collected only during the colder months (quarter 1 and 4), which may influence some of the detected patterns.

By integrating structural and functional indicators, this study advances current approaches to community state assessment in the Baltic Sea. The MFA results demonstrate that functional and structural dimensions contribute complementary

information, reinforcing previous calls to account for functional traits when evaluating ecosystem change (Smit *et al.*, 2021). These findings underscore the value of including functional indicators in community-specific assessments and thereby complementing broader ecosystem-wide evaluations, such as those used HELCOM and other regional assessments (Blenckner *et al.*, 2021; HELCOM, 2023), which often cannot resolve patterns at similarly fine spatial and temporal scales. Functional diversity is increasingly recognized as a key determinant of ecosystem resilience, stability and energy flow in marine fish communities and often responds to environmental change in ways that taxonomic metrics alone cannot (Chillo *et al.*, 2011; Mori *et al.*, 2013; Stuart-Smith *et al.*, 2013). Several studies also demonstrate functional reorganization of fish communities under warming and exploitation (McLean *et al.*, 2019; Coulon *et al.*, 2023), further underscoring the value of trait-based indicators for detecting early ecological change. A key limitation of our work is the incomplete availability of trait data specifically for Baltic Sea fish. We therefore used trait data from North Sea populations of the same species, under the assumption that trait-based differences among species are broadly comparable between these neighboring ecosystems. This approach is commonly used in marine trait research, as many life-history traits show broad geographic consistency within species. Nonetheless, our results highlight the need for more complete and region-specific trait inventories to support future functional assessments.

Our results further emphasize the importance of combining temporal and spatial perspectives. The indicator selection protocol (Otto *et al.*, 2018), which is based on spatially aggregated time series, identified a partly different set of drivers than the spatiotemporal models. This discrepancy is not unexpected, as purely temporal analyses assume spatial uniformity and are limited in capturing fine-scale spatial complexity (Chen *et al.*, 2011). In contrast, our high-resolution spatiotemporal framework revealed distinct environmental gradients and spatially structured changes. Multi-criteria indicator evaluation frameworks that assess indicators in terms of sensitivity, robustness, redundancy and management relevance are well established in marine ecosystem assessments and align with international recommendations for indicator development (Kershner *et al.*, 2011; Queirós *et al.*,

2016). Our spatiotemporal GLMM approach fits within recent methodological advances in marine ecology, where SPDE-based models have proved powerful tools for capturing fine-scale species–environment relationships (Thompson *et al.*, 2023). Finally, our results suggest that order-level CPUE may be more suitable for tracking community-level change than single-species abundance indicators, which can be strongly influenced by targeted management interventions.

While spatial indices of the indicators showed divers temporal trajectories, their integration into a cumulative state score allowed us to identify areas where the fish community changed most strongly. Many of these areas show little overlap with existing HELCOM MPAs or the fisheries closure area. This spatial mismatch is concerning in light of global evidence that shifting species distributions can undermine the effectiveness of static MPAs (Cashion *et al.*, 2020) and that climate adaptation principles remain insufficiently integrated into MPA planning (O'Regan *et al.*, 2021). Similar mismatches between static protected areas and shifting distributions have been documented in many marine regions and are increasingly recognized as a major challenge for conservation under climate change (Pinsky *et al.*, 2018; Bates *et al.*, 2019). Dynamic spatial management, which allows management measures to shift in space and time, has been proposed as a promising response to such challenges (Maxwell *et al.*, 2015; Dunn *et al.*, 2016; Gilman *et al.*, 2019; Oestreich *et al.*, 2020). In the Baltic Sea, simply relocating existing HELCOM MPAs to align them with the areas of strongest fish community change would risk eroding the conservation benefits these sites already provide, and the spatial footprint of the identified change zones is too extensive for relocation to be practical. Instead, our findings support calls for an expansion of spatial protection, potentially including dynamic elements that can better track shifting community states. Effective enforcement will be essential to ensure that such measures deliver ecological benefits, particularly in light of previous challenges in implementing regional actions such as the Baltic Sea Action Plan (Brady *et al.*, 2022). Recent initiatives such as the PROTECT BALTIC project (https://protectbaltic.eu) (Baltic Marine Environment Protection Commission, n.d.) represent important steps towards improving MPA planning and management in the region.

Several of the areas where we detected strong community state changes are also projected to experience substantial expansion of offshore wind farms. A recent review of wind farm effects in European waters, including the Baltic Sea, suggests that turbines can locally increase the abundance of demersal fishes via reef effects that provide shelter and foraging opportunities (Knorrn *et al.*, 2024). However, broader ecosystem-level consequences remain uncertain due to limited evidence on impacts on apex predators, species interactions and physiological or behavioral responses of marine organisms. Offshore wind farms may also interact with other anthropogenic pressures—such as noise, bottom disturbance or altered food webs—creating cumulative impacts that can amplify or counteract local habitat effects (Korpinen and Andersen, 2016; Galparsoro *et al.*, 2022). Moreover, interactions with other uses may further influence habitat suitability for different taxonomic and functional groups. Given the expected scale of offshore wind expansion to meet decarbonization targets (European Environment Agency, 2024), it is likely that the Baltic fish community will increasingly experience cumulative effects of wind farm development. Our results therefore highlight priority areas where ecological change coincides with expanding marine uses and where cumulative impacts warrant careful evaluation.

Conclusion

Our study provides an integrated, high-resolution assessment of recent structural and functional changes in the Baltic Sea fish community. The strong influence of climate-driven environmental change, together with pronounced spatial heterogeneity, highlights the need for adaptive management approaches that account for shifting community states. Incorporating functional indicators alongside traditional structural metrics, and resolving spatial dynamics at fine scales, can substantially improve the appraisal of ecosystem change and its drivers. Order-level abundance indicators also offer a robust means of tracking community-level responses. Finally, priority areas where substantial ecological change coincides with limited protection require coordinated cross-national action to maintain the biodiversity and productivity of the Baltic Sea under increasing anthropogenic pressures.

REFERENCES

Abdi, H., Williams, L. J., and Valentin, D. 2013. Multiple factor analysis: principal component analysis for multitable and multiblock data sets. WIREs Computational Statistics, 5: 149–179.

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. preprint. Ecology. http://biorxiv.org/lookup/doi/10.1101/2022.03.24.485545 (Accessed 2 January 2024).

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., *et al.* 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO, 44: 345–356.

Baltic Marine Environment Protection Commission. (n.d.). PROTECT BALTIC: Preserve, revive, thrive. https://protectbaltic.eu (Accessed 8 June 2025).

Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M., *et al.* 2019. Climate resilience in marine protected areas and the 'Protection Paradox'. Biological Conservation, 236: 305–314.

Belkin, I. M. 2009. Rapid warming of Large Marine Ecosystems. Progress in Oceanography, 81: 207–213.

Beukhof, E., Dencker, T. S., Palomares, M. L. D., and Maureaud, A. 2019a. A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas [dataset]. PANGAEA.

Beukhof, E., Dencker, T., Pecuchet, L., and Lindegren, M. 2019b. Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series, 610: 205–222.

Blenckner, T., Möllmann, C., Stewart Lowndes, J., Griffiths, J. R., Campbell, E., De Cervo, A., Belgrano, A., *et al.* 2021. The Baltic Health Index (BHI): Assessing the social–ecological status of the Baltic Sea. People and Nature, 3: 359–375.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science, 16: 533–540.

Brady, M. V., Andersen, M. S., Andersson, A., Kilis, E., Saarela, S.-R., and Hvarregaard Thorsøe, M. 2022. Strengthening the policy framework to resolve lax implementation of the Baltic Sea Action Plan for agriculture. Ambio, 51: 69–83.

Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J., *et al.* 2022. Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? Ocean & Coastal Management, 223: 106154.

Cashion, T., Nguyen, T., Ten Brink, T., Mook, A., Palacios-Abrantes, J., and Roberts, S. M. 2020. Shifting seas, shifting boundaries: Dynamic marine protected area designs for a changing climate. PLOS ONE, 15: e0241771.

Casini, M., and Larson, N. 2013. HELCOM Core Indicator.

Chen, Q., Han, R., Ye, F., and Li, W. 2011. Spatio-temporal ecological models. Ecological Informatics, 6: 37–43.

Chillo, V., Anand, M., and Ojeda, R. A. 2011. Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands. Ecosystems, 14: 1168–1177.

Conley, D. J., Carstensen, J., Ærtebjerg, G., Christensen, P. B., Dalsgaard, T., Hansen, J. L. S., and Josefson, A. B. 2007. LONG-TERM CHANGES AND IMPACTS OF HYPOXIA IN DANISH COASTAL WATERS. Ecological Applications, 17. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/05-0766.1 (Accessed 16 January 2025).

Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., *et al.* 2009. Hypoxia-related Processes in the Baltic Sea. Environmental Science & Technology, 43: 3412–3420.

Coulon, N., Lindegren, M., Goberville, E., Toussaint, A., Receveur, A., and Auber, A. 2023. Threatened fish species in the Northeast Atlantic are functionally rare. Global Ecology and Biogeography, 32: 1827–1845.

Domínguez-Tejo, E. 2016. Marine Spatial Planning advancing the Ecosystem-Based Approach to coastal zone management_ A review. Marine Policy.

Dunn, D. C., Maxwell, S. M., Boustany, A. M., and Halpin, P. N. 2016. Dynamic ocean management increases the efficiency and efficacy of fisheries

management. Proceedings of the National Academy of Sciences, 113: 668–673.

Eilola, K., Meier, H. E. M., and Almroth, E. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. Journal of Marine Systems, 75: 163–184.

EMODnet. 2024. EMODnet Human Activities.

European Environment Agency. 2024. Harnessing Offshore Wind While Preserving the Seas. https://www.eea.europa.eu/en/analysis/publications/harnessing-offshore-wind-while-preserving-the-seas (Accessed 8 June 2025).

Fey, D. P., Hiller, A., Margonski, P., Moll, D., Nilsson, H., Pongolini, L., Stybel, N., *et al.* 2014. HERRING Impact Report Herring spawning areas - present and future challenges.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Froese, R., and Pauly, D. 2024. FishBase. www.fishbase.org.

Galparsoro, I., Menchaca, I., Garmendia, J. M., Borja, Á., Maldonado, A. D., Iglesias, G., and Bald, J. 2022. Reviewing the ecological impacts of offshore wind farms. npj Ocean Sustainability, 1: 1.

Gilman, E., Kaiser, M. J., and Chaloupka, M. 2019. Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives? Ecosphere, 10: e02968.

Gini, C. 1912. Variabilità e mutabilità. Studi Economico-Giuridici della R. Università de Cagliari, 3: 1–158.

HELCOM. 2008. Baltic Sea fisheries closure.

HELCOM. 2023. HELCOM MPAs.

HELCOM. 2023. State of the Baltic Sea. Third HELCOM holistic assessment 2016-2021. Baltic Sea Environment Proceedings n°194.

HELCOM. (n.d.). Marine Protected Areas. https://helcom.fi/action-areas/marine-protected-areas/ (Accessed 8 June 2025).

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G., *et al.* 2013. Projected impacts of climate change on marine fish and fisheries. ICES Journal of Marine Science, 70: 1023–1037.

ICES. 2017. Manual for the Baltic International Trawl Surveys (BITS). Series of ICES Survey Protocols SISP 7 - BITS: 95. ICES.

ICES. 2022. Baltic Sea ecoregion – fisheries overview. ICES Advice: Fisheries Overviews. https://ices-library.figshare.com/articles/report/Baltic_Sea_ecoregion_fisheries_overview/21646934 (Accessed 26 February 2024).

ICES. 2024. Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Herring_i_Clupea_harengus_i_in_subdivisions_20_24_spring_spawners_Skagerrak_Kattegat_and_western_Baltic_/25019273 (Accessed 16 January 2025).

Kershner, J., Samhouri, J. F., James, C. A., and Levin, P. S. 2011. Selecting Indicator Portfolios for Marine Species and Food Webs: A Puget Sound Case Study. PLoS ONE, 6: e25248.

Knorrn, A. H., Teder, T., Kaasik, A., and Kreitsberg, R. 2024. Beneath the blades: Marine wind farms support parts of local biodiversity - a systematic review. Science of The Total Environment, 935: 173241.

Korpinen, S., and Andersen, J. H. 2016. A Global Review of Cumulative Pressure and Impact Assessments in Marine Environments. Frontiers in Marine Science, 3. http://journal.frontiersin.org/Article/10.3389/fmars.2016.00153/abstract (Accessed 3 December 2025).

Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment – the impact of climate variability on key processes. ICES Journal of Marine Science, 62: 1408–1425.

Laliberte, E., and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits, 91.

Link, J. S., and Watson, R. A. 2019. Global ecosystem overfishing: Clear delineation within real limits to production. Science Advances, 5: eaav0474.

Liu, Y., Meier, H. E. M., and Eilola, K. 2017. Nutrient transports in the Baltic Sea – results from a 30-year physical–biogeochemical reanalysis. Biogeosciences, 14: 2113–2131.

Lowerre-Barbieri, S. K., Catalan, I. A., Opdal, A. F., and Jørgensen, C. 2019. Preparing for the future: integrating spatial ecology into ecosystem-based management. ICES Journal of Marine Science, 76: 467-476.

Mackenzie, B. R., Gislason, H., Möllmann, C., and Köster, F. W. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Global Change Biology, 13: 1348–1367.

MacNeil, L., Madiraca, F., Otto, S., and Scotti, M. 2025. Spatial Change of Dominant Baltic Sea Demersal Fish Across Two Decades. Ecology and Evolution, 15: e71309.

Madiraca, F., MacNeil, L., Scotti, M., Möllmann, C., and Otto, S. A. in preparation. Environmentally driven shifts of Baltic fish distributions and their impact on spatiotemporal overlap between species.

Madiraca, F., MacNeil, L., Dutheil, C., Meier, H. E. M., Scotti, M., Möllmann, C., and Otto, S. A. in preparation. Shifting Baltic Sea fish distributions under future environmental change.

Maestro, M., Pérez-Cayeiro, M. L., Chica-Ruiz, J. A., and Reyes, H. 2019. Marine protected areas in the 21st century: Current situation and trends. Ocean & Coastal Management, 171: 28–36.

Magurran, A. E. 2003. Measuring biological diversity. John Wiley & Sons.

Mason, N. W. H., Mouillot, D., Lee, W. G., and Wilson, J. B. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity.

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., *et al.* 2015. Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. Marine Policy, 58: 42–50.

Mbaru, E. K., Graham, N. A. J., McClanahan, T. R., and Cinner, J. E. 2020. Functional traits illuminate the selective impacts of different fishing gears on coral reefs. Journal of Applied Ecology, 57: 241–252.

McLean, M. J., Mouillot, D., Goascoz, N., Schlaich, I., and Auber, A. 2019. Functional reorganization of marine fish nurseries under climate warming. Global Change Biology, 25: 660–674.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Mori, A. S., Furukawa, T., and Sasaki, T. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews, 88: 349–364.

Mouchet, M. A., Villéger, S., Mason, N. W. H., and Mouillot, D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24: 867–876.

Nagelkerken, I., Allan, B. J. M., Booth, D. J., Donelson, J. M., Edgar, G. J., Ravasi, T., Rummer, J. L., *et al.* 2023. The effects of climate change on the ecology of fishes. PLOS Climate, 2: e0000258.

Oesterwind, D., Psuty, I., Pachur, M., von Dorrien, C., Lejk, A., Casini, M., and Larson, N. 2013. HELCOM Core Indicator Report.

Oestreich, W. K., Chapman, M. S., and Crowder, L. B. 2020. A comparative analysis of dynamic management in marine and terrestrial systems. Frontiers in Ecology and the Environment, 18: 496–504.

Ojaveer, E., and Kalejs, M. 2005. The impact of climate change on the adaptation of marine fish in the Baltic Sea. ICES Journal of Marine Science, 62: 1492–1500.

O'Regan, S. M., Archer, S. K., Friesen, S. K., and Hunter, K. L. 2021. A Global Assessment of Climate Change Adaptation in Marine Protected Area Management Plans. Frontiers in Marine Science, 8: 711085.

Orio, A., Bergström, U., Florin, A., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap between interacting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Otto, S. A., Kadin, M., Casini, M., Torres, M. A., and Blenckner, T. 2018. A quantitative framework for selecting and validating food web indicators. Ecological Indicators, 84: 619–631.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., *et al.* 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., *et al.* 2020. Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography, 43: 197–208.

Pielou, E. C. 1966. The Measurement of Diversity in Different Types of Biological Colledions, 13: 131–144.

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung, W. W. L. 2018. Preparing ocean governance for species on the move. Science, 360: 1189–1191.

Priya, A. K., M, M., Rajamanickam, S., Sivarethinamohan, S., Gaddam, M. K. R., Velusamy, P., R, G., *et al.* 2023. Impact of climate change and anthropogenic activities on aquatic ecosystem – A review. Environmental Research, 238: 117233.

Queirós, A. M., Strong, J. A., Mazik, K., Carstensen, J., Bruun, J., Somerfield, P. J., Bruhn, A., *et al.* 2016. An Objective Framework to Test the Quality of Candidate Indicators of Good Environmental Status. Frontiers in Marine Science, 3. http://journal.frontiersin.org/Article/10.3389/fmars.2016.00073/abstract (Accessed 3 December 2025).

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Receveur, A., Leprieur, F., Ellingsen, K. E., Keith, D., Kleisner, K. M., McLean, M., Mérigot, B., *et al.* 2024. Long-term changes in taxonomic and functional composition of European marine fish communities. Ecography, 2024: e07234.

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., and Pavoine, S. 2016. Measuring the functional redundancy of biological communities: a quantitative guide. Methods in Ecology and Evolution.

Ricotta, C. 2022. Functional imbalance not functional evenness is the third component of community structure. Ecological Indicators.

Serif. 2023. Affinity Photo 2. Serif (Europe) Ltd.

Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Ryberg, M. P., Lindegren, M., Durant, J. M., *et al.* 2019. Catastrophic dynamics limit Atlantic cod recovery. Proceedings of the Royal Society B: Biological Sciences, 286: 20182877.

Shannon, C. E. 1948. A Mathematical Theory of Communication. The Bell System Technical Journal, 27.

Smit, K. P., Bernard, A. T. F., Lombard, A. T., and Sink, K. J. 2021. Assessing marine ecosystem condition: A review to support indicator choice and framework development. Ecological Indicators, 121: 107148.

Souza, A. T., Dias, E., Antunes, C., and Ilarri, M. 2023. Disruptions caused by invasive species and climate change on the functional diversity of a fish community. NeoBiota, 88: 211–244.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., *et al.* 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature, 501: 539–542.

Thompson, P. L., Rooper, C. N., Nephin, J., Park, A. E., Christian, J. R., Davies, S. C., Hunter, K., *et al.* 2023. Response of Pacific halibut (Hippoglossus stenolepis) to future climate scenarios in the Northeast Pacific Ocean. Fisheries Research, 258: 106540.

Törnroos, A., Pecuchet, L., Olsson, J., Gårdmark, A., Blomqvist, M., Lindegren, M., and Bonsdorff, E. 2019. Four decades of functional community change

reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem. Global Change Biology, 25: 1235–1246.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B: Biological Sciences, 281: 20140846.

Villéger, S., Mason, N. W. H., and Mouillot, D. 2008. NEW MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL ECOLOGY. Ecology, 89: 2290–2301.

Willis, K. A., Serra-Gonçalves, C., Richardson, K., Schuyler, Q. A., Pedersen, H., Anderson, K., Stark, J. S., *et al.* 2022. Cleaner seas: reducing marine pollution. Reviews in Fish Biology and Fisheries, 32: 145–160.

Woillez, M., Rivoirard, J., and Petitgas, P. 2009. Notes on survey-based spatial indicators for monitoring fish populations. Aquatic Living Resources, 22: 155–164.

Wright, G., Ardron, J., Gjerde, K., Currie, D., and Rochette, J. 2015. Advancing marine biodiversity protection through regional fisheries management: A review of bottom fisheries closures in areas beyond national jurisdiction. Marine Policy, 61: 134–148.

Zhao, K., Gaines, S. D., García Molinos, J., Zhang, M., and Xu, J. 2022. Climate change and fishing are pulling the functional diversity of the world's largest marine fisheries to opposite extremes. Global Ecology and Biogeography, 31: 1616–1629.

ACKNOWLEDGEMENTS

We would like to thank Dr. Daniel Oesterwind for his help with providing further background information on the development of large fish indicators (LFIs) in the Baltic Sea.

SUPPLEMENTARY MATERIAL

Model input

Table S1. Overview of traits used for calculating functional indicators including information of how they are named in R scripts, their format, ecological category, applied transformations and sources from which they were extracted.

Trait	*Name in R scripts*	*Format*	*Category*	*Applied transformations*	*Source*
Mouth position	mouth.position	Categorical	Trophic		Froese and Pauly, 2024
Feeding mode	feeding.mode	Categorical	Trophic		Beukhof *et al.*, 2019
Trophic level	tl	Numerical	Trophic	Yeo-Johnson	Beukhof *et al.*, 2019
Eye diameter	eye.diameter	Numerical	Trophic		Froese and Pauly, 2024
Habitat	habitat	Categorical	Life history		Froese and Pauly, 2024
Salinity habitat	salhab	Categorical	Life history		Beukhof *et al.*, 2019
Preferred modelled temperature	modtemp	Numerical	Life history	Yeo-Johnson	Froese and Pauly, 2024
Growth coefficient	growth.coefficient	Numerical	Life history	Yeo-Johnson	Beukhof *et al.*, 2019
Spawning type	spawning.type	Categorical	Reproductive		Beukhof *et al.*, 2019
Fertilization type	fert	Categorical	Reproductive		Froese and Pauly, 2024
Age at maturity	age.maturity	Numerical	Reproductive	Yeo-Johnson	Beukhof *et al.*, 2019
Fecundity	fecundity	Numerical	Reproductive	Yeo-Johnson	Beukhof *et al.*, 2019
Offspring size	offspring.size	Numerical	Reproductive	Yeo-Johnson	Beukhof *et al.*, 2019
Fin shape	fin.shape	Categorical	Trophic, mobility		Beukhof *et al.*, 2019
Aspect ratio of caudal fin	AR	Numerical	Trophic, mobility	Yeo-Johnson	Beukhof *et al.*, 2019
Body shape	body.shape	Categorical	Multiple		Beukhof *et al.*, 2019
Maximum length	length.max	Numerical	Multiple	Yeo-Johnson	Beukhof *et al.*, 2019
Maximum age	age.max	Numerical	Multiple	Yeo-Johnson	Beukhof *et al.*, 2019

Table S2. Overview of single species included in the study and the file names of images used for extracting and, where necessary, calculating the species-specific eye diameter trait from Froese and Pauly (2024).

Species	*Image file name*
Agonus cataphractus	Agcat_u3.jpg
Alosa fallax	Alfal_u4.jpg
Ammodytes marinus	Ammodytes_marinus3.jpg
Ammodytes tobianus	Amtob_u2.jpg
Anarhichas lupus	1406026447579Au0FqWazXy27NY8W.jpeg
Aphia minuta	Apmin_f0.jpg
Argentina silus	Arsil_u0.jpg
Argentina sphyraena	1505227784063KJwohCEfJtaJiBme.jpeg
Arnoglossus laterna	Arlat_u4.jpg
Atherina presbyter	1406027930006tlikILSVUlVqKLNL.jpeg
Belone belone	1406026645267H1mll4kByOreoVI0.jpeg
Buglossidium luteum	Bulut_u0.jpg
Callionymus lyra	Calyr_u5.jpg
Callionymus maculatus	ce-CMAC-001a.jpeg
Chelidonichthys cuculus	Chcuc_u3.jpg
Chelidonichthys lucerna	1406026893361ISfZ8Fmezc6rBDii.jpeg
Chelon labrosus	Chlab_u4.jpg
Ciliata mustela	1391990559_217.120.237.5.jpeg
Clupea harengus	1406027928618WwYuTjsUO5XoDlgK.jpeg
Crystallogobius linearis	Crlin_u3.jpg
Ctenolabrus rupestris	1406026454583uYCYxICCkjCXn0lH.jpeg
Cyclopterus lumpus	Cylum_u3.jpg
Dicentrarchus labrax	1406026893603X8KnWKb4Nsf7ZkdA.jpeg
Enchelyopus cimbrius	1406026441005ybiiRGNU3eE38Kug.jpeg
Engraulis encrasicolus	1406027028260pEOMggBGzlrzibbs.jpeg
Entelurus aequoreus	Eaequoreus.jpeg
Etmopterus spinax	Etspi_u0.jpg
Eutrigla gurnardus	Chgur_u2.jpg
Gadus morhua	Gamor_ub.jpg
Gaidropsarus macrophthalmus	Gamac_u7.jpg
Gaidropsarus vulgaris	DSC01058.jpeg
Gasterosteus aculeatus	Gaacu_u2.jpg
Glyptocephalus cynoglossus	Glcyn_u1.jpg
Gobius niger	Gonig_u5.jpg
Hippoglossoides platessoides	Hipla_u3.jpg
Hippoglossus hippoglossus	Hihip_u3.jpg
Hyperoplus immaculatus	Hyimm_u0.jpg
Hyperoplus lanceolatus	Hylan_u0.jpg
Labrus bergylta	DSC01057.jpeg
Lampetra fluviatilis	14060266529685lYvSO7cm8c7opfT.jpeg
Lepidorhombus whiffiagonis	Lewhi_u0.jpg

Leptoclinus maculatus	Lemac_ue.jpg
Limanda limanda	Lilim_f0.jpg
Liparis montagui	Limon_u4.jpg
Lumpenus lampretaeformis	Lulum_u0.jpg
Melanogrammus aeglefinus	Meaeg_u5.jpg
Merlangius merlangus	Memer_u0.jpg
Merluccius merluccius	merluzzo.640.jpeg
Micromesistius poutassou	Mipou_u4.jpg
Microstomus kitt	Mikit_u0.jpg
Molva molva	Molvamolva32cmx.jpeg
Mullus surmuletus	Musur_ua.jpg
Mustelus mustelus	Mumus_f0.jpg
Myoxocephalus quadricornis	Trqua_u2.jpg
Myoxocephalus scorpius	Mysco_u3.jpg
Nerophis ophidion	Neoph_u4.jpg
Osmerus eperlanus	Osepe_u7.jpg
Pegusa lascaris	1406026894031fAKtcvNnjUt5eWym.jpeg
Petromyzon marinus	1406026440078YHvX62LsPmLaXPoi.jpeg
Platichthys flesus	Plfle_u0.jpg
Pleuronectes platessa	Plpla_u1.jpg
Pollachius pollachius	1406027847808bYnH7ZqMGu793kz9.jpeg
Pollachius virens	1551217875_141.101.77.64.jpeg
Pomatoschistus microps	Pomatoschistus_microps_3.jpeg
Pomatoschistus minutus	Pomin_m0.jpg
Raniceps raninus	Raran_u4.jpg
Salmo salar	Sasal_u3.jpg
Sardina pilchardus	1406026643304lRLlPefRzZzOslKx.jpeg
Scomber scombrus	Scsco_u1.jpg
Scophthalmus maximus	1406027927108kKSyF6y1746jFXwC.jpeg
Scyliorhinus canicula	Sccan_m0.jpg
Scyliorhinus stellaris	Scste_u5.jpg
Sebastes viviparus	Seviv_u2.jpg
Solea solea	Sosol_u7.jpg
Spinachia spinachia	Spspi_u0.jpg
Sprattus sprattus	1406027030197bdLUzCtRkwFXwnpX.jpeg
Squalus acanthias	Sqaca_u1.jpg
Symphodus melops	Symel_m0.jpg
Syngnathus acus	Syngnathusacus.jpeg
Syngnathus rostellatus	Syngnathus_rostellatus_2.jpeg
Syngnathus typhle	Sytyp_u1.jpg
Trachinus draco	TRADRA.jpeg
Trachurus trachurus	Trtra_u4.jpg
Trisopterus esmarkii	Tresm_u0.jpg
Trisopterus luscus	Trisopterusluscus.jpeg
Trisopterus minutus	poorcod.jpeg
Zeus faber	Zefab_f0.jpg

Indicator transformation

Several indicators were transformed to improve distributional properties. To assess the necessity of these transformations we investigated histograms of indicators post-aggregation. If normality of distributions was not improved, we transformed the pre-aggregated data. In the end, Mean CPUE, CPUE of cod, CPUE of whiting, CPUE of plaice, and CPUE of functional group 2 were transformed with the log (x + 1) transformation. Species richness and community-weighted mean (CWM) of trophic level were log-transformed. Large Fish Index (LFI) of the whole community and of cod over 30 centimeters were arcsine-transformed. CWM of fecundity was transformed with the Yeo-Johnson power transformation (Yeo, 2000).

Model output

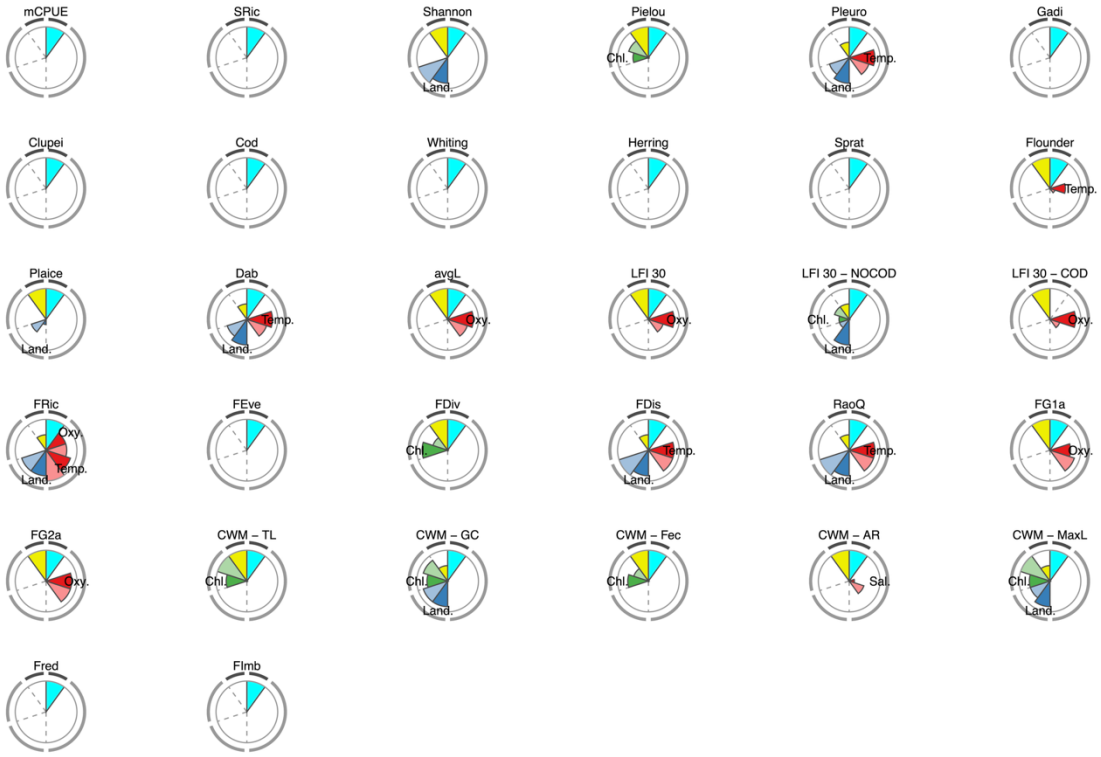


Figure S1. Spie charts of tested indicators showing their performance. Yellow color corresponds to link to management, and aqua to indication of trend score. Red, green, and blue denote pressure groups, namely climate, eutrophication, and fisheries related pressures, respectively. Darker shades of these colors show indicator sensitivity, and lighter ones show robustness to highlighted pressure.

Temperature is abbreviated as “Temp.”, salinity as “Sal.”, oxygen as “Oxy.”, chlorophyll *a* as “Chl.”, and fisheries landings as “Land.”. Full indicator names are available in the main text (Table 1).

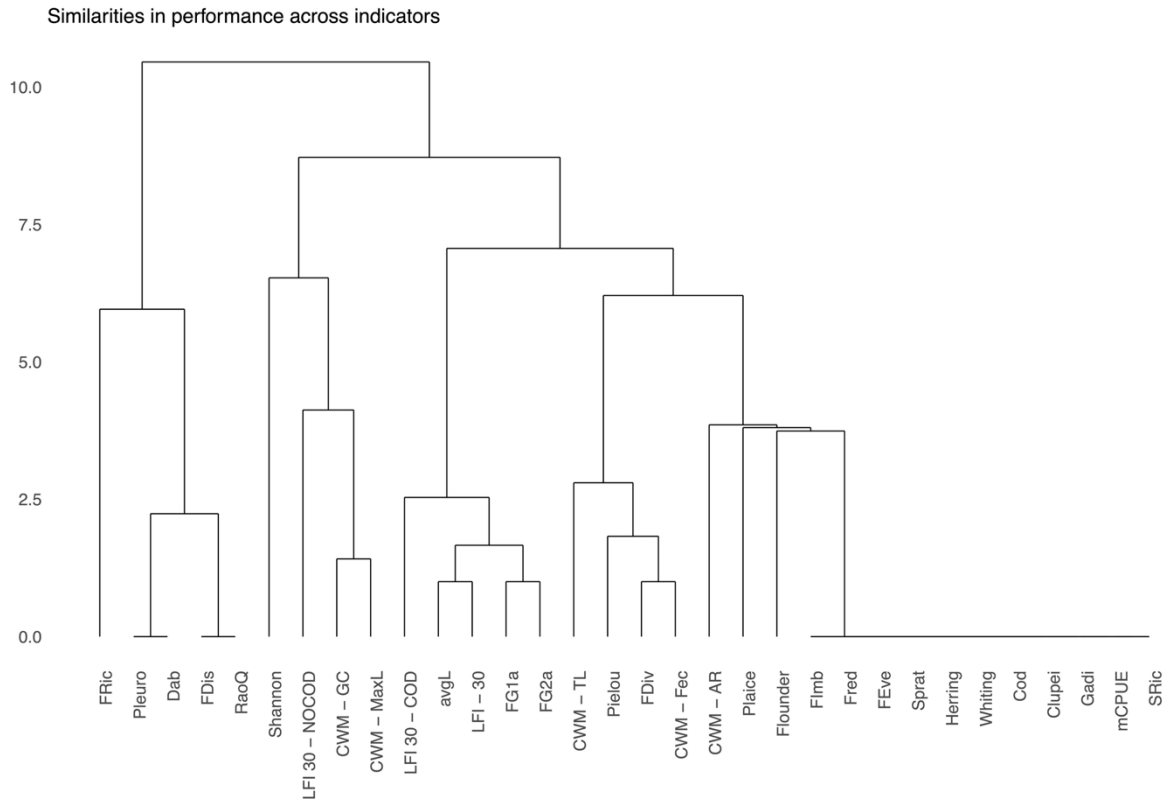


Figure S2. Dendrogram from the hierarchical cluster analysis showing similarities in indicator performance.

Table S3. Extended overview of the final models’ structure. Additional information includes Normalized Root Mean Squared Error (NRMSE) values in the training “Train” and testing “Test” period, distributions used in the models, and random effects used in the models where “SP” denotes spatial random effects and “SPT” spatiotemporal random effects. “Temp.” denotes temperature, “Sal.” salinity, “Oxy.” Oxy, “Chl.” Chlorophyll *a*, and “Land.” denotes landings. The numbers reported in the table represent coefficient estimates obtained from the models, those noted with “*” and in bold are deem statistically significant ($p \leq 0.05$). Response curve types are written underneath covariate coefficients where “Li” stands for linear and “Sm” for smoother. Full indicator names are available in the main text (Table 1).

					Covariates in spatiotemporal models				
Indicator	*Covariates determining temporal indicator dynamics (INDperform)*	*NRMSE*	*Distribution*	*Random effects*	*Temp.*	*Sal.*	*Oxy.*	*Chl.*	*Land.*
Pleuro	**Temp.**, Land.	Train: 0.67 Test: 0.70	Gaussian	SPT-AR1	**0.14*** **Li**	**0.61*** **Li**	-2.45 Sm		
Gadi		Train: 0.66 Test: 0.72	Gaussian	SPT-AR1	**0.21*** **Li**	-0.17 Li	**29.40*** **Sm**		
Clupei		Train: 0.74 Test: 0.85	Tweedie	SPT-AR1	**0.09*** **Cv**		**0.20*** **Cv**	**-0.07*** **Cv**	
Shannon	Land.	Train: 0.69 Test: 0.73	Gaussian	SPT-AR1	**0.04*** **Li**	**0.13*** **Li**	**0.05*** **Li**	0.01 Li	
Pielou	Chl.	Train: 0.88 Test: 0.85	Gaussian	SPT-AR1				-0.00 Li	0.00 Li
LFI 30	Oxy.	Train: 0.72 Test: 0.72	Tweedie	SP + SPT-AR1	**-0.05*** **Li**		0.01 Li	**-0.04*** **Li**	
FRic	**Temp.**, Oxy., Land.	Train: 0.68 Test: 0.85	Gaussian	SPT-IID	**0.00*** **Li**	**-0.18*** **Sm**	0.00 Sm	**0.01*** **Li**	
FEve		Train: 0.87 Test: 0.95	Gaussian	SPT-AR1	**-0.02*** **Li**		**-0.03*** **Li**		
FDiv	**Chl.**	Train: 0.86 Test: 0.89	Gaussian	SPT-AR1		-0.00 Li	**0.02*** **Li**	**-0.01*** **Li**	0.00 Li
CWM - MaxL	**Chl.**, Land.	Train: 0.75 Test: 0.81	Gaussian	SPT-AR1			0.01 Li	**0.02*** **Li**	

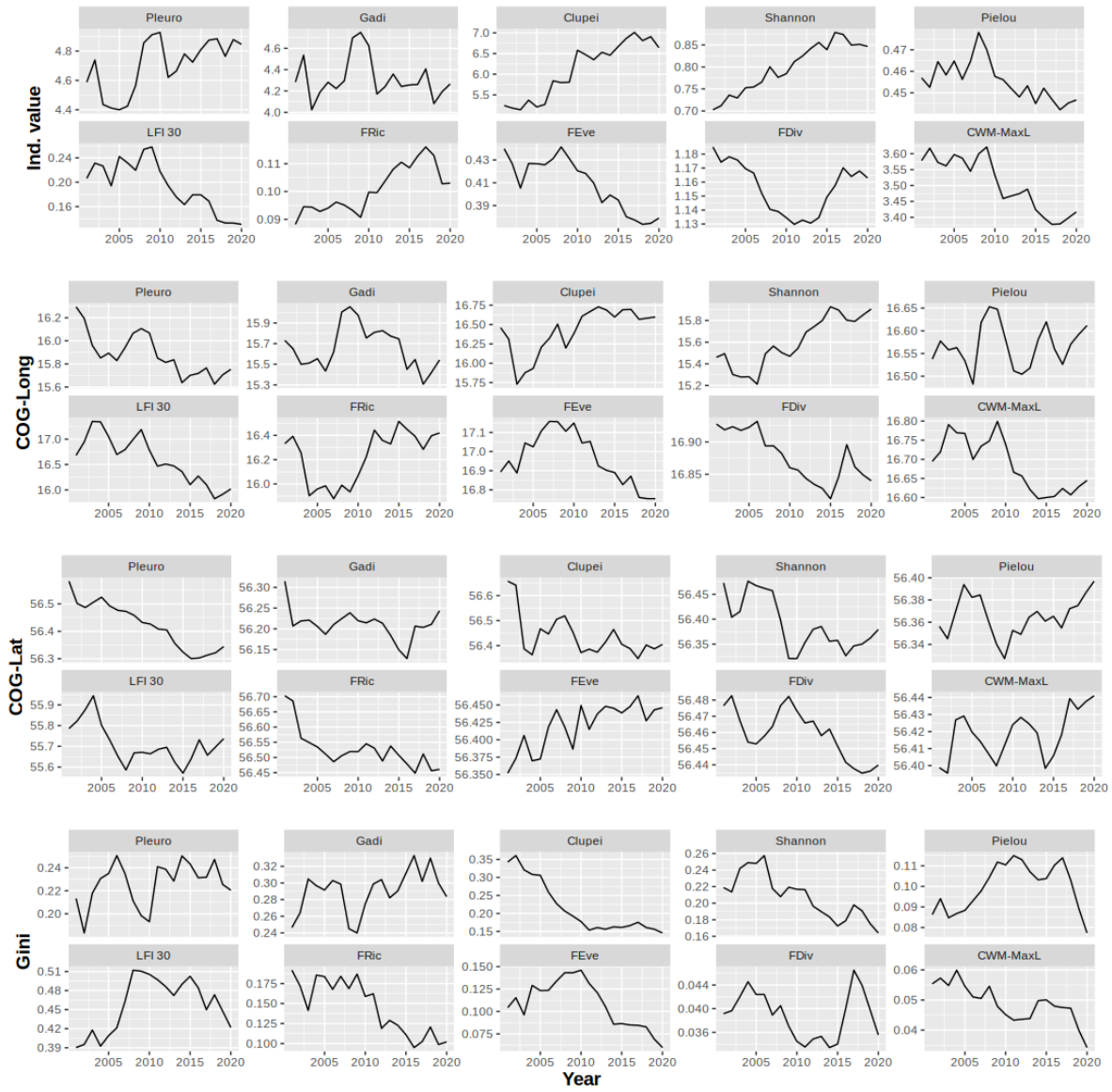


Figure S3. Interannual changes in spatial indices of the used indicators. The mean estimated value of the indicator is denoted with “Ind. value”, “COG-Long” represent center of gravity in longitude and “COG-Lat” in latitude, and “Gini” is the Gini index of aggregation.

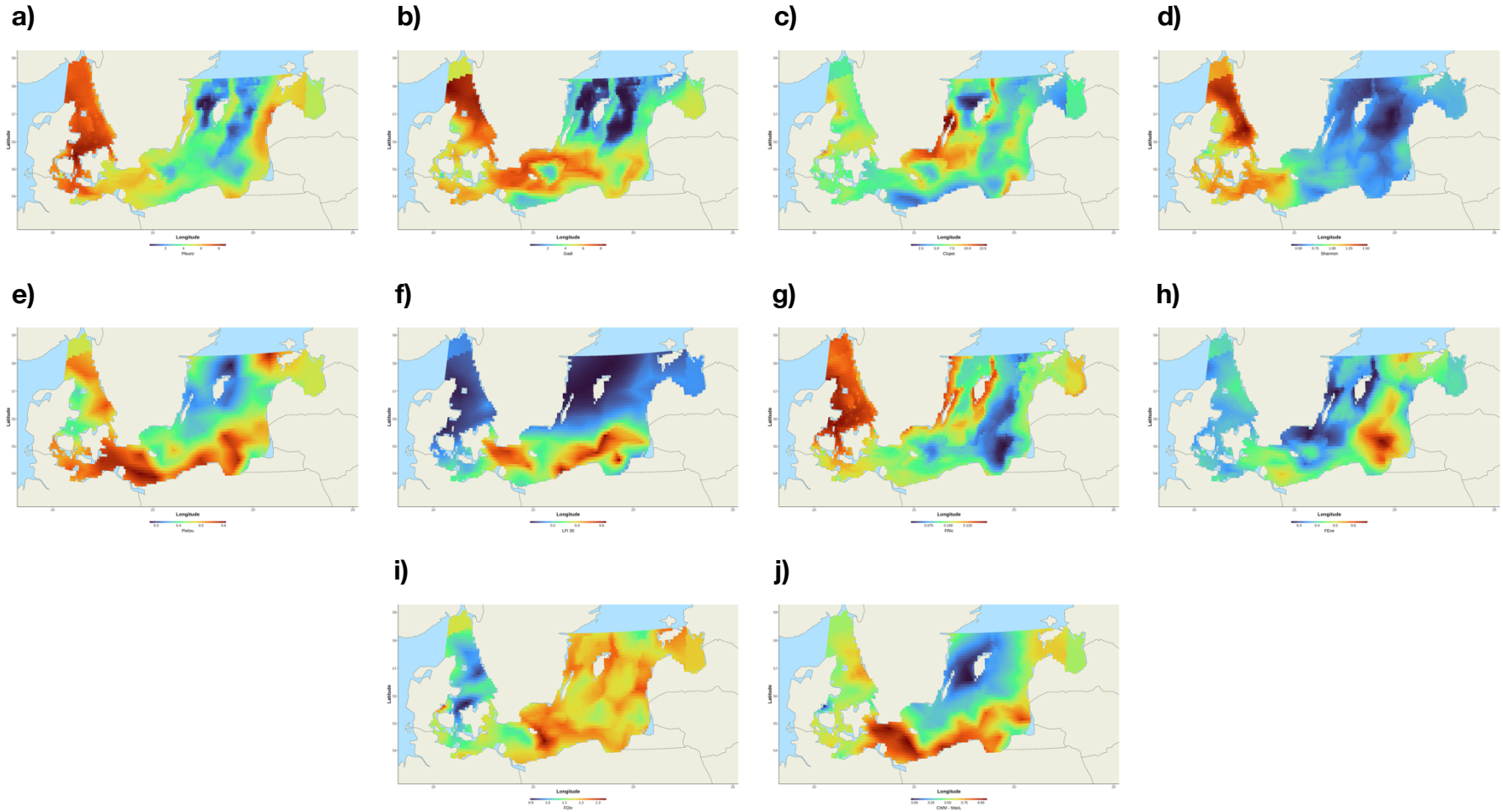


Figure S4. Indicators in the Baltic Sea between 2001 and 2020: a) Pleuronectiformes CPUE, b) Gadiformes CPUE, c) Clupeiformes CPUE, d) Shannon's diversity, e) Pielou's eveness, f) Large Fish Index of all fish over 30 cm, g) Functional richness, h) Functional evenness, i) Functional divergence, and j) CWM maximum length.

REFERENCES

Beukhof, E., Dencker, T. S., Palomares, M. L. D., and Maureaud, A. 2019. A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas [dataset]. PANGAEA.

Froese, R., and Pauly, D. 2024. FishBase. www.fishbase.org.

Yeo, I.-K. 2000. A new family of power transformations to improve normality or symmetry. Biometrika, 87: 954–959.

CHAPTER 4

A climate vulnerability assessment of the fish community in the Western Baltic Sea

Dorothee Moll[1], Harald Asmus[2], Alexandra Blöcker[3], Uwe Böttcher[1], Jan Conradt[3], Leonie Färber[3], Nicole Funk[3], Steffen Funk[3], Helene M. Gutte[3], Hans-Harald Hinrichsen[4], Paul Kotterba[1], Uwe Krumme[1], **Frane Madiraca**[3], H.E. Markus Meier[5], Steffi Meyer[3,6], Timo Moritz[7], Saskia A. Otto[3], Guilherme Pinto[8], Patrick Polte[1], Marie-Catherine Riekhof[9], Victoria Sarrazin[10], Heike Schwermer[9], Marco Scotti[4,11], Rudi Voss[8,9], Helmut Winkler[12], Christian Möllmann[3]✉

[1] Thuenen Institute of Baltic Sea fisheries, Rostock, Germany

[2] Alfred-Wegener Institute for Polar and Marine Research, Wadden Sea Station Sylt, List, Germany

[3] Institute of Marine Ecosystem and Fishery Science, Center for Earth System Research and Sustainability (CEN), Hamburg University, Hamburg

[4] Marine Ecology Research Division, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

[5] Department of Physical Oceanography and Instrumentation, Leibniz Institute for Baltic Sea Research Warnemünde, Rostock, Germany

[6] BioConsult GmbH C Co. KG, Bremen, Germany

[7] Stiftung Deutsches Meeresmuseum – Museum für Meereskunde und Fischerei, Deutsches Meeresmuseum, Stralsund, Germany

[8] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany.

[9] Center for Ocean and Society (CeOS), Christian-Albrechts-University Kiel, Kiel, Germany

[10] Leibniz Institute for Biodiversity Change Analysis (LIB), Museum of Nature – Zoology, Germany, Hamburg

[11] Institute of Biosciences and Bioresources, National Research Council of Italy, Firenze, Italy

[12] University of Rostock, Department of Zoology, Rostock, Germany

✉christian.moellmann@uni-hamburg.de

ABSTRACT

Marine fisheries are increasingly impacted by climate change, affecting species distribution and productivity, and necessitating urgent adaptation efforts. Climate vulnerability assessments (CVA), integrating expert knowledge, are vital for identifying species that could thrive or suffer under changing environmental conditions. This study presents a first CVA for the Western Baltic Sea's fish community, a crucial fishing area for Denmark and Germany. Characterized by a unique mix of marine, brackish, and freshwater species, this coastal ecosystem faces significant changes due to the combined effects of overfishing, eutrophication and climate change. Our CVA involved a qualitative expert scoring of 22 fish species, assessing their sensitivity and exposure to climate change. Our study revealed a dichotomy in climate change vulnerability within the fish community of the Western Baltic Sea because traditional fishing targets cod and herring as well as other species with complex life histories are considered to face increased risks, whereas invasive or better adaptable species might thrive under changing conditions. Our findings hence demonstrate the complex interplay between life-history traits and climate change vulnerability in marine fish communities. Eventually, our study provides critical knowledge for the urgent development of tailored adaptation efforts addressing existing but especially future effects of climate change on fish and fisheries in the Western Baltic Sea, to navigate this endangered fisheries systems into a sustainable future.

Keywords: Climate change, climate vulnerability assessment, fish community, trait-based sensitivity, Western Baltic Sea

INTRODUCTION

Marine fisheries are vulnerable to climate change because of its impacts on the distribution and productivity of living marine resources (Free *et al.*, 2019). As a consequence, adaptation efforts addressing existing but especially future effects of climate change are crucially required to navigate fisheries systems into a sustainable future (IPCC, 2023). Climate vulnerability assessments (CVA) based on expert knowledge contribute to adaptation planning because they may identify species potentially flourishing or suffering under future novel environmental conditions. CVAs are related to climate risk assessments that evaluate the potential impact of one or multiple hazards on species, habitats or ecosystems, either with a qualitative (based on expert opinion), semi-quantitative (based on data and expert opinion) or quantitative approaches (based on data only) (Holsman *et al.*, 2017). In case of assessing the potential climate impact on entire fish communities where limited quantitative data is often available for a large number of local species, CVAs have proven efficient and been applied to many areas of the world ocean (Pecl *et al.*, 2014; Hare *et al.*, 2016; Spencer *et al.*, 2019; Bueno-Pardo *et al.*, 2021; Ramos *et al.*, 2022; Carroll *et al.*, 2023). In CVAs vulnerability is usually assessed as the combination of trait-based sensitivity of individual species and their exposure to climate change due to spatial overlap with a hazard such as warming (Hare *et al.*, 2016).

Here we report on a first CVA for the fish community of the Western Baltic Sea, an important fishing ground for fisheries mainly in Denmark and Germany. The Western Baltic Sea is a transition area between the more saline areas bordering the North Sea (i.e. Skagerrak and Kattegat) and the low saline Baltic proper. Similar to most areas of the Baltic Sea, the Western Baltic Sea experienced significant climate-related warming that is expected to continue in the future (Dutheil *et al.*, 2022; Meier *et al.*, 2022). Along with the warming more frequent and longer marine heatwaves are reported that may play a role in the appearance of local hypoxic areas (Piehl *et al.*, 2023; Gröger *et al.*, 2024; Pinto *et al.*, 2024). Due to its dynamic physical oceanography (Leppäranta and Myrberg, 2009), the fish community of the Western Baltic Sea contains a peculiar mix of marine, brackish and freshwater species (Frelat

et al., 2018). Traditionally stocks of cod (*Gadus morhua*) and herring (*Clupea harengus*) supported profitable local fisheries that provided income and cultural identity for coastal communities (Döring *et al.*, 2020). Recently, both stocks collapsed due to the combined effects of overfishing and climate change (Möllmann *et al.*, 2021; Polte *et al.*, 2021) which caused an ongoing demise of local fisheries with important implications for local communities (Döring *et al.*, 2020; Lewin *et al.*, 2023). However, how future climate change will likely affect the entire fish community of the Western Baltic Sea is largely unknown. Consequently, knowledge is lacking about which species are critically endangered or may even be profitable resources under future novel environmental conditions. Lacking knowledge on the vulnerability of the Western Baltic fish community presently hampers efforts to transition the remaining fisheries towards a more sustainable future.

Our CVA involved a qualitative expert scoring of 22 fish species, assessing their sensitivity and exposure to climate change. Our study revealed a dichotomy in climate change vulnerability within the fish community of the Western Baltic Sea because traditional fishing targets and species with complex life histories are considered to face increased risks, whereas invasive or better adaptable species might thrive under changing conditions. Our findings hence demonstrate the complex interplay between life-history traits and climate change vulnerability in marine fish communities. Eventually, our study provides critical knowledge for the urgent development of tailored adaptation efforts addressing existing but especially future effects of climate change on fish and fisheries in the Western Baltic Sea, to navigate this endangered coastal fisheries systems into a sustainable future.

MATERIALS AND METHODS

Approach

We conducted a climate vulnerability assessment (CVA) for the fish community in the Western Baltic Sea, including the Belt Sea, the Sound and the Arkona Sea, covering the International Council for the Exploration of the Sea (www.ices.dk) sub-divisions 22-24 (Figure 1). The Western Baltic Sea is a mesohaline transition zone (salinities of

~20 PSU in the Belt Sea and ~7-10 PSU in the Arkona Sea/Pomeranian Bight) between the species-rich marine waters of the Kattegat-Skagerrak and the rather species-poor brackish Baltic Proper (Frelat *et al.*, 2018). We largely followed the CVA approach for fish communities developed for other areas that combines expert scorings of trait-based sensitivity of species with exposure scorings to locally important climate factors (Hare *et al.*, 2016; Spencer *et al.*, 2019). Similarly to these studies we considered adaptive capacity of the fish species to be covered by sensitivity attributes (Hare *et al.*, 2016).

Expert ratings of sensitivity were supported by detailed species profiles (see below – Sensitivity) that were prepared based on a comprehensive literature review. Species profiles were drafted by scientists within the balt_ADAPT project ("Adaptation of the Western Baltic Coastal Fishery to Climate Change"), who also conducted a preliminary test of the sensitivity scoring exercise. Afterwards species profiles were reviewed in a targeted workshop with additional experts on Baltic fish ecology external to the balt_ADAPT project. The final sensitivity scoring was developed by a combined group of balt_ADAPT and external scientists. Exposure scoring was conducted during two targeted project workshops by a sub-group within balt_ADAPT and prepared by analyses of available projections of physical-oceanographic variables (Saraiva *et al.*, 2019) and fish species distribution maps. Scoring exercises were conducted using online questionnaires prepared on the "Survey Solutions" online platform (https://mysurvey.solutions/en/). Background material on the questionnaire is available at https://github.com/GuiSPinto/cva_baltADAPT.

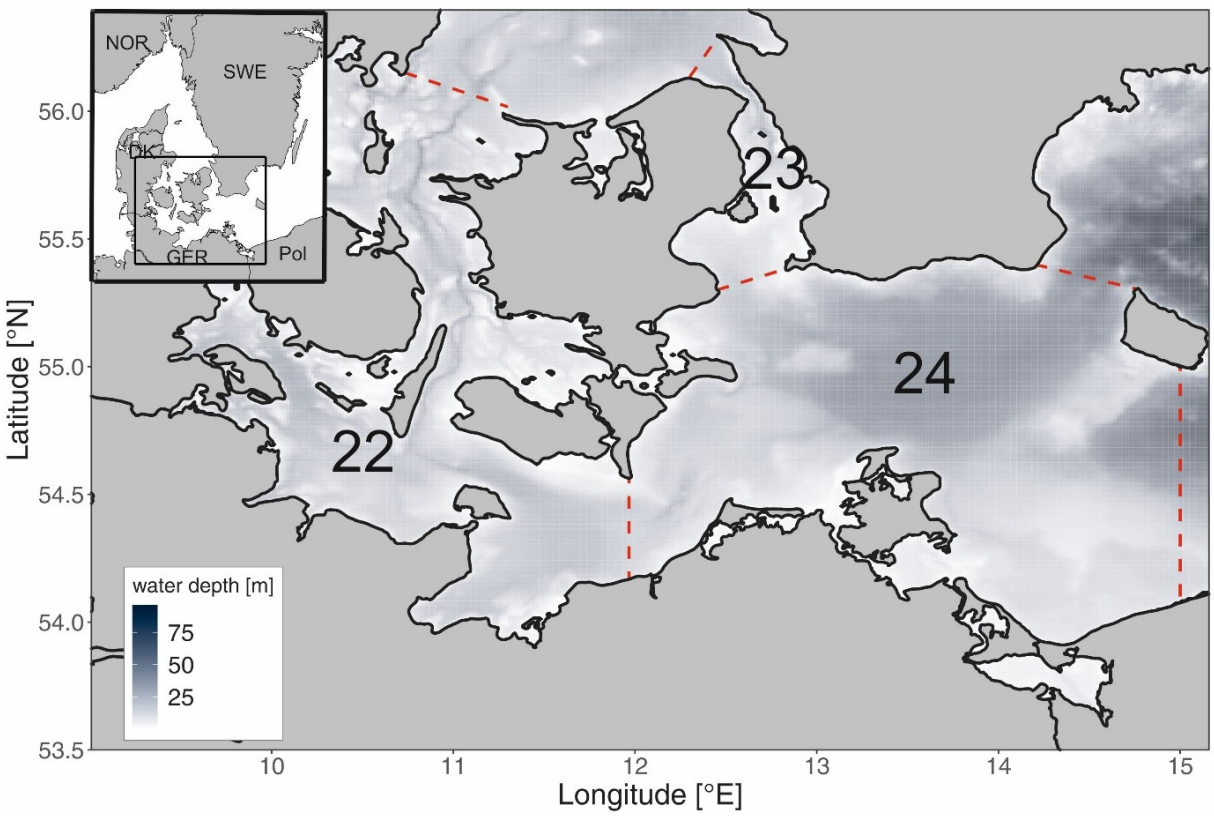


Figure 1. Study area. Map of the Western Baltic Sea with International Council for the Exploration of the Sea (ICES) management units (Sub-divisions: 22 – Belt Sea, 23 – Sound and 24 – Arkona Sea).

Sensitivity

Species list and profiles

As a first step of our study we selected fish species to be included in the CVA based on monitoring data on the local fish communities from the Baltic International Trawl Survey (BITS), accessible through the DATRAS webportal (https://datras.ices.dk). Based on species distribution maps (see below – Exposure) we selected species that persistently occur in the Western Baltic Sea. We additionally included fish species with lacking population data (mostly coastal fish species not covered by BITS) when local experts confirmed their occurrence and/or habitat use for distinct life stages (early life stage and/or adult stage) within our study area. Our species list contained 22 commercially-exploited marine, but also non-exploited marine and freshwater/brackish fish species (Table 1).

As a basis for the expert-based sensitivity scoring we developed profiles for each species based on an extensive literature research. Profiles contain comprehensive information with regard to 12 selected sensitivity attributes (Table 2). If available, we added distribution ranges within the study area as well as information on stock size, recruitment and growth to provide further background during the scoring process. We initially focused our literature research on local information for each fish species. However, in case regional information on certain biological traits of a species were lacking, we added information from adjacent and other regions of the world ocean. Fish profiles are available at https://github.com/GuiSPinto/cva_baltADAPT.

Attributes and scoring categories

Sensitivity attributes are biological traits/life history characteristics that show the capacity of a species to respond to a changing environment (Hare *et al.*, 2016). We included a set of 12 sensitivity attributes referring to specific environmental requirements during fish life history and modified these to fit within the scope of the Western Baltic Sea ecosystem (Table 2). Furthermore, we developed descriptions for the four different scoring categories (bins), i.e. low, moderate, high and very high, representing the different degrees of sensitivity for each attribute (see below – Data Analysis).

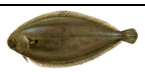
Exposure

Climate exposure maps

We initially aimed at exploring the exposure of fish species to climate-induced changes in temperature, salinity and oxygen, because these three oceanographic factors are known to strongly influence Baltic Sea fish communities (Frelat *et al.*, 2018; Möllmann, 2019). We hence explored oceanographic projections that are based on four regional climate models coupled to a regional three-dimensional ocean circulation model (Meier *et al.*, 2019; Saraiva *et al.*, 2019). The horizontal and vertical resolutions of the ocean model are 3.7 km and 3 m, respectively. Initial explorative analyses did not reveal clear future climate-related trends in salinity and oxygen in the Western Baltic Sea, which confirmed earlier analyses of projection outputs revealing difficulties in modelling salinity (Saraiva *et al.*, 2019), and the dominating

dependence of oxygen conditions on natural variability and eutrophication abatement strategies (Meier *et al.*, 2019, 2021). We hence focused our CVA on future climate-induced temperature changes (surface and bottom; °C).

Table 1. Fish species included in the Climate Vulnerability Assessment for the Western Baltic Sea. Pictures are from https://fish-commercial-names.ec.europa.eu/fish-names/; bold parts of the common names are used for simplicity in the further course of the paper.

Picture	*Scientific name*	*Common name*	*Ecotype*
	*Gadus morhua*	Atlantic **cod**	marine
	*Clupea harengus*	Atlantic **herring**	marine
	*Sprattus sprattus*	European **sprat**	marine
	*Merlangius merlangus*	**Whiting**	marine
	*Scophthalmus maximus*	**Turbot**	marine
	*Scophthalmus rhombus*	**Brill**	marine
	*Limanda limanda*	Common **dab**	marine
	*Platichthys flesus*	European **flounder**	marine
	*Pleuronectes platessa*	European **plaice**	marine
	*Solea solea*	Common **sole**	marine
	*Scomber scombrus*	Atlantic **mackerel**	marine
	*Chelon labrosus*	Thicklip grey **mullet**	marine
	*Belone belone*	**Garfish**	marine
	*Cyclopterus lumpus*	**Lumpsucker**	marine
	*Zoarces viviparus*	**Eelpout**	marine
	*Salmo salar*	Atlantic **salmon**	marine-freshwater (anadromous)

	*Salmo trutta*	Sea **trout**	marine-freshwater (anadromous)
	*Anguilla Anguilla*	European **eel**	freshwater-marine (catadromous)
	*Perca fluviatilis*	European **perch**	freshwater-brackish
	*Sander lucioperca*	**Pikeperch**	freshwater-brackish
	*Esox lucius*	Northern **pike**	freshwater-brackish
	*Neogobius melanostomus*	Round **goby**	freshwater-brackish

Seasonal and annual exposure maps were developed based on temperature projections according to Representative Concentration Pathways (RCP) scenarios RCP4.5 and RCP8.5 (Van Vuuren *et al.*, 2011). We explored differences in mean bottom and surface temperatures for a "mid of century" (MOC, 2040-2049) and an "end of century" (EOC, 2080-2089) period in relation to a reference period (2010-2019). For the MOC analysis, we used RCP4.5. only, since temperature trajectories of both RCPs only diverge later in the century (Saraiva *et al.*, 2019). We used Z-scores to measure the amount of future change relative to the reference period (Hare *et al.*, 2016; Spencer *et al.*, 2019):

$$|Z| = \left| \frac{\bar{X}_f - \bar{X}_r}{\sigma_r} \right| \quad (1)$$

where $\bar{X}_f$ is the mean of the future period, $\bar{X}_r$ is the mean of the reference period, and σ_r is the standard deviation of the reference period. Similar to Spencer *et al.* (2019), Z-scores were classified into four exposure bin categories: low ($|Z| \leq 0.5$), moderate ($0.5 < |Z| \leq 1.5$), high ($1.5 < |Z| \leq 2.0$), and very high ($|Z| > 2.0$). The direction of the changes in temperature was not considered since we only aimed at analyzing the amount of change. We mapped the data for all RCP and MOC/EOC combinations in a quartile fashion with mean layers (Spencer *et al.*, 2019). In total 6 maps of annual means (Figure 2.) and 24 quarterly maps (indicating seasonal changes) were produced as a basis for the exposure assessments of the Western Baltic Sea fish

species. All exposure maps are available at https://github.com/GuiSPinto/cva_baltADAPT.

Species distribution maps

We developed species distribution maps for comparison with exposure factor maps as a basis for the exposure scoring. We acquired data from ICES BITS and BIAS (Baltic International Acoustic Survey) as well as the Baltic Acoustic Sprat Survey (BASS), all accessible via DATRAS (https://datras.ices.dk). For our study, we included catch per unit effort (CPUE) data from 2010 to 2019 for BITS and BIAS, and from 2015 to 2019 for BASS. Inverse distance weighting (IDW) was applied for interpolating species distributions according to a grid of 0.05° longitude × 0.05° latitude (~3×6 km2). Each cell reports the median of annual values recorded across the entire period for that specific cell. Species distribution maps are available at https://github.com/GuiSPinto/cva_baltADAPT.

Expert scoring

Sensitivity scoring was conducted by a sub-group of the co-authors (20) representing expert knowledge with different educational/scientific backgrounds (aquatic ecology, fish and fisheries biology/ecology/oceanography). The heterogeneity of the group was assumed to cover expertise for the 22 different species selected. A sub-group of six co-authors familiar with Baltic Sea physical oceanography conducted the exposure scoring. A single questionnaire was prepared for the sensitivity assessment and exposure assessments were conducted in three separate questionnaires according to the three projection scenarios used (RCP4.5 MOC and EOC, RCP8.5 EOC).

We used a tally system for both expert sensitivity and exposure scorings (Hare *et al.*, 2016). Each expert distributed five tallies among the four different sensitivity/exposure categories (low, moderate, high, and very high) allowing the participants to express their expert certainty. Additionally, experts placed four tallies in three bin categories (negative, neutral and positive) to assess *Directional Effects* of climate-related environmental changes on the fish community during the sensitivity

assessment. Eventually, experts also assessed *Data Quality* for both sensitivity and exposure assessments using scores from 0 to 3 with 3 = adequate data, 2 = limited data, 1 = scoring based on expert judgement only, 0 = no data available (Hare *et al.*, 2016). Results of the scoring exercises were exported from the online platform into the free software environment for statistical computing and graphics R (R Core Team, 2023) for analysis.

Data analysis

Sensitivity and exposure scores

For each species i, we calculated a weighted mean of the individual expert scores on each sensitivity attribute (SA) and exposure factor (EF) (Hare *et al.*, 2016):

$$X_i = \frac{\big((L \times 1) + (M \times 2) + (H \times 3) + (VH \times 4)\big)}{(L + M + H + VH)} \quad (2)$$

where $X_i$indicates either SA_i or EF_i L, M, H and VH are the number of tallies in the "low", "moderate", "high" and "very high" scoring bins, respectively.

Table 2. List of sensitivity attributes and corresponding descriptions as baseline for the scoring process. Short versions of the attribute names in brackets as used in Figure 5.

Biological Attributes	*Description*	*Low sensitivity*	*High sensitivity*
Habitat Specificity [Habitat]	Relative dependence of a population to a habitat and the abundance of key habitats	Population is a habitat generalist and utilizes very common habitats during the entire ontogeny	Population is a specialist on an abundant habitat
Prey Specificity [Prey]	Population is a prey generalist or specialist	Population eats a large variety of prey (opportunistic feeder)	Population is partial to a single prey type (prey specialist)
Adult Mobility [Mobility]	Ability of the population to move if their current location becomes unsuitable (homing behavior excluded)	Highly mobile and non-site dependent adults	Site dependent adults with limited mobillty
Dispersal of Early Life Stages [Dispersal]	Ability of the population to colonize new habitats	High egg and larvae dispersal	Low egg and larval dispersal
Early Life History Survival and Settlement Requirements [ELH]	Relative importance of early life history requirements for the population	Eggs and larvae have minimal requirements	Eggs and larvae have some specific requirements
Complexity in Reproductive Strategy [Complexity]	Sensitivity of reproductive strategy to climate change. Reproductive characteristics are (e.g.): Diadromous migration, parental care/guarding nest behavior, homing behavior)	Simple reproductive strategy (no more than one characteristic)	Complex reproductive strategy (three characteristics)
Population Spawning Cycle [Spawning]	Spawning strategies are sensitive to climatic changes (focus on the dominant population within the system)	Consistent throughout the year without a defined spawning season	One spawning event per year within a confined time frame
Sensitivity to Temperature [Temperature]	Known temperature of occurrence or the distribution of the species as a proxy for sensitivity to temperature	Wide temperature range throughout ontogeny and adapted to warmer water temperatures/no impact on spawning phenology	Somewhat limited temperature range throughout ontogeny and adapted to colder water temperatures/moderate/high impact on spawning phenology
Sensitivity to Salinity [Salinity]	Known salinity tolerance or the distribution of the species as a proxy for sensitivity to salinity	Euryhaline/life stages occurring in the Baltic Sea are euryhaline	Limited salinity range/life stages occurring in the Baltic Sea show a limited salinity range

Sensitivity to Ocean Acidification [Acidification]	Sensitivity or tolerance against decreased pH (relationship to "sensitive taxa")	Population either does not rely on pH sensitive taxa (for food), or is expected to show no effect/impact to ocean acidification	Population is reliant on sensitive taxa and/or certain life stage is negatively affect by a decrease in pH
Population Growth Rate [Growth]	Productivity of the population, using distinct parameters (max. growth rate, von Bertalanffy K, age at maturity, max. age, natural mortality M, measured max. length)	Population growth rate is high, high productivity.	Population growth rate is low, low productivity, affected to any environmental changes.
Additional stressors [Other]	Other factors that could limit population responses to climate change (other than fishing pressure)	Population is experiencing limited stress (no/ no more than one known stressor, i.e., sensitivity to low oxygen, predation pressure, cannibalism, pollutants, anthropogenic stressors (eutrophication, habitat modification))	Population is experiencing moderate/high stress (no more than tow to three known stressors, i.e., sensitivity to low oxygen, predation pressure, cannibalism, pollutants, anthropogenic stressors (eutrophication, habitat modification))

Based on individual SA_i scores, we calculated sensitivity scores for each species by numerical averaging and additionally by using a logic rule (Hare *et al.*, 2016). According to the latter, species are scored into the VH category when ≥ 3 individual attributes have mean values ≥ 3.5, into the H category when ≥ 2 of the attributes have mean values ≥ 3.0, into the M category when ≥ 2 attributes have mean values ≥ 2.5, and into the L category when < 2 attributes have mean values ≥ 2.5. Usually a logic rule is preferred over numeric averages because attributes and factors are not intended to be correlated (Johnson and Welch, 2009). However, using numeric values allowed us to analyse the variability of SA_i between species using Principal Component Analysis (PCA) and Hierarchical Clustering (see below).

Since we only used temperature as an EF_i we could not apply the original logic rule (Hare et al., 2016). We hence distributed scores into categories based on their mean numeric values (VH = >3.25, H = 2.50 – 3.25, M = 1.75 – 2.49, L = 1.00 – 1.74).

Directional effects

We computed directional effects (DE) as a weighted mean of the individual expert scorings (Hare *et al.*, 2016):

$$DE_i = \frac{\big((Pos \times 1) + (Neu \times 0) + (Neu \times -1)\big)}{P + Neu + Neg} \quad (3)$$

where Pos are the tallies scored in the "positive category", Neu are the tallies scored in the "neutral category", and Neu are the tallies scored in the "negative category". We classified an overall negative effect when the score was < -0.333, a neutral effect between - 0.333 – 0.333 and a positive effect when the score was > 0.333.

Vulnerability

We calculated the overall vulnerability of each species by multiplying the mean sensitivity and exposure scores. We distributed scores into vulnerability categories based on their mean numeric values (VH ≥ 3.25, H = 2.50 – 3.25, M = 1.75 – 2.49, L = 1.00 – 1.74).

Certainty analysis

We explored the variability of the assessments between experts based on a bootstrap analysis (Hare *et al.*, 2016). Scores were resampled 103 times with replacement from the sensitivity and exposure assessments, and the process was repeated for each sensitivity and exposure category. Subsequently, we combined each run to calculate the final vulnerability score. The final certainty score represents the highest percentage of the computed vulnerability score distribution. We used the same approach to evaluate certainty for the direction of effects of climate on each fish species.

Software tool and libraries

All analyses and visualizations were performed in the free software environment for statistical computing and graphics R (R Core Team, 2023) using Rstudio (Posit Team, 2024) and the packages "tidyverse" (Wickham *et al.*, 2019), "factoextra" (Kassambra and Mundt, 2020), "cluster" (Maechler *et al.*, 2023) and "pheatmap" (Kolde, 2019).

RESULTS

Sensitivity

Thermal tolerance of species and scoring of individual attributes

Figure 3 provides an overview of thermal tolerances and mean (across all experts) scores for the 12 attributes quantifying the sensitivity to climate change of 22 fish species inhabiting the Western Baltic Sea. Thermal tolerances are indicated because of our focus on exposure to temperature changes. Scores of individual climate sensitivity attributes provide the basis for the evaluation of overall species' sensitivity (Figures 4 & 5).

Sensitivity scores and directional effects

Mean numeric sensitivity scores derived from our expert assessment largely match the categorization according to the logic rule (Figure 4A). 10 out of 22 species were assessed to have a high or very high sensitivity to climate change. In addition to salmon, trout and eelpout, the sensitivity of eel to climate change was rated as very

high while the numeric score is a little lower compared to the other three species. Other species considered to be of high sensitivity were two traditional fishing targets as cod and herring, pike and pikeperch (freshwater origin), and lumpsucker. Additionally, the seasonally immigrating mackerel was rated to have a high sensitivity while the numeric score was comparatively low. The high sensitivity of mackerel resulted from high scores for the three attributes Spawning (full names of the attributes given in Table 2), Temperature and Salinity, while other attributes were assessed to be relatively low (Figure 5). On the other end, experts scored mullet and sprat to be least sensitive. Overall, 10 out of 22 species were assessed to have a moderate sensitivity to climate change, including all flatfish species.

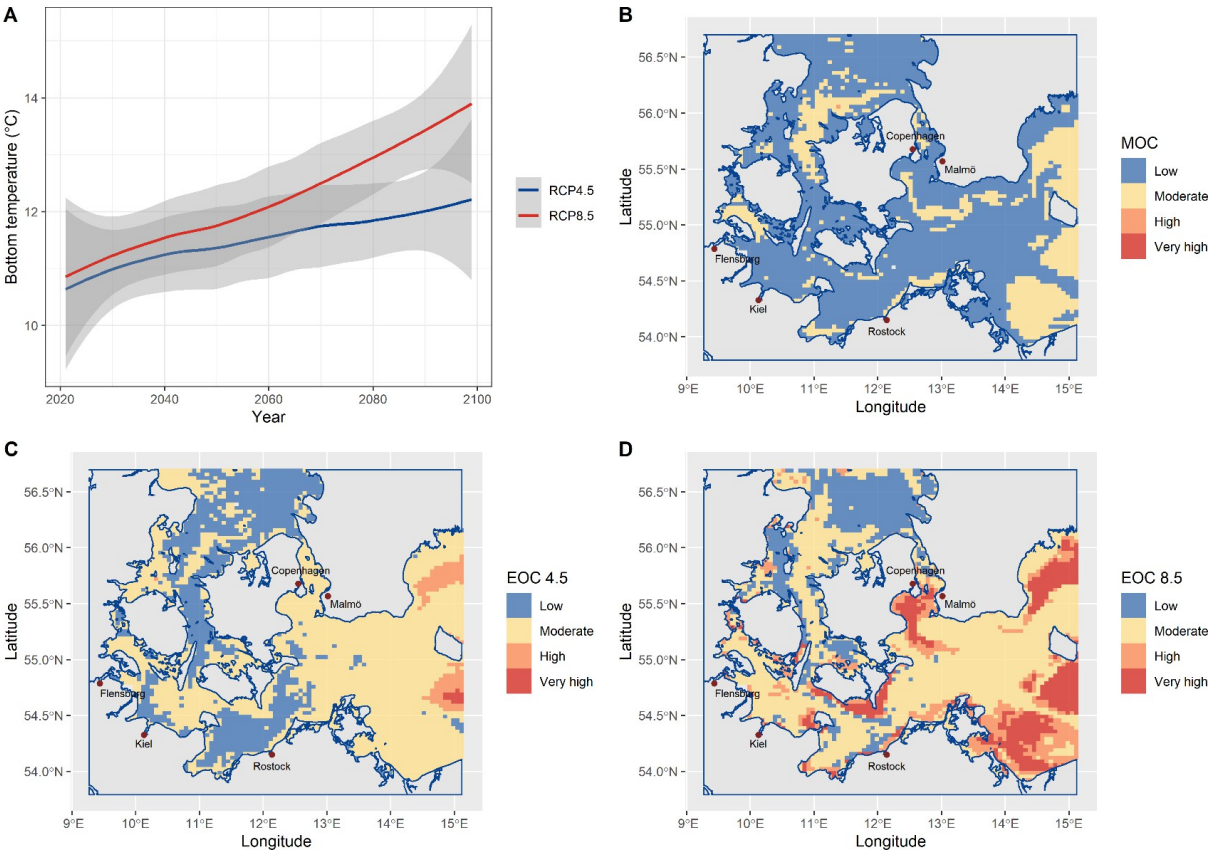


Figure 2. Future temperature changes in the Western Baltic Sea. Example maps illustrating future bottom summer temperature changes used to assess the exposure of the fish community. (A) Temperature projections for mean bottom temperature under emission scenarios RCP4.5 and RCP8.5. (B) Map of Z-scores for the "mid of century" (MOC, 2040-2049) scenario. (C) Map of Z-scores for the "end of century" (EOC, 2080-2089) scenario under RCP4.5. (D) Map of Z-scores for the "end of

century" (EOC, 2080-2089) scenario under RCP8.5. Z-scores in B – D are categorized into Low, Moderate, High and Very High.

Numeric scores for the directional effects of climate change matched the categorization according to the logic rule and all neutral scores were significantly higher than the negative and lower than the positive scores (Figure 4B). Furthermore, directional effects largely reflect the assessment of overall fish sensitivity. Very highly and highly sensitive species were generally assessed to be negatively affected by climate change with the exception of pike and pikeperch, which were categorized as neutral (Figure 4A). Cod and herring, the traditionally most important fisheries targets, were rated to likely experience the strongest negative effects due to climate change. On the other end of the spectrum, species with the lowest sensitivity as mullet and sprat were assessed to profit from climate change (positive effect). The highest positive effect of climate change is indicated for the invasive goby that was rated with being only moderately sensitive, but with a very low numeric score.

Importance of sensitivity attributes

We analysed the importance of individual attributes for the sensitivity of fish species to climate change using Hierarchical Clustering (HC) and Principal Component Analysis (PCA). According to the expert assessment, life-cycle attributes mainly determine the sensitivity of species to climate change. A main "attribute" cluster (upper left part of the heatmap in Figure 5A) groups together species displaying complex reproductive strategies (Complexity), including temporally-restricted and few spawning events (Spawning) and low dispersal rates of early life stages (Dispersal), which additionally have specific survival and settlement requirements (ELH). Further attributes of species lumped together in this cluster are specific habitat requirements (Habitat) and additional stress factors (Other). Typically, these attributes are distinctive of fish that have a high or very high sensitivity to climate change. Main representatives of these sensitive groups (denoted by 1 and 2 in Figure 5B) include (a) salmon, trout and eel, which have diadromous life-cycles; (b) herring (specific habitats are required for their benthic eggs); (c) eelpout and lumpsucker as they do depend on a form of brood care; and (d) pike and pikeperch, which have freshwater

origin and in the Western Baltic Sea live at the limits of their distribution. Species of group 1 differ from those of group 2 mainly because of the sensitivity to temperature, which characterizes the second cluster (Figure 5B).

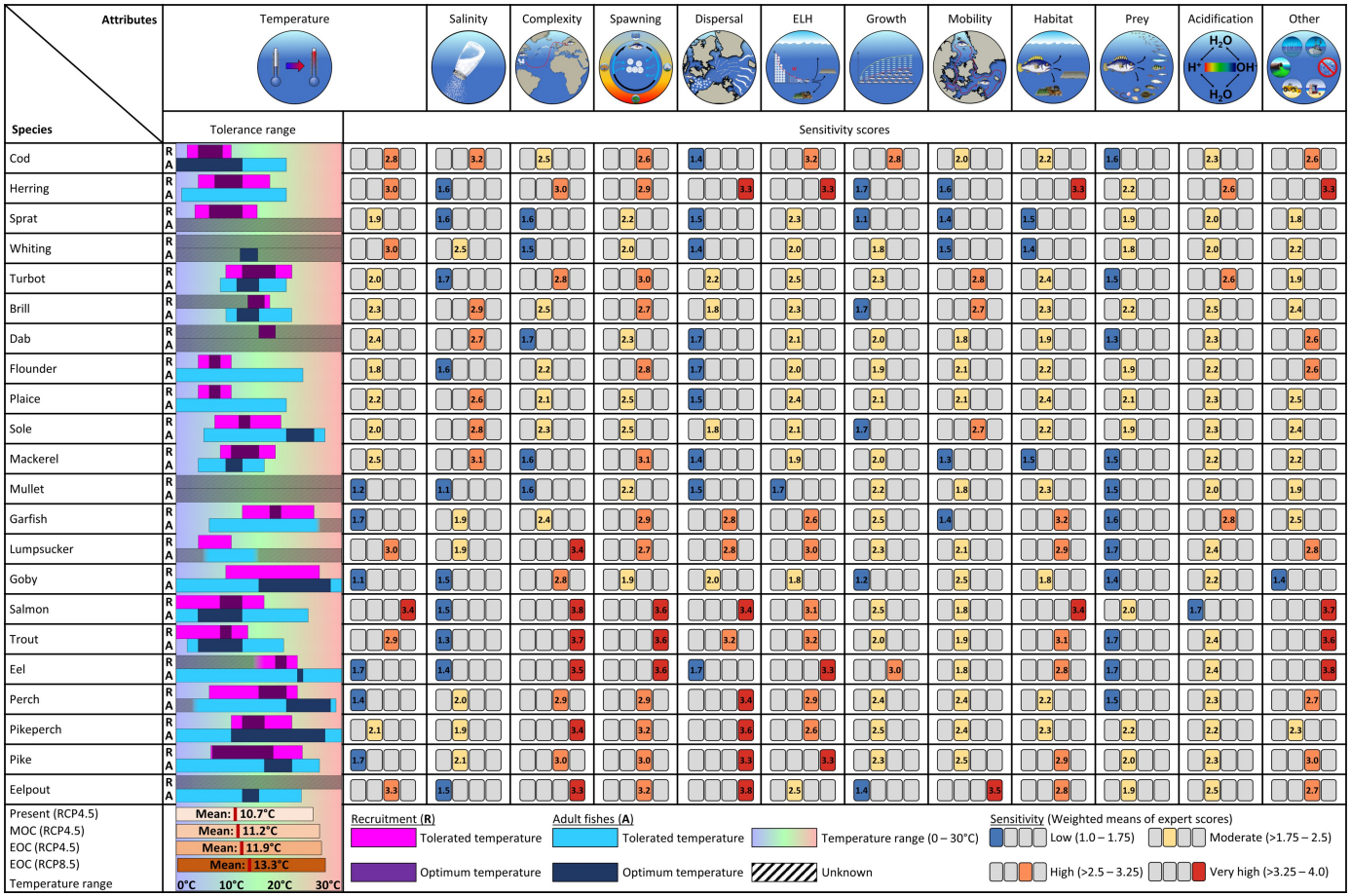


Figure 3. Summary of thermal tolerances and attribute-based sensitivity scores of Western Baltic fish species. Species names are according to Table 1; thermal tolerance ranges reflect the needs of species for recruitment (R) and adult stages (A) as found in the literature (see species profiles); sensitivity scorings represent the means calculated over the values provided by all experts; RCP4.5 and 8.5 represent emission scenarios (see Material and Methods); MOC – middle of the century; EOC – end of century.

The relationship between complex life-cyles and the sensitivity to climate change is also demonstrated by the results of the PCA (Figure 5B). Species considered to be of high and very high sensitivity (groups 1 and 2) are positively related to the dominant mode of variability (Dim1) as are the traits from the main "sensitivity attribute" cluster (upper cluster in Figure 5A). Species of low to moderate sensitivity (groups 3 and 4) are consequently negatively related to Dim1. These groups contain almost exclusively marine species (and goby), including almost all flatfish species (except turbot) that generally have less challenging life-cycles (Figure 5A). A sub-cluster (group 3, Figure 5B) is positively related to the second mode of variability (Dim2) and hence characterized by high sensitivity to salinity. Species of this groups include mackerel (pelagic), two bottom-dwelling flatfish as dab and plaice, and the demersal gadids cod and whiting. Negatively related to Dim2 are species considered to be of low mobility such as the highly-sensitive eelpout and the low-sensitive goby.

Experts additionally rated the quality of the data available for assessing the sensitivity of the species (https://github.com/GuiSPinto/cva_baltADAPT). The two commercially-important species cod and herring are considered as those best studied. A general lack of information on the attribute Acidification. Data availability on some sensitivity attributes (Other, ELH, Temperature, Complexity) was limited for some species.

Exposure to temperature change

Exposure to climate-related warming was rated based on the overlap of individual spatial distributions of fish species with temperature projections according to "mid of century" (MOC; only RCP4.5) and "end of century" (EOC; RCP4.5 and 8.5) scenarios (Figure 6). Similar to the sensitivity, numeric scores of exposure largely match the categorization obtained using our modified logic rule. Exposure to temperature under both RCP4.5 (MOC and EOC) scenarios was generally rated to be low, with a slight increase in the mean numeric score towards later in the century (1.2 and 1.5 for MOC and EOC, respectively). Exposure scores for EOC increase under RCP8.5 to largely moderate (mean score of 2.2), except for cod that is rated as highly exposed (mean score of 2.9). The commercially important species cod, herring and sprat have

generally the highest exposure values. Species such as dab and mullet are often found at the lower exposure range. Data quality for the exposure ratings was high for the traditional target species of the fishery but low for less abundant marine, freshwater-marine, and freshwater-brackish species (Table 1; https://github.com/GuiSPinto/cva_baltADAPT).

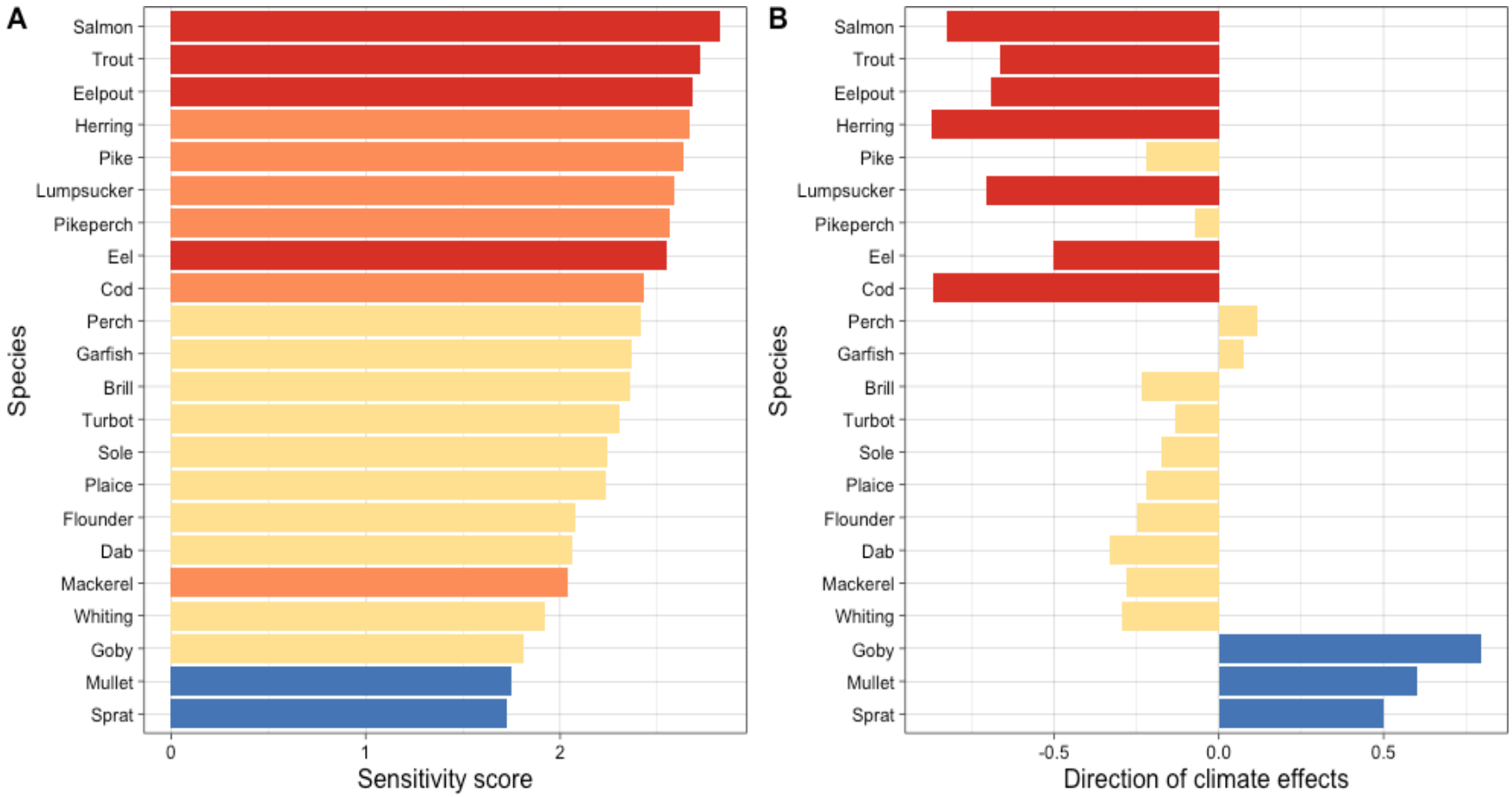


Figure 4. Sensitivity of Western Baltic fish species to climate change. (A) Species' sensitivity calculated as the weighted mean over 12 individual sensitivity attributes and using all expert scores; colours represent sensitivity scores according to the logic rule: red – very high, orange – high, yellow – moderate, blue – low. (B) Directional effects of climate change obtained as weighted means over all expert scores; colours represent categorization according to the logic rule: red – negative, yellow – neutral, blue – positive.

Vulnerability

Combing scores on overall sensitivity for each of the 22 fish species with those on the exposure to future warming yielded in the final assessment of their vulnerability to climate change (Figure 7). Numeric scores (mean = 1.6) as well as the categorization according to the logic rule indicate a low vulnerability of all species until the mid of the century (Figure 7A). Vulnerability increases towards the end of the century and varies according to emission scenario. Under RCP4.5, the overall numeric score only slightly increased compared to the earlier period (mean = 1.8) but the categorization according to the logic rule indicates a split of the fish community in species with low and moderate vulnerability (Figure 7B). Under the high emission scenario (RCP8.5; mean = 2.2), most of the fish species are rated to be moderately vulnerable and only goby and mullet stay with low vulnerability (Figure 7C). The commercially important cod and herring, the diadromous fish as salmon and trout, eelpout, and lumpsucker all exhibit a high vulnerability to climate change.

We also investigated the certainty of vulnerability scores using bootstrapping and found high values close to 1 (Figure 7). Notable exceptions are the mostly freshwater species perch, pike and pikeperch as well as a catadromous species as eel under the MOC scenario, and some species under the RCP8.5 scenario at the end of the century (i.e., salmon, cod, and trout).

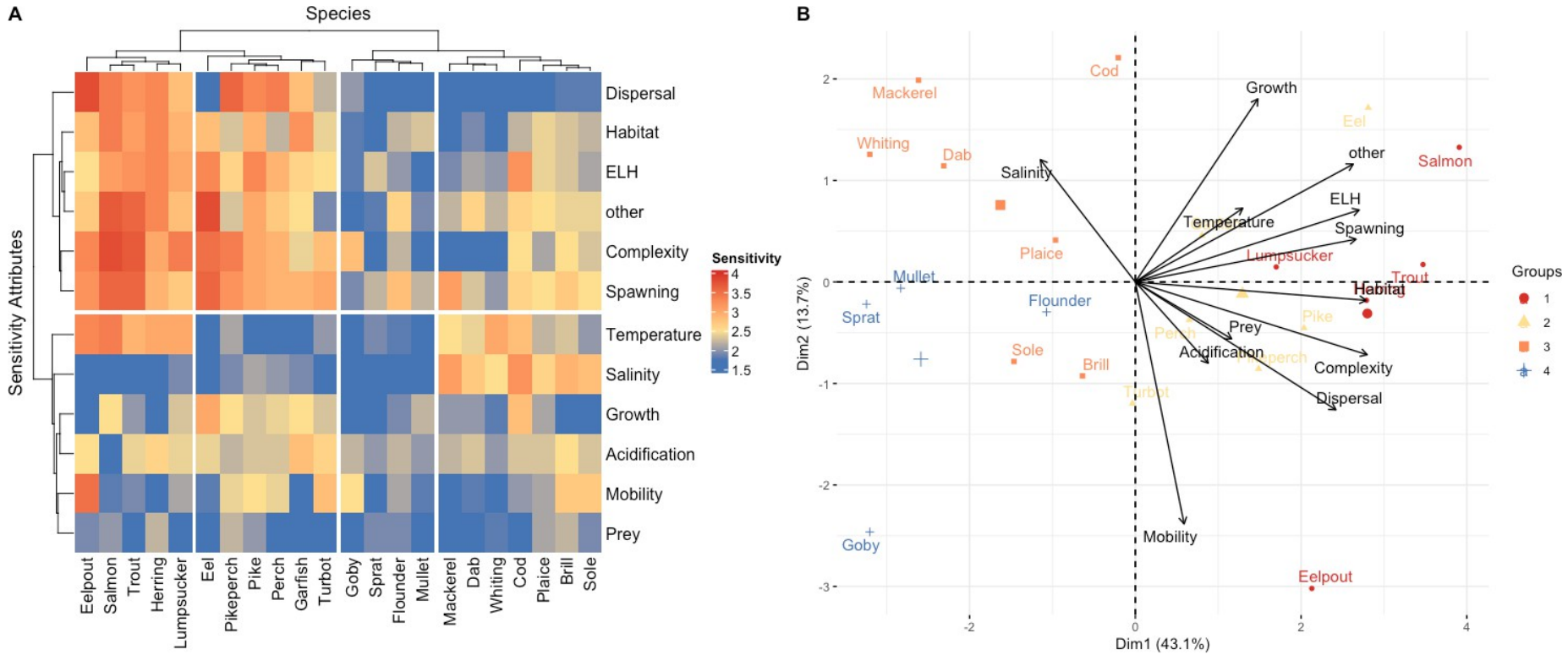


Figure 5. Relationships between sensitivity attributes and Western Baltic fish species. (A) Heatmap showing sensitivity attributes (rows) and species (columns); dendrograms and map splitting reflect the hierarchical clustering. (B) Principal Component Analysis biplot projecting attributes and species on the first two dimensions (Dim1, Dim2); colours of species groups assigned according to hierarchical clustering; complete attribute names and descriptions are provided in Table 2; species overplotted by "Habitat" is "Herring".

DISCUSSION

We here report on a first climate vulnerability assessment (CVA) of a fish community in the Baltic Sea where knowledge on how climate change will likely affect entire fish communities is deficient. A general lack of quantitative data for many of the fish species is also characteristic for our study area, the Western Baltic Sea, and we hence implemented a qualitative, expert-based approach that has been applied to many areas of the world ocean and returned promising results (Pecl *et al.*, 2014; Hare *et al.*, 2016; Spencer *et al.*, 2019; Bueno-Pardo *et al.*, 2021; Ramos *et al.*, 2022). Because of the uniqueness of the Western Baltic Sea ecosystem, a transition basin between the more saline areas bordering the North Sea (i.e., Skagerrak and Kattegat) and the low saline Baltic proper (Lehmann *et al.*, 2022), we had to adjust the attribute and category descriptions for the sensitivity assessment to the special conditions of our study region. We supported the assessment of the 12 species attributes by comprehensive fish profiles that were the result of an extensive review of the available literature. The literature is unsurprisingly dominated by studies on cod and herring, the two traditional commercial targets, an aspect that may have contributed to the dominant perception of their high sensitivity to climate change. Data quality assessments especially also revealed a lack of information on the potential effects on single attributes, and especially on ocean acidification as an important climate change effect for almost all species (but see Stiasny *et al.*, 2016). To provide a reliable CVA, we made an effort to assemble a group of participating scientists that represented broad ecological expertise on the 22 fish species considered. Nevertheless, a broader and more international participation of experts may contribute to sharpening potential future CVA outcomes.

A major result of our study is that marine and freshwater species with complex life-cycles attributes were assessed to have high and very high sensitivity to climate change effects. Highly sensitive species are especially anadromous salmonids (salmon and trout), and the catadromous eel. Such diadromous life-cycles are characterized by complex spawning migrations between freshand seawater habitats, with distinct spawning periods and specific requirements for the well-being and

survival of their early life stages (Sternecker *et al.*, 2014; Heessen *et al.*, 2015; Smialek *et al.*, 2021). The typically long migrations of diadromous species expose them to a multitude of anthropogenic and natural pressures limiting e.g. connectivity between habitats (Kappel, 2005; Van Puijenbroek *et al.*, 2019; Costa *et al.*, 2021). The state of European eel populations showcases their high sensitivity, not only to climate change, but to a multitude of cumulative pressures. European eel is currently assessed as critically endangered with a dramatic decline in recruitment and no signs of recovery (ICES, 2020).

Additionally to diadromous species, fish displaying further aspects characteristic of complex life-history strategies have been rated highly sensitive by experts. This group includes species typically requiring specialised habitats for benthic egg deposition such as in herring and garfish (Von Nordheim *et al.*, 2018; Veneranta and Urho, 2021), and species conducting a form of brood care like eelpout and lumpsucker (Manica and Johnstone, 2004; Hedman *et al.*, 2011). Also species of freshwater origin that live in the Western Baltic Sea at the limits of their salinity tolerance (i.e., pike, perch, and pikeperch) are considered highly sensitive. These latter species display complex reproductive strategies, require special vegetation for spawning (Balon, 1985), and have a pronounced homing behavior (Jepsen *et al.*, 1999; Lappalainen *et al.*, 2003; Engstedt *et al.*, 2014; Christensen *et al.*, 2021).

In contrast to species with complex life-history stategies, successful invaders to the Baltic Sea such as goby, mullet and sprat were assessed to be least sensitive and may hence profit from climate change. For goby, low sensitivity scores are in accordance with the literature that reports this species to benefit from climate-related environmental changes (Tomczak and Sapota, 2006), because of a broad thermal tolerance (Kornis *et al.*, 2012; Christensen *et al.*, 2021) and a high potential for adaptation to local environmental conditions (Björklund and Almqvist, 2010). In contrast to the invading goby, the two least sensitive species in our assessment, i.e. mullet and sprat, reached the Baltic Sea by range expansions and both species adapted to the wide range of salinities and temperatures. Sprat is widely established and occupies a broad range of the basin, from southern to northern areas (Parmanne

et al., 1994), while a regular occurrence of mullet in the north of the Baltic Sea is a recent phenomenon (Schaber *et al.*, 2011).

A further obvious result of our study is that experts assessed the traditionally dominating fishing targets in the Western Baltic, cod and herring, as highly sensitive to climate change. In contrast to other highly sensitive species, the sensitivity of cod is not related to any complex life-cycle attributes, but to its dependence on higher salinities (Nissling and Westin, 1997). Generally, cod is considered to suffer from the effects of climate change in the Western Baltic Sea, especially warming, while the exact process is still unclear (Funk *et al.*, 2020, 2023; Möllmann *et al.*, 2021; Receveur *et al.*, 2022). In contrast, herring is tolerant to a wide range of salinity changes (Klinkhardt, 1986a, 1986b), but belongs to the group of climate sensitive species because of its rather complex life cycle. Demersal spawning of herring requires specific habitats such as vegetated coastal waters, i.e., estuaries, lagoons, and bays (Polte *et al.*, 2017). Egg development and recruitment are therefore highly dependent on environmental conditions and especially the temperature regime in the littoral zone. Our exposure analysis revealed that essential inshore nursery habitats will face drastic future warming, potentially limiting recruitment and reducing stock productivity. Furthermore, milder winter temperatures in recent years have likely caused a shift in spawning phenology, resulting in a potential mismatch of prey items for herring larvae during their critical first-feeding stage (Polte *et al.*, 2021).

In contrast to cod and herring, our expert-based assessment revealed flatfish species to be less sensitive to the effects of climate change in the Western Baltic Sea. The recent drastic increase in plaice in the area may be a result of their low climate sensitivity (ICES, 2023). The increase in the bottom living plaice stock is surprising given the increasing extension of hypoxic bottom zones in the Western Baltic Sea (Piehl *et al.*, 2023; Gröger *et al.*, 2024; Pinto *et al.*, 2024). Hypoxic conditions are expected to decrease the availability of suitable habitats for flatfish, but also cod. However, physiological studies point towards a stronger resilience of flatfish compares to the combined effects of warming and deoxygenation compared to cod (Seibel, 2023).

Experts considered exposure of Western Baltic fish species to warming to be mainly low under the moderate RCP4.5 scenario, increasing to largely moderate only under the most severe emission scenario RCP8.5. The overall low to moderate exposure mainly reflect that temperature projections indicate a weaker warming for the Western Baltic Sea compared to the eastern and northern Baltic Sea areas (Dutheil *et al.*, 2022). As a result most of the area considered in our study fell within the low or moderate warming category. A further reason for the low exposure is that we considered the period of 2010 – 2019 as the baseline for the categorization of warming. This decade already experienced a significant degree of warming compared to pre-industrial times thus reducing the chances of detecting major significant differences when contrasted with future projections (Dutheil *et al.*, 2022). Our exposure rating hence quantifies the extent of additional future warming in the Western Baltic Sea.

The exposure assessment generally bears most of the room for improvement in a future CVA for the Western Baltic fish community. We used the best available survey data to assess the spatial overlap of the species with future thermal conditions, however these surveys do not sufficiently cover the distribution ranges of all species as especially known for cod (Funk *et al.*, 2020, 2021). Moreover, the data cover only some seasons, not accounting for seasonal migrations. Additionally, many of the species that are traditionally of no high commercial importance such as pike, perch and pikeperch are not targeted by the existing monitoring programmes, hence no numeric information on their distribution exists.

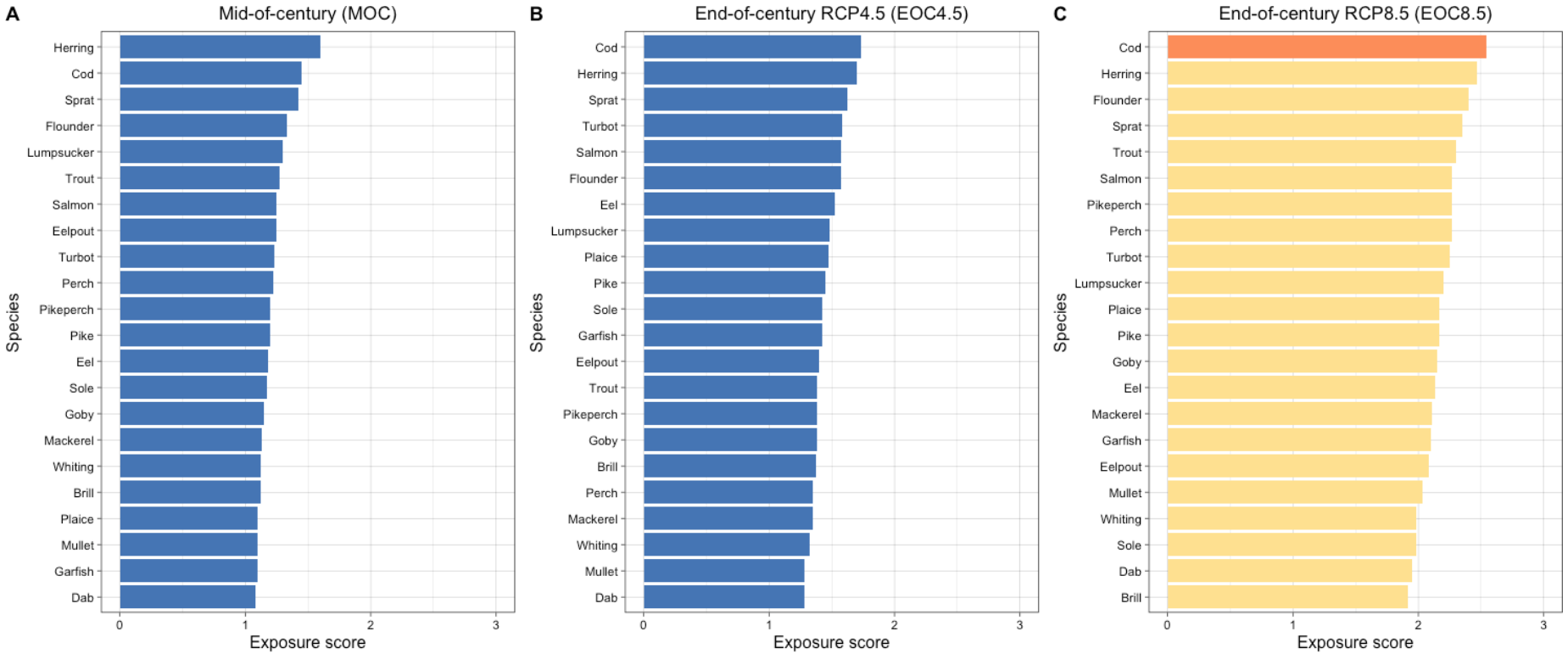


Figure 6. Exposure of the Western Baltic fish species to climate change. Exposure scores for (A) RCP4.5 mid-of-century climate scenario, (B) RCP4.5 end-of-century climate scenario, and (C) RCP8.5 end-of-century climate scenario. Colours represent sensitivity scores according to the logic rule: orange – high, yellow – moderate, blue – low.

A further limitation of our assessment is that we only focused on the exposure to warming because of uncertainties in the future projections of salinity and oxygen conditions (Saraiva *et al.*, 2019; Meier *et al.*, 2021; Dutheil *et al.*, 2022). Furthermore, detrimental oxygen conditions are assumed to be mainly determined by eutrophication, while the importance of ocean warming for the increased occurrence of oxygen minimum zones needs further investigations (Friedland *et al.*, 2023; Piehl *et al.*, 2023). Variability in salinity is also crucially important for fish species in the Western Baltic Sea, an area with a dynamic hydrography (Leppäranta and Myrberg, 2009), since they will likely affect the productivity and distribution of all the species (documented for each species in the species profiles; see Material and Methods). Future exposure ratings need to better include these in the CVA when more reliable projections of salinity and oxygen are available. Future assessments may additionally comprise indices for future changes in plankton productivity and ocean acidification (Hare *et al.*, 2016).

Combing sensitivity and exposure provided vulnerability assessments of the Western Baltic fish species to climate change. Vulnerability is expected to be generally low until the middle of the century, and increased to moderately or high depending of emission scenario and species considered. Vulnerability assessments largely reflect the sensitivity of the species, because exposure was generally less variable. The most vulnerable species include the traditional fishing targets cod and herring as well as the salmonids salmon and trout, which altogether are also found under the species with highest sensitivity and exposure scores. Highly vulnerable outcomes are also found for lumpsucker and eelpout, two species with a high sensitivity but comparatively lower exposure scores. Other highly sensitive species like the mainly freshwater species (i.e. pike, perch, and pikeperch) are categorized as moderately vulnerable due to their lower exposure ratings, a result that holds true also for eel. Lowest vulnerability is found for goby and mullet, mainly because of their low sensitivity scores.

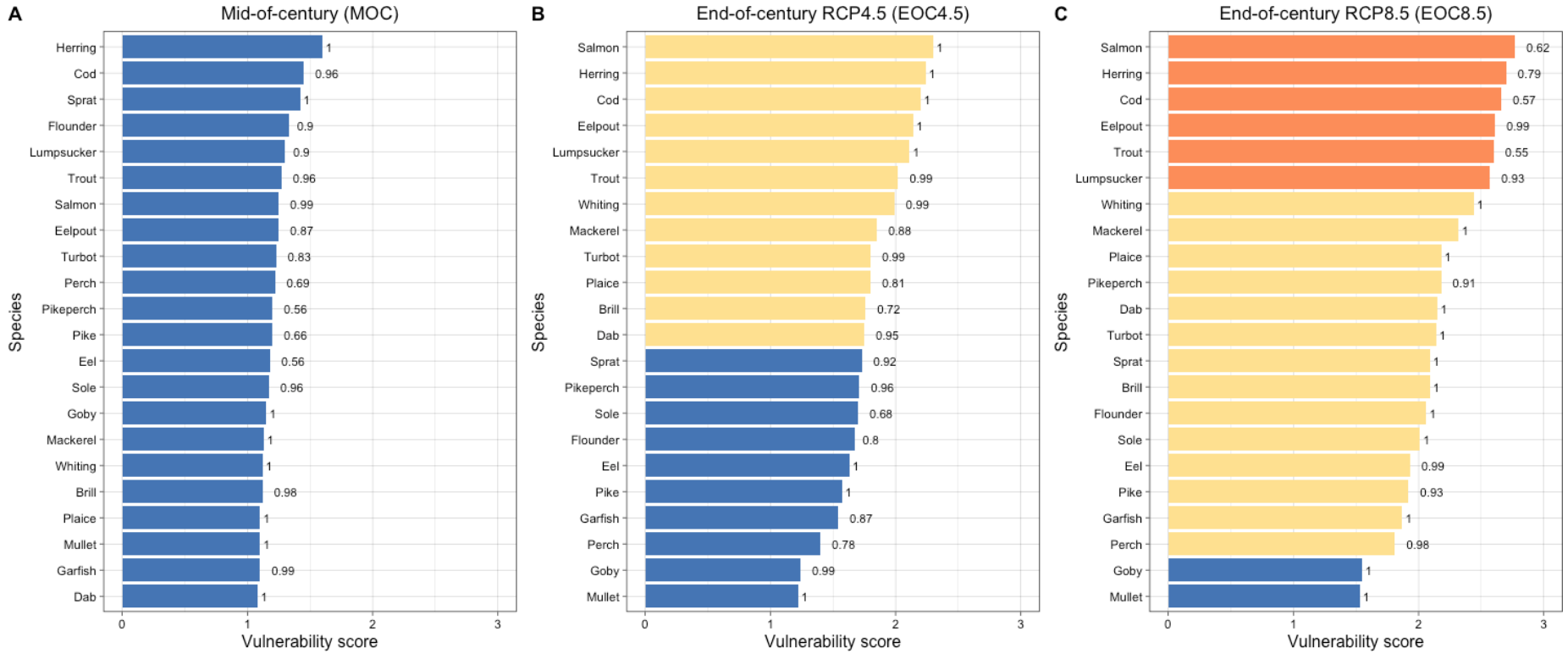


Figure 7. Vulnerability of Western Baltic fish species to climate change. Vulnerability scores are reported for (A) RCP4.5 mid-of-century climate scenario, (B) RCP4.5 end-of-century climate scenario, and (C) RCP8.5 end-of-century climate scenario. Colours describe the intensity of sensitivity scores according to the logic rule: orange – high, yellow – moderate, blue – low. Certainty estimates derived by bootstrapping are added as numbers next to individual bars.

Conclusions

Our study revealed a dichotomy in climate change vulnerability within the fish community of the Western Baltic Sea. Traditional fishing targets and species with complex life histories face heightened risks, whereas invasive or adaptable species might thrive under changing conditions. Such a scenario presents significant ecological and economic implications, particularly for local fisheries traditionally reliant on sensitive species like cod and herring. Our findings furthermore demonstrate the complex interplay between life-history traits and climate change vulnerability in marine fish communities. Our analysis, while methodologically robust, also highlights the limitations inherent in such assessments. The dearth of comprehensive ecological data, particularly on non-commercial species, and the focus on temperature as a primary climate factor without fully integrating other critical parameters like salinity and oxygen levels, suggest areas for improvement in future studies. Overall, our study is a call for the urgent development of tailored adaptation efforts addressing existing but especially future effects of climate change on fish and fisheries in the Western Baltic Sea to navigate this endangered fisheries systems into a sustainable future.

REFERENCES

Balon, E. K. 1985. Early ontogeny of Labeotropheus Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *In* Early life histories of fishes: New developmental, ecological and evolutionary perspectives, pp. 207–236. Ed. by E. K. Balon. Springer Netherlands, Dordrecht. http://link.springer.com/10.1007/978-94-010-9258-6_11 (Accessed 11 December 2025).

Björklund, M., and Almqvist, G. 2010. Rapid spatial genetic differentiation in an invasive species, the round goby Neogobius melanostomus in the Baltic Sea. Biological Invasions, 12: 2609–2618.

Bueno-Pardo, J., Nobre, D., Monteiro, J. N., Sousa, P. M., Costa, E. F. S., Baptista, V., Ovelheiro, A., *et al.* 2021. Climate change vulnerability assessment of the

main marine commercial fish and invertebrates of Portugal. Scientific Reports, 11: 2958.

Carroll, G., Eurich, J. G., Sherman, K. D., Glazer, R., Braynen, M. T., Callwood, K. A., Castañeda, A., *et al.* 2023. A participatory climate vulnerability assessment for recreational tidal flats fisheries in Belize and The Bahamas. Frontiers in Marine Science, 10: 1177715.

Christensen, E. A. F., Svendsen, M. B. S., and Steffensen, J. F. 2021. Population ecology, growth, and physico-chemical habitat of anadromous European perch Perca fluviatilis. Estuarine, Coastal and Shelf Science, 249: 107091.

Costa, M. J., Duarte, G., Segurado, P., and Branco, P. 2021. Major threats to European freshwater fish species. Science of the Total Environment, 797: 149105. Elsevier.

Döring, R., Berkenhagen, J., Hentsch, S., and Kraus, G. 2020. Small-Scale Fisheries in Germany: A Disappearing Profession? *In* Small-Scale Fisheries in Europe: Status, Resilience and Governance, pp. 483–502. Ed. by J. J. Pascual-Fernández, C. Pita, and M. Bavinck. Springer International Publishing, Cham. http://link.springer.com/10.1007/978-3-030-37371-9_23 (Accessed 15 December 2025).

Dutheil, C., Meier, H. E. M., Gröger, M., and Börgel, F. 2022. Understanding past and future sea surface temperature trends in the Baltic Sea. Climate Dynamics, 58: 3021–3039.

Engstedt, O., Engkvist, R., and Larsson, P. 2014. Elemental fingerprinting in otoliths reveals natal homing of anadromous B altic S ea pike (*E sox lucius* L .). Ecology of Freshwater Fish, 23: 313–321.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. 2019. Impacts of historical warming on marine fisheries production. Science, 363: 979–983.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Friedland, R., Vock, C., and Piehl, S. 2023. Estimation of hypoxic areas in the Western Baltic Sea with geostatistical models. Water, 15: 3235. MDPI.

Funk, S., Krumme, U., Temming, A., and Möllmann, C. 2020. Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (Gadus morhua) in the Western Baltic Sea. ICES Journal of Marine Science, 77: 1816–1829.

Funk, S., Frelat, R., Möllmann, C., Temming, A., and Krumme, U. 2021. The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod Gadus morhua in the western Baltic Sea. Journal of Fish Biology, 98: 707–722.

Funk, S., Funk, N., Herrmann, J., Hinrichsen, H., Krumme, U., Möllmann, C., and Temming, A. 2023. Tracing growth patterns in cod (Gadus morhua L.) using bioenergetic modelling. Ecology and Evolution, 13: e10751.

Gröger, M., Dutheil, C., Börgel, F., and Meier, M. H. E. 2024. Drivers of marine heatwaves in a stratified marginal sea. Climate Dynamics, 62: 3231–3243.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., *et al.* 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PLOS ONE.

Hedman, J. E., Rüdel, H., Gercken, J., Bergek, S., Strand, J., Quack, M., Appelberg, M., *et al.* 2011. Eelpout (Zoarces viviparus) in marine environmental monitoring. Marine Pollution Bulletin, 62: 2015–2029.

Heessen, H. J. L., Daan, N., and Ellis, J. R. (Eds). 2015. Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys. Brill | Wageningen Academic. https://brill.com/view/title/68532 (Accessed 2 January 2024).

Holsman, K., Samhouri, J., Cook, G., Hazen, E., Olsen, E., Dillard, M., Kasperski, S., *et al.* 2017. An ecosystem-based approach to marine risk assessment. Ecosystem Health and Sustainability, 3: e01256.

ICES. 2020. Guide to ICES Advisory Framework and Principles. https://doi.org/10.17895/ICES.ADVICE.7648.

ICES. 2023. Baltic Fisheries Assessment Working Group (WGBFAS). https://doi.org/10.17895/ICES.PUB.23123768.

IPCC. 2023. Climate Change 2022: Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Jepsen, N., Koed, A., and ØKland, F. 1999. The movements of pikeperch in a shallow reservoir. Journal of Fish Biology, 54: 1083–1093.

Johnson, J. E., and Welch, D. J. 2009. Marine Fisheries Management in a Changing Climate: A Review of Vulnerability and Future Options. Reviews in Fisheries Science, 18: 106–124.

Kappel, C. V. 2005. Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. Frontiers in Ecology and the Environment, 3: 275–282.

Kassambra, A., and Mundt, F. 2020. Factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Klinkhardt, M. 1986a. Ergebnisse von untersuchungen zur schlupf-und dottersackphase der larven von rügenschen frühjahrsheringen (Clupea harengus L.). Fischereiforschung, 24: 28–30.

Klinkhardt, M. 1986b. Gedanken zur abhängigkeit der laichentwicklung rügenscher frühjahrsheringe (Clupea harengus L.) von umweltparametern. Fischerei-Forschung, 24: 22–27.

Kolde, R. 2019. pheatmap: Pretty heatmaps.

Kornis, M. S., Mercado-Silva, N., and Vander Zanden, M. J. 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology, 80: 235–285.

Lappalainen, J., Dörner, H., and Wysujack, K. 2003. Reproduction biology of pikeperch (Sander lucioperca (L.)) – a review. Ecology of Freshwater Fish, 12: 95–106.

Lehmann, A., Myrberg, K., Post, P., Chubarenko, I., Dailidiene, I., Hinrichsen, H.-H., Hüssy, K., *et al.* 2022. Salinity dynamics of the Baltic Sea. Earth System Dynamics, 13: 373–392. Copernicus Publications Göttingen, Germany.

Leppäranta, M., and Myrberg, K. 2009. Topography and hydrography of the Baltic Sea. Physical oceanography of the Baltic Sea: 41–88. Springer Berlin Heidelberg.

Lewin, W.-C., Barz, F., Weltersbach, M. S., and Strehlow, H. V. 2023. Trends in a European coastal fishery with a special focus on small-scale fishers–Implications for fisheries policies and management. Marine Policy, 155: 105680. Elsevier.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., and Hornik, K. 2023. cluster: cluster analysis basics and extensions.

Manica, A., and Johnstone, R. A. 2004. The Evolution of Paternal Care with Overlapping Broods. The American Naturalist, 164: 517–530.

Meier, H. E. M., Eilola, K., Almroth-Rosell, E., Schimanke, S., Kniebusch, M., Höglund, A., Pemberton, P., *et al.* 2019. Disentangling the impact of nutrient load and climate changes on Baltic Sea hypoxia and eutrophication since 1850. Climate Dynamics, 53: 1145–1166.

Meier, H. E. M., Dieterich, C., and Gröger, M. 2021. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. Communications Earth & Environment, 2: 50.

Meier, H. M., Dieterich, C., Gröger, M., Dutheil, C., Börgel, F., Safonova, K., Christensen, O. B., *et al.* 2022. Oceanographic regional climate projections for the Baltic Sea until 2100. Earth System Dynamics Discussions, 2021: 1–66. Göttingen, Germany.

Möllmann, C. 2019. Effects of climate change and fisheries on the marine ecosystem of the Baltic Sea. *In* Oxford Research encyclopedia of climate science. https://oxfordre.com/climatescience/display/10.1093/acrefore/9780190228620.001.0001/acrefore-9780190228620-e-682 (Accessed 15 December 2025).

Möllmann, C., Cormon, X., Funk, S., Otto, S. A., Schmidt, J. O., Schwermer, H., Sguotti, C., *et al.* 2021. Tipping point realized in cod fishery. Scientific Reports, 11: 14259.

Nissling, A., and Westin, L. 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. Marine Ecology Progress Series, 152: 261–271.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana, 10: 29–59.

Pecl, G. T., Ward, T. M., Doubleday, Z. A., Clarke, S., Day, J., Dixon, C., Frusher, S., *et al.* 2014. Rapid assessment of fisheries species sensitivity to climate change. Climatic Change, 127: 505–520.

Piehl, S., Friedland, R., Heyden, B., Leujak, W., Neumann, T., and Schernewski, G. 2023. Modeling of Water Quality Indicators in the Western Baltic Sea: Seasonal Oxygen Deficiency. Environmental Modeling & Assessment, 28: 429–446.

Pinto, G., Möllmann, C., Hinrichsen, H.-H., Lehmann, A., Quaas, M., and Voss, R. 2024. Longer and more frequent marine heatwaves in the Western Baltic Sea. https://assets-eu.researchsquare.com/files/rs-3910435/v1_covered_4003d6e5-036d-4efa-bc2f-b6be9841fa7b.pdf (Accessed 15 December 2025).

Polte, P., Kotterba, P., Moll, D., and von Nordheim, L. 2017. Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters. Scientific Reports, 7: 42709. Nature Publishing Group UK London.

Polte, P., Gröhsler, T., Kotterba, P., Von Nordheim, L., Moll, D., Santos, J., Rodriguez-Tress, P., *et al.* 2021. Reduced Reproductive Success of Western Baltic Herring (Clupea harengus) as a Response to Warming Winters. Frontiers in Marine Science, 8: 589242.

Posit Team. 2024. .

R Core Team. 2023. R: A Language and Environment for Statistical Computing.

Ramos, J. E., Tam, J., Aramayo, V., Briceño, F. A., Bandin, R., Buitron, B., Cuba, A., *et al.* 2022. Climate vulnerability assessment of key fishery resources in the Northern Humboldt Current System. Scientific Reports, 12: 4800.

Receveur, A., Bleil, M., Funk, S., Stötera, S., Gräwe, U., Naumann, M., Dutheil, C., *et al.* 2022. Western Baltic cod in distress: decline in energy reserves since

1977. ICES Journal of Marine Science, 79: 1187–1201. Oxford University Press (OUP).

Saraiva, S., Meier, H. M., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R., *et al.* 2019. Uncertainties in projections of the Baltic Sea ecosystem driven by an ensemble of global climate models. Frontiers in Earth Science, 6: 244. Frontiers Media SA.

Schaber, M., Marohn, L., Petereit, C., Schroeder, J. P., Zumholz, K., and Hanel, R. 2011. Newcomers in the Baltic Sea: an attempt to trace the origins and whereabouts of thicklip grey mullet Chelon labrosus. Fisheries Science, 77: 757–764.

Seibel, B. A. 2023. Animal response to hypoxia in estuaries and effects of climate change. Climate change and estuaries: 545–562. CRC Press.

Smialek, N., Pander, J., and Geist, J. 2021. Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. Fisheries Management and Ecology, 28: 437–467.

Spencer, P. D., Hollowed, A. B., Sigler, M. F., Hermann, A. J., and Nelson, M. W. 2019. Trait-based climate vulnerability assessments in data-rich systems: An application to eastern Bering Sea fish and invertebrate stocks. Global Change Biology, 25: 3954–3971.

Sternecker, K., Denic, M., and Geist, J. 2014. Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. Ecology and Evolution, 4: 2749–2758.

Stiasny, M. H., Mittermayer, F. H., Sswat, M., Voss, R., Jutfelt, F., Chierici, M., Puvanendran, V., *et al.* 2016. Ocean acidification effects on Atlantic cod larval survival and recruitment to the fished population. PloS one, 11: e0155448. Public Library of Science San Francisco, CA USA.

Tomczak, M. T., and Sapota, M. R. 2006. The fecundity and gonad development cycle of the round goby (Neogobius melanostomus Pallas 1811) from the Gulf of Gdańsk. International Journal of Oceanography and Hydrobiology, 35: 353–367.

Van Puijenbroek, P. J. T. M., Buijse, A. D., Kraak, M. H. S., and Verdonschot, P. F. M. 2019. Species and river specific effects of river fragmentation on European anadromous fish species. River Research and Applications, 35: 68–77.

Van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., *et al.* 2011. The representative concentration pathways: an overview. Climatic Change, 109: 5–31.

Veneranta, L., and Urho, L. 2021. Reproduction range of garfish, Belone belone (L.), in the northern Baltic Sea. Memoranda Societatis pro Fauna et Flora Fennica, 97: 1–10.

Von Nordheim, L., Kotterba, P., Moll, D., and Polte, P. 2018. Impact of Spawning Substrate Complexity on Egg Survival of Atlantic Herring (Clupea harengus, L.) in the Baltic Sea. Estuaries and Coasts, 41: 549–559.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., *et al.* 2019. Welcome to the Tidyverse. JOSS 4 (43): 1686.

ACKNOWLEDGEMENTS

This study is a contribution to the balt_ADAPT (Adaptation of the Western Baltic Coastal Fishery to Climate Change; Grant no. 03F0863) project funded by the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung, BMBF). Further funding is acknowledged from project SeaUseTip (Spatial and temporal analysis of tipping points of the socio-ecological system of the German North Sea under different management scenarios; Grant Grant No. 01LC1825) for AB, and SpaCeParti (Coastal Fishery, Biodiversity, Spatial Use and Climate Change: A Participative Approach to navigate the Western Baltic Sea into a Sustainable Future; Grant no. 03F0914) for SF, both funded by BMBF. JC and HG received funding from the EU H2020 projects COMFORT (Grant No. 820989) and MISSION ATLANTIC (Grant No. 862428), respectively. The study reflects only the authors' view; the European Commission and their executive agency are not responsible for any use that may be made of the information the work contains. LF received funding from the

Cluster of Excellence CLICCS (Climate, Climatic Change, and Society) coordinated through University of Hamburg's Center for Earth System Research and Sustainability (CEN) in close collaboration with multiple partner institutions and is funded by the Deutsche Forschungsgemeinschaft (DFG; Grant No. 390683824).

AUTHOR CONTRIBUTIONS

DM, PP and CM conceptualized the study. DM and NF conducted the literature research underlying the species profiles. HA, UB, UK, TM, MP, VS and HW evaluated and improved species profiles. GP designed and constructed online questionnaires and mapped temperature projections provided by MEEM. FM and SO provided species distribution maps. Figure 2 is designed by PK. All authors conducted sensitivity assessments. Exposure assessments were performed by DM, HHH, FM, GP, PP, RV and CM. DM, GP, PP and CM conducted the data analysis. DM, PP and CM provided the initial manuscript. All authors reviewed and commented on the manuscript.

FUNDING

Open Access funding enabled and organized by Projekt DEAL. We acknowledge financial support from the Open Access Publication Fund of Universität Hamburg.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

Correspondence and requests for materials should be addressed to C.M.

DISCUSSION

Changing environmental conditions worldwide are expected to shift fish distributions likely altering biotic interactions as a result (Pinsky *et al.*, 2020). As a result, the structure and functioning of the marine communities are likely to change considerably with multiple studies supporting this outlook (Vergés *et al.*, 2014; Pecl *et al.*, 2017; McLean *et al.*, 2019; Zhao *et al.*, 2022; Souza *et al.*, 2023). On a regional scale, the Baltic Sea is a clear example of an ecosystem heavily affected by diverse anthropogenic impacts such as temperature increases, expansions of hypoxic zones, eutrophication, and overexploitation, among others (Möllmann *et al.*, 2009; Reusch *et al.*, 2018; Pecuchet *et al.*, 2020). These issues are likely to advance in the future with the addition of decreasing salinity (Andersson *et al.*, 2015), although highly uncertain (Meier *et al.*, 2021). Salinity is one of the most important factors contributing to the community composition observed in the Baltic characterized by a coexistence of marine and freshwater species (Frelat *et al.*, 2018). Even though these issues are being increasingly studied, important knowledge gaps still remain. Often, studies and assessments of the Baltic Sea fish community are limited by coarse spatial scales, lacking understanding of overlap dynamics between species and stocks, and by disproportionally high focus on single species and aggregated biomass trends (Orio *et al.*, 2020; Blenckner *et al.*, 2021; HELCOM, 2023). In parallel, implementing adequate ecosystem-based management of the Baltic is a goal of high priority. In order that this can be achieved, further holistic understanding of the fish community is highly needed. The aim of this dissertation is to address the identified knowledge gaps through four complementary research studies studying the past and the future of the Baltic Sea fish community under changing environmental conditions.

Summary of the main findings

In **chapter 1**, the use of advanced species distribution models (SDMs) and spatial indices derived from model-based predictions strongly suggests distributional shifts to have occurred in European flounder, European plaice and Eastern Baltic Sea (EBS) cod stock between 2001 and 2020. These are largely reflected in increased habitat

size and dispersal, together with declining CPUE during the autumn/winter period and are considered primarily driven by changes in temperature and oxygen.

Our results for flounder show a pronounced abundance hotspot along the eastern coast of the Baltic states. However, this area experienced a decline in abundance which is generally consistent with MacNeil *et al.* (2025). We found both the presence and abundance of flounder highly influenced by temperature aligning with Rau *et al.* (2019) who identified temperature a primary driver of flatfish distributions in the western Baltic Sea. We found oxygen to also play an important role in the observed changes. However, areas of higher flounder abundance that we identified differ from those in Orio *et al.* (2019) as they report the species to be more concentrated along the southern Baltic coast.

EBS cod demonstrated westward and northward shifts and expanded its habitat. Hence, our results stand at odds with contractions demonstrated by Orio *et al.* (2019) but we do agree on oxygen being an important driver. Thus, the spatiotemporal shifts that we observe are likely a result of the increasing oxygen concentrations in areas such as east of Gotland. Overall, we find this cod stock to be sensitive to environmental constraints such as oxygen and temperature, in line with the available literature (Heessen *et al.*, 2015; Bryhn *et al.*, 2022). However, we also found a positive relationship between rising temperature and EBS cod which contradicts existing knowledge on the species (Bryhn *et al.*, 2022) and apparently contributed to the observed expansion.

European plaice is another expanding species but toward the south and the east with highest abundance in the WBS, similar to what MacNeil *et al.* (2025) observed. Salinity is an important driver of its distribution but while other flatfish are constrained by low salinity, plaice appears to tolerate brackish waters more easily. In addition to salinity, temperature and oxygen are also important drivers as reflected in the literature (Heessen *et al.*, 2015; Rau *et al.*, 2019).

Other species and stocks; namely Western Baltic Sea (WBS) cod, whiting, European sprat, and three-spined stickleback; do not show notable spatiotemporal changes implying that their habitat preferences and tolerances are largely met during the study period. Their distributional patterns are also heavily dependent on dynamic environmental conditions (temperature, salinity, oxygen, and chlorophyll *a*). Dab is strongly influenced by salinity and depth, consistent with Heessen *et al.* (2015) and Rau *et al.* (2019). Whiting is driven by more variables than expected, with depth not playing and important role. Temperature is the only significant driver for WBS cod and there is a negative relationship between the two, in line with Bryhn *et al.* (2022). Thus, we observe the two Baltic cod stocks to react differently to rising temperature.

For Atlantic herring we only identified depth as a significant covariate driving its occurrence and none for its abundance. The results strongly suggest that other dynamics, likely captured by the spatial random fields of the applied model, might explain its abundance patterns. Competition for prey items with sprat might be an important factor as herring growth was shown to be considerably lower when sprat abundance is high (Casini *et al.*, 2010). Sprat prefers lower salinity and higher temperatures, the importance of these drivers echoed in the available literature (Cardinale *et al.*, 2002; MacKenzie and Köster, 2004; MacKenzie *et al.*, 2008; Petereit *et al.*, 2008; Ojaveer and Kalejs, 2010). Temperature was the only significant driver for stickleback, supported by Lefébure *et al.* (2014) but species interactions might also play an important. When norther pike (*Esox lucius*) and European perch (*Perca fluviatilis*) decline the abundance of stickleback increases, as noted by Bergström *et al.* (2015) and Eriksson *et al.* (2021).

Furthermore, we investigated spatial overlap between species and stocks as it is likely to play and important role in shaping ecological interactions and competitive outcomes (Brodeur *et al.*, 2008). We find that the majority of overlap cases to occur between the WBS cod stock and species which are most abundant in ICES Division IIIa and subdivisions 22-24, a rather small portion of the total study area where increased overlap is most likely due to the concentration of populations (Deane, 2022). Species with more dispersed distributions and the EBS cod stock are more

often involved in cases of spatial separation. Particularly interesting are cases where plaice is involved. Over time, it overlaps less with dab and whiting possibly making their interaction less frequent. At the same time, its interactions with flounder might be intensifying as a result of increasing overlap between the two.

In **chapter 2**, we used the framework from **chapter 1** by refitting SDMs of the same species and stocks and applying the same model structures as in **chapter 1**. In doing so, we were able to provide one of the first comprehensive projections of distributional changes for the aforementioned eight species (including two cod stocks) in the Baltic under combined future climate and nutrient scenarios (RCP4.5-BSAP, RCP4.5-REF, RCP8.5-BSAP, and RCP8.5-REF). Interestingly, we find that most species respond consistently across scenarios and time periods (mid-century (2053 – 2059) and end-century (2092 – 2098) relative to the baseline (2014 - 2020)) with differences observable more often in the magnitude than in the direction of change. We identified, with the exception of plaice, a lack of longitudinal and latitudinal shifts standing in contrast with globally reported poleward shifts (Horta E Costa *et al.*, 2014; Verges *et al.*, 2014; Frainer *et al.*, 2017; Pecl *et al.*, 2017; Hastings *et al.*, 2020; Pinsky *et al.*, 2020), likely a result of salinity (Frelat *et al.*, 2018) and the basin coastlines, similar as in the Adriatic (Cavraro *et al.*, 2022), constraining large-scale shifts.

We also identified distinct groups of potential “winners” and “losers” of future environmental change. Dab, flounder and whiting constitute the latter owing to predicted reductions in habitat size and abundance. WBS cod and Atlantic herring, while still being in the losing group, will experience low levels of change. However, both stocks have already undergone severe biomass declines (Fey *et al.*, 2014; Birgersson *et al.*, 2022; Bryhn *et al.*, 2022; ICES, 2024a) and our models do not suggest a recovery under any tested scenario likely considerably limiting their resilience to existing and any new pressures. Furthermore, the absence of significant dynamic covariates in the herring model reduces confidence in scenario-specific interpretations. Bauer *et al.* (2018) also had limited success in reproducing its distribution and reasoned that such issues in modelling are a result of species such

as herring exhibiting wide tolerances to environmental conditions (Somodi *et al.*, 2017) and due to pelagic species usually having more variable distributions than demersal ones (Thorson *et al.*, 2016).

The relative "winners" group consisted of European plaice, EBS cod and European sprat which are projected to expand their habitat and disperse more under most scenarios. Of these, plaice demonstrates the largest shifts, especially under RCP8.5-BSAP where it benefits from rising temperature, reduced nutrients and increased oxygen while sprat stands to benefit most from the RCP8.5-REF due to a combination of higher temperature and reduced salinity in the Baltic. Interestingly, EBS cod is one of the only two populations that might, together with habitat size, increase in abundance depending on the scenario. However, the modeled positive response to rising temperature is not supported by known physiological constraints (Bryhn *et al.*, 2022) and the results need to be interpreted with caution.

The second species that might increase in abundance is the stickleback. It should, however, be regarded as a distinct case given that it is the only species that exhibits directional changes between the two climate scenarios, seemingly doing best under RCP8.5-BSAP characterized by stable habitat size, reduced aggregation and increased CPUE. Even though temperature was identified as the only significant driver, interactions with other non-significant covariates – particularly salinity – might further shape its responses.

In addition to analyzing species- and stock-based distributional changes across the examined scenarios, changes in spatial overlap between species and stock pairs were investigated. We find that the Spatial Overlap Index (SOI) changes over time for all pairs, however they are typically consistent across scenarios and primarily driven by gradual warming, aligning with other studies that suggest moderate, although ecologically relevant, shifts in species co-occurrence under climate change (Jones *et al.*, 2013; Pecl *et al.*, 2017). Overall, our results indicate stronger overlap between the species in the "losers" group as well as plaice and EBS cod. WBS cod and sprat, its important prey, are projected to become more separate potentially negatively

impacting the recovery of WBS cod (Sparholt, 1994; Receveur *et al.*, 2022). EBS cod is expected to overlap less with flounder contrasting with observations by Orio *et al.* (2020). The inter-stock competition between the two cod stocks might also diminish as a result of the projected decrease in spatial overlap. However, our model training design excludes ICES Subdivision 24, a known area where the two mix. Regardless, we still generated predictions in this area but these should be interpreted with caution given that such decisions might limit the transferability of the model (Lee-Yaw *et al.*, 2022). Furthermore, a recent study also suggested that the two stocks might differ in habitat use based on depth, with WBS cod being more frequent in shallower and EBS cod in deeper areas thus potentially facilitating their coexistence (Schade *et al.*, 2022).

In **chapter 3**, we moved beyond single species and stocks analyses and provided a comprehensive assessment of recent changes (2001-2020) in the wider Baltic fish community by combining high spatiotemporal resolution with an integrated indicator framework. Our approach is underpinned by the spatiotemporal modelling framework adapted from **chapters 1** and **2** as well as by the use of structural and functional indicators, the latter of which are derived using functional traits. Our findings support the conclusions from other research that climate change and eutrophication played a significant role in alterations to the structure and functioning of the Baltic Sea ecosystem (Conley *et al.*, 2009; Möllmann *et al.*, 2009; Pecuchet *et al.*, 2020) and in documented distributional shifts and changing overlap in fish species (Orio *et al.*, 2019, 2020; MacNeil *et al.*, 2025; **Chapter 1**; **Chapter 2**). Temperature is identified as the strongest and most frequent driver of changes in the fish community by our spatiotemporal models with oxygen, chlorophyll *a*, and salinity also often important.

The indicator selection protocol (Otto *et al.*, 2018) that we used in **chapter 3**, which is based on spatially aggregated time series, identified a partly different set of drivers than the spatiotemporal models. This is not unexpected, as purely temporal analyses assume spatial uniformity and are limited in capturing fine-scale spatial complexity (Chen *et al.*, 2011). However, using multi-criteria indicator evaluation frameworks that assess indicators in terms of sensitivity, robustness, redundancy and management relevance is a well-established practice in marine ecosystem assessments and aligns

with international recommendations for indicator development (Kershner *et al.*, 2011; Queirós *et al.*, 2016). Thus, we consider it a key part of the assessment process that is further extended with the use of spatiotemporal SPDE-based GLMMs that can capture fine-scale species–environment relationships (Thompson *et al.*, 2023).

A key part of the study is the integration of both structural and functional indicators. Results of the Multiple Factor Analysis (MFA) show that functional and structural dimensions offer complementary information, strengthening the argument to consider functional traits when assessing ecosystem condition (Smit *et al.*, 2021). Indeed, they often respond to environmental change differently from taxonomic metrics and capture information these traditional indicators cannot (Chillo *et al.*, 2011; Mori *et al.*, 2013; Stuart-Smith *et al.*, 2013). We also find order-level abundance indicators to offer a robust means of tracking community-level responses when compared with species- and stock-level indicators. In addition, the high spatiotemporal resolution of this study also complements other ecosystem-wide and regional assessments (Blenckner *et al.*, 2021; HELCOM, 2023) which often cannot resolve patterns at such fine scales.

In the end, we used indicator spatiotemporal predictions to derive a cumulative community state score resolved in space and time. This allowed us to calculate how this score changed between an early (2001-2005) and a late (2016-2020) period and to map it to the study area. In doing so, we were able to demonstrate a mismatch between areas where the structure and functioning of the fish community changed the most and protected areas - HELCOM Marine Protected Areas (MPAs) and a fisheries closure area. In addition, in several areas with strong community state changes, substantial expansions of offshore wind farms are planned.

Lastly, in **chapter 4**, we provided a first climate vulnerability assessment (CVA) for a Baltic Sea fish community under future warming scenarios (RCP4.5 and RCP8.5), focusing on the WBS and using trait-based information for 22 species. A general lack of quantitative data of the fish species in our study area supported the decision to utilize a qualitative, expert-approach already employed in other areas of the world

(Pecl *et al.*, 2014; Hare *et al.*, 2016; Spencer *et al.*, 2019; Bueno-Pardo *et al.*, 2021; Ramos *et al.*, 2022).

Our results suggest that marine and freshwater species with complex life cycles have a high and very high sensitivity to climate change. These include anadromous salmonids (Atlantic salmon and sea trout) and the catadromous European eel which exhibit complex spawning migrations, distinct spawning periods and specific requirement during their early life stages (Sternecker *et al.*, 2014; Heessen *et al.*, 2015; Smialek *et al.*, 2021). In addition to these diadromous species, several others were rated highly sensitive by the experts given that they display complex life-history aspects. These include herring and garfish due to their need for specialized habitats for benthic egg deposition (Von Nordheim *et al.*, 2018; Veneranta and Urho, 2021) and eelpout and lumpsucker which conduct a form of brood care (Manica and Johnstone, 2004; Hedman *et al.*, 2011). Freshwater species (northern pike, European perch and pikeperch) are considered highly sensitive due to their limited salinity tolerances, complex reproductive strategies, need for special vegetation for spawning (Balon, 1985), and pronounced homing behavior (Jepsen *et al.*, 1999; Lappalainen *et al.*, 2003; Engstedt *et al.*, 2014; Christensen *et al.*, 2021). Cod is also considered highly sensitive due to its dependence on higher salinities (Nissling and Westin, 1997) and given that it is considered to suffer under the effects of climate change, especially warming, despite the exact process still remaining unclear (Funk *et al.*, 2020, 2023; Möllmann *et al.*, 2021; Receveur *et al.*, 2022).

Species that successfully invaded the Baltic (round goby, thicklip grey mullet and sprat) are considered less sensitive and may even profit from climate change. The goby has a broad thermal tolerance (Kornis *et al.*, 2012) and high potential for adaptation to local environmental conditions (Björklund and Almqvist, 2010) explaining the reports on this species benefiting from climate-related changes (Tomczak and Sapota, 2006). Mullet and sprat are species that reached the Baltic through range expansions and adapted to a wide range of salinities and temperature. Sprat occupies a broad range from southern to northern areas of the basin (Parmanne *et al.*, 1994) while the mullet recently started to become a regular occurrence in the

north (Schaber *et al.*, 2011). Flatfishes are considered a less sensitive group to climate change in the assessment with the recent drastic increase of plaice effectively demonstrating this attribute (ICES, 2024b).

Exposure of the species to warming is considered mostly low under RCP4.5 and increased to mostly moderate under RCP8.5 possibly reflecting temperature projections indicating weaker warming in the WBS when compared to eastern and norther Baltic areas (Dutheil *et al.*, 2022). Alternatively, using the 2010-2019 period as the baseline could explain the overall low scores as this period already experienced significant warming compared to pre-industrial times and lowering the chances of detecting major differences when compared to future projections (Dutheil *et al.*, 2022). Lastly, we combined species sensitivity and exposure to provide vulnerability assessments for each species which resulted with low scores until the middle of the century and moderate or high scores depending on RCP scenario and species. Given the low variability of the exposure, the vulnerability assessments largely reflect species sensitivity.

Management implications and limitations

Distributional shifts in marine ecosystems are increasingly documented (Perry *et al.*, 2005; Cheung *et al.*, 2013; Baudron *et al.*, 2020; Hastings *et al.*, 2020; Pinsky *et al.*, 2020). They pose serious issues for management efforts influencing quota allocations, threatening established fisheries but also opening opportunities for new ones (Astthorsson *et al.*, 2012; Pinsky and Fogarty, 2012; Pinsky *et al.*, 2018; Baudron *et al.*, 2020). However, even positive effects need costly societal adjustments (Weiskopf *et al.*, 2020). Furthermore, adapting management strategies often takes a long time when compared to the speed of distributional shifts. Such is the case in the northeast of United States, where fisheries have shifted only 10 to 30% as their target species (Pinsky and Fogarty, 2012). Distributional shifts documented in **chapter 1** and projected in **chapter 2** will likely complicate management efforts in the Baltic Sea since our study area is shared by 10 countries. This makes co-management of fish resources under future environmental change an important but likely difficult task, especially in the current political context.

Changing distributions in the Baltic have resulted with changes in spatial overlap and are likely to continue in the future putting strain on important species and stocks (Orio *et al.*, 2020; **Chapter 1**; **Chapter 2**). Such developments can be seen in other parts of the world as well. For example, in the northern California Current, there are regions with high spatial overlap between jellyfish and pelagic species. Diet studies showed high trophic overlap with small pelagic fish that prey copepods and euphasiid eggs and stable isotope analysis suggested that both these fish and the jellyfish occupy the same trophic level (Brodeur *et al.*, 2008). WBS cod is a prime example of a stock likely at additional risk since it is already depleted and is simultaneously expected to overlap more with potential competitors and become more separated from sprat, an important prey item (Sparholt, 1994; Orio *et al.*, 2020). Changes in biotic interactions can have even more profound consequences by impacting ecosystem structure and functioning (Eriksson *et al.*, 2011; Hollowed *et al.*, 2013; Weiskopf *et al.*, 2020; Dimitriadis *et al.*, 2021) thus potentially putting additional pressure on the WBS cod stock. Plaice, on the other hand, is consistently shown to have adapted well to the current state of the Baltic Sea, also supported by other studies (ICES, 2024b; Rosciszewski-Dodgson and Cirella, 2024; MacNeil *et al.*, 2025). It appears to have a strong capacity to thrive in the future as well - likely a result of its recent and projected habitat expansion and reduction in spatial overlap with some of its potential prey item competitors (**Chapter 1**; **Chapter 2**, **Chapter 4**).

In **chapter 2** we demonstrate that the most favorable of the investigated scenarios of future environmental change is RCP4.5-BSAP benefiting a wide range of species including common dab, European flounder, European plaice, WBS cod, EBS cod, and whiting. This is supported by other studies indicating the profound effects of increasing temperature, decreasing salinity (Blenckner *et al.*, 2015) - although highly uncertain (Meier *et al.*, 2021), and heightened nutrient loads (Niiranen *et al.*, 2013). RCP4.5 is expected to result with high biodiversity and catch value in the Baltic Sea (Bauer *et al.*, 2019) and would likely be beneficial to species with high and very high sensitivity to climate change (**Chapter 4**). RCP4.5-BSAP would likely curb the future dominance of the stickleback, a species showing a recent increase in abundance (Bergström *et al.*, 2015; Olin *et al.*, 2022). This scenario would also reduce the

abundance of sprat which might benefit herring due to a negative relationship between sprat abundance and herring growth (Casini *et al.*, 2010). Whether this is desirable is open to debate due to concerns raised by exceptionally low sprat recruitment between 2001 and 2023 (ICES, 2024c). Herring might further benefit from this scenario due to its suggested preference for colder, more saline conditions (Illing *et al.*, 2016; Dodson *et al.*, 2019; Polte *et al.*, 2021; Ory *et al.*, 2022). RCP8.5-REF is least favorable as it would benefit opportunistic species (**Chapter 2**) and successful invaders (**Chapter 4**). Despite the benefits of RCP4.5, our findings still reveal more reasons for concern and more ambitious mitigation pathways such as RCP2.6 or RCP3.4 could potentially improve outcomes. However, their feasibility remains uncertain given the current global policy trajectories.

A further issue for Baltic species is the apparent lack of longitudinal and latitudinal shifts (**Chapter 2**) standing in contrast to a global pattern of poleward shifts (Horta E Costa *et al.*, 2014; Verges *et al.*, 2014; Frainer *et al.*, 2017; Pecl *et al.*, 2017; Hastings *et al.*, 2020; Pinsky *et al.*, 2020). We consider this to likely be a result of the Baltic coastline constraining large-scale redistributions, much like in the Adriatic Sea (Cavraro *et al.*, 2022). The strong horizontal salinity gradient that plays a key role in structuring fish communities is an additional factor that likely further limits substantial range shifts (Frelat *et al.*, 2018). Under these constraints, the affected species effectively become trapped.

The uncertainty of global climate change mitigation efforts and the semi-enclosed nature of the Baltic limiting large-scale redistributions emphasize the importance of reducing eutrophication. In addition, we propose reducing exploitation of vulnerable species given that such actions can enhance stock resilience, even when environmental conditions are not optimal (Sumaila and Tai, 2020). Plenty examples demonstrate the detrimental effects of combined impacts. (Sumaila and Tai, 2020). For example, in the Northern Hemisphere, multiple cases of marine regime shifts likely originates as a result of combined effects of overfishing and environmental change. On the other side of the world, in Tasmania, it was observed that overfishing of lobsters has reduced the resilience of kelp beds to climate-driven sea urchin

outbreaks. This resulted with an increasing the risk of the catastrophic shifts from kelp beds to sea urchin barrens (Ling *et al.*, 2009). In the southwest Indian Ocean, extinction risks for endemic sharks and rays are being increased by the overfishing and climate change acting together (Pollom *et al.*, 2024). In the Baltic itself, it was found that regional management, under environmental change, would likely play a major role in its future (Niiranen *et al.*, 2013). In addition to reducing exploitation of vulnerable species, simultaneous targeting of abundant species might help rebalance trophic interactions. In the Baltic, sprat could be a good candidate given it known negative effects on herring (Casini *et al.*, 2010). However, as already mentioned, this would require a cautious approach given the concerns related to its exceptionally low recruitment between 2021 and 2023 (ICES, 2024c).

A key tool in managing marine ecosystems in order to strengthen their resilience to environmental change are protection measures such as MPAs. However, changing distributions might render them ineffective (Cashion *et al.*, 2020) and they largely do not incorporate common climate change adaptation principles in their design (O'Regan *et al.*, 2021). Furthermore, in **chapter 3**, by integrating both structural and functional indicators into a highly resolved spatiotemporal state assessment of the fish community, we find a mismatch between areas where the community state has changed the most and established protection areas (HELCOM MPAs and a fisheries closure area). Similar mismatches between static protected areas and shifting distributions have been documented in many marine regions and are increasingly recognized as a major challenge for conservation under climate change (Pinsky *et al.*, 2018; Bates *et al.*, 2019). Simply relocating existing protection areas would risk eroding the conservation benefits these sites already provide, and areas of considerable change are too large in surface for this to be a viable solution. Instead, we suggest further expansion of spatial protection, potentially including dynamic spatial management which allows management measures to shift in space and time as needed (Maxwell *et al.*, 2015; Dunn *et al.*, 2016; Gilman *et al.*, 2019; Oestreich *et al.*, 2020). Dynamic management could be integrated with adaptive management which uses a structured, iterative framework supported by monitoring and assessment for decision making (Walters and Holling, 1990; Ban *et al.*, 2014).

Adaptive management defines management goals as well as rules to meet management objectives. An example would be the amount of habitat that should be closed to fishing in order to protect a particular species. At the implementation stage of adaptive management, dynamic management couples into its framework by updating spatial management areas quickly using the already defined protocols through the adaptive management process. For example, it would identify where habitat closures would occur on a daily, weekly or monthly scales. Dynamic management enables the rapid change of space-time scale at which the rules are implemented. These changes can be implemented via dynamic management without needing to return to the decision making process (Maxwell *et al.*, 2015).

In **chapter 3**, we also find that several areas with strong community state changes are projected to experience substantial expansion of offshore wind farms. While these might locally increase the abundance of demersal fishes via reef effects that provide shelter and foraging opportunities (Knorrn *et al.*, 2024), broader ecosystem-level consequences remain uncertain. They may also interact with other anthropogenic pressures—such as noise, bottom disturbance or altered food webs—creating cumulative impacts that can amplify or counteract local habitat effects (Korpinen and Andersen, 2016; Galparsoro *et al.*, 2022). Moreover, interactions with other uses may further influence habitat suitability for different taxonomic and functional groups.

The presented data-driven approaches come with several limitations that need to be addressed. Firstly, ICES surveys (BITS and BIAS) are largely not carried out during the warmer months likely preventing the capture of the whole relationship between investigated species and temperature. This is effectively seen in EBS cod, where we found a positive relationship with temperature (**Chapter 1**; **Chapter 2**) which strongly contradicts the current understanding of its physiological preferences (Bryhn *et al.*, 2022). Revising survey protocols to include data from this period and expanding coverage to shallow coastal areas are critical steps for improving data accuracy and model predictions. Secondly, to include fisheries exploitation in the applied models, in **chapters 1** to **3**, we used non-resolved landings data which limited our ability to disentangle these effects. Bauer *et al.* (2018) integrated fisheries effort at a constant

value but spatially redistributed it within the area at every time-step following the changes in spatial distributions of the targeted fish. The need for utilizing such approaches and the need for understanding long-term drivers and informing sustainable management strategies underpins the value of any future efforts to reconstruct spatially resolved fisheries data. Thirdly, while the models we employed incorporate spatiotemporal dependencies that can capture some indirect effects of species interactions (Anderson *et al.*, 2022), they do not explicitly account for direct trophic or competitive relationships. Depending on the perspective, this may be considered a notable limitation (Dormann *et al.*, 2018; Moullec *et al.*, 2022). Lastly, in **chapters 3** and **4**, we are confronted with a considerable lack of trait data from the Baltic Sea basin. Given this, in **chapter 3** we use trait data from the North Sea, while, in **chapter 4**, Baltic Sea data is supplemented with data from other ecosystems, including the Mediterranean. We do not consider this ideal and strongly advise for a targeted collection of trait data in the Baltic Sea basin.

Conclusion

The analyses carried out as part of this doctoral thesis effectively demonstrate the fundamental connectedness between the environment and the spatiotemporal dynamics of the Baltic Sea fish community. The results strongly indicate that changing conditions, with temperature often acting as the lead driver, have led to apparent distributional shifts in at least three species and more are projected to do so under future climate and nutrient scenarios. These shifts have and will likely result with further changes to spatial overlap between species and stock pairs possibly affecting established biotic interactions. Such developments are expected to put strain on individual species and stocks, such as the ecologically and commercially important WBS cod, but also on the broader ecosystem structure and functioning.

For many species, the future appears bleak even under the relatively moderate warming scenarios such as RCP4.5 strengthening the arguments for reducing greenhouse gas emission even further. Traditional fishing targets and species with complex life histories are particularly at risk whereas invasive or adaptable species might benefit from changing conditions. In addition, the semi-enclosed nature of the

Baltic Sea and its salinity gradient likely limit large-scale distributions of the affected species. Given the uncertainties related to the global efforts to mitigate climate change, reducing nutrient loads and strong regulation of fisheries exploitation are certainly warranted. A potential way for managing the fisheries sector could combine reduced exploitation of vulnerable species and increased fishing of abundant species. However, effective oversight would be necessary for ensuring the health and resilience of the ecosystem given that there is evidence that global stock assessments may systematically overestimate the sustainability of fisheries (Edgar *et al.*, 2024). MPAs, in particular, are prominent tools that can be used in such endeavors; however, our analyses suggest that there is a mismatch between protected areas and areas of high change in the structure and functioning of the fish community. Adaptive strategies such as dynamic spatial management, i.e. management measures that are allowed to shift in space and time, might prove useful here (Maxwell *et al.*, 2015; Dunn *et al.*, 2016; Gilman *et al.*, 2019; Oestreich *et al.*, 2020). Several areas of fish community change are also projected to undergo an extensive expansion of offshore wind farms highlighting yet another potential driver of change to watch over.

We also provide strong evidence supporting the addition of functional indicators alongside traditional metrics and resolving spatial dynamics at fine scales in state assessment. Such approaches can substantially improve the appraisal of ecosystem change and its drivers. In addition, order-level abundance indicators also offer a robust means of tracking community-level responses. Lastly, we advocate for expansions of survey protocols, reconstruction of spatially resolved fisheries data, inclusion of biotic interactions, and targeted collection of trait data in the Baltic Sea so that future data-driven approaches, similar to the ones employed as part of this thesis, could improve in accuracy and robustness. In the end, the goals of the necessary collaborative management directed towards safeguarding the biodiversity and ensuring the sustainable future of the Baltic Sea remain hard to attain without the continuous advancement of our understanding of this ecosystem.

REFERENCES

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. K. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. preprint. Ecology. http://biorxiv.org/lookup/doi/10.1101/2022.03.24.485545 (Accessed 2 January 2024).

Andersson, A., Meier, H. E. M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., *et al.* 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO, 44: 345–356.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., and Óskarsson, G. J. 2012. Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. ICES Journal of Marine Science, 69: 1289–1297.

Balon, E. K. 1985. Early ontogeny of Labeotropheus Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. *In* Early life histories of fishes: New developmental, ecological and evolutionary perspectives, pp. 207–236. Ed. by E. K. Balon. Springer Netherlands, Dordrecht. http://link.springer.com/10.1007/978-94-010-9258-6_11 (Accessed 11 December 2025).

Ban, N. C., Maxwell, S. M., Dunn, D. C., Hobday, A. J., Bax, N. J., Ardron, J., Gjerde, K. M., *et al.* 2014. Better integration of sectoral planning and management approaches for the interlinked ecology of the open oceans. Marine Policy, 49: 127–136. Elsevier.

Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M., *et al.* 2019. Climate resilience in marine protected areas and the 'Protection Paradox'. Biological Conservation, 236: 305–314.

Baudron, A. R., Brunel, T., Blanchet, M., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., *et al.* 2020. Changing fish distributions challenge the effective management of European fisheries. Ecography, 43: 494–505.

Bauer, B., Meier, H. E. M., Casini, M., Hoff, A., Margoński, P., Orio, A., Saraiva, S., *et al.* 2018. Reducing eutrophication increases spatial extent of communities supporting commercial fisheries: a model case study. ICES Journal of Marine Science, 75: 1306–1317.

Bauer, B., Gustafsson, B. G., Hyytiäinen, K., Meier, H. E. M., Müller-Karulis, B., Saraiva, S., and Tomczak, M. T. 2019. Food web and fisheries in the future Baltic Sea. Ambio, 48: 1337–1349.

Bergström, U., Olsson, J., Casini, M., Eriksson, B. K., Fredriksson, R., Wennhage, H., and Appelberg, M. 2015. Stickleback increase in the Baltic Sea – A thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science, 163: 134–142.

Birgersson, L., Söderström, S., and Belhaj, M. 2022. The Decline of Cod in the Baltic Sea - A Review of Biology, Fisheries and Management, Including Recommendations for Cod Recovery. The Fisheries Secretariat, Stockholm, Sweden.

Björklund, M., and Almqvist, G. 2010. Rapid spatial genetic differentiation in an invasive species, the round goby Neogobius melanostomus in the Baltic Sea. Biological Invasions, 12: 2609–2618.

Blenckner, T., Llope, M., Möllmann, C., Voss, R., Quaas, M. F., Casini, M., Lindegren, M., *et al.* 2015. Climate and fishing steer ecosystem regeneration to uncertain economic futures. Proceedings of the Royal Society B: Biological Sciences, 282: 20142809.

Blenckner, T., Möllmann, C., Stewart Lowndes, J., Griffiths, J. R., Campbell, E., De Cervo, A., Belgrano, A., *et al.* 2021. The Baltic Health Index (BHI): Assessing the social–ecological status of the Baltic Sea. People and Nature, 3: 359–375.

Brodeur, R. D., Suchman, C. L., Reese, D. C., Miller, T. W., and Daly, E. A. 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Marine Biology, 154: 649–659.

Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J., *et al.* 2022. Which factors can affect the productivity and dynamics of cod

stocks in the Baltic Sea, Kattegat and Skagerrak? Ocean & Coastal Management, 223: 106154.

Bueno-Pardo, J., Nobre, D., Monteiro, J. N., Sousa, P. M., Costa, E. F. S., Baptista, V., Ovelheiro, A., *et al.* 2021. Climate change vulnerability assessment of the main marine commercial fish and invertebrates of Portugal. Scientific Reports, 11: 2958.

Cardinale, M., Casini, M., and Arrhenius, F. 2002. The influence of biotic and abiotic factors on the growth of sprat (Sprattus sprattus) in the Baltic Sea. Aquatic Living Resources, 15: 273–281.

Cashion, T., Nguyen, T., Ten Brink, T., Mook, A., Palacios-Abrantes, J., and Roberts, S. M. 2020. Shifting seas, shifting boundaries: Dynamic marine protected area designs for a changing climate. PLOS ONE, 15: e0241771.

Casini, M., Bartolino, V., Molinero, J. C., and Kornilovs, G. 2010. Linking fisheries, trophic interactions and climate: threshold dynamics drive herring Clupea harengus growth in the central Baltic Sea. Marine Ecology Progress Series, 413: 241–252.

Cavraro, F., Anelli Monti, M., Matić-Skoko, S., Caccin, A., and Pranovi, F. 2022. Vulnerability of the Small-Scale Fishery to Climate Changes in the Northern-Central Adriatic Sea (Mediterranean Sea). Fishes, 8: 9.

Chen, Q., Han, R., Ye, F., and Li, W. 2011. Spatio-temporal ecological models. Ecological Informatics, 6: 37–43.

Cheung, W. W. L., Watson, R., and Pauly, D. 2013. Signature of ocean warming in global fisheries catch. Nature, 497: 365–368.

Chillo, V., Anand, M., and Ojeda, R. A. 2011. Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands. Ecosystems, 14: 1168–1177.

Christensen, E. A. F., Svendsen, M. B. S., and Steffensen, J. F. 2021. Population ecology, growth, and physico-chemical habitat of anadromous European perch Perca fluviatilis. Estuarine, Coastal and Shelf Science, 249: 107091.

Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., *et al.* 2009. Hypoxia-related Processes in the Baltic Sea. Environmental Science & Technology, 43: 3412–3420.

Deane, D. C. 2022. Species accumulation in small–large vs large–small order: more species but not all species? Oecologia, 200: 273–284.

Dimitriadis, C., Fournari-Konstantinidou, I., Sourbès, L., Koutsoubas, D., and Katsanevakis, S. 2021. Long Term Interactions of Native and Invasive Species in a Marine Protected Area Suggest Complex Cascading Effects Challenging Conservation Outcomes. Diversity, 13: 71.

Dodson, J. J., Daigle, G., Hammer, C., Polte, P., Kotterba, P., Winkler, G., and Zimmermann, C. 2019. Environmental determinants of larval herring (Clupea harengus) abundance and distribution in the western Baltic Sea. Limnology and Oceanography, 64: 317–329.

Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., and Moretti, M. D. 2018. Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions.

Dunn, D. C., Maxwell, S. M., Boustany, A. M., and Halpin, P. N. 2016. Dynamic ocean management increases the efficiency and efficacy of fisheries management. Proceedings of the National Academy of Sciences, 113: 668–673.

Dutheil, C., Meier, H. E. M., Gröger, M., and Börgel, F. 2022. Understanding past and future sea surface temperature trends in the Baltic Sea. Climate Dynamics, 58: 3021–3039.

Edgar, G. J., Bates, A. E., Krueck, N. C., Baker, S. C., Stuart-Smith, R. D., and Brown, C. J. 2024. Stock assessment models overstate sustainability of the world's fisheries.

Engstedt, O., Engkvist, R., and Larsson, P. 2014. Elemental fingerprinting in otoliths reveals natal homing of anadromous B altic S ea pike (*E sox lucius* L .). Ecology of Freshwater Fish, 23: 313–321.

Eriksson, B. K., Sieben, K., Eklöf, J., Ljunggren, L., Olsson, J., Casini, M., and Bergström, U. 2011. Effects of Altered Offshore Food Webs on Coastal Ecosystems Emphasize the Need for Cross-Ecosystem Management. AMBIO, 40: 786–797.

Eriksson, B. K., Yanos, C., Bourlat, S. J., Donadi, S., Fontaine, M. C., Hansen, J. P., Jakubavičiūtė, E., *et al.* 2021. Habitat segregation of plate phenotypes in a

rapidly expanding population of three-spined stickleback. Ecosphere, 12: e03561.

Fey, D. P., Hiller, A., Margonski, P., Moll, D., Nilsson, H., Pongolini, L., Stybel, N., *et al.* 2014. HERRING Impact Report Herring spawning areas - present and future challenges.

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., and Aschan, M. M. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. Proceedings of the National Academy of Sciences, 114: 12202–12207.

Frelat, R., Orio, A., Casini, M., Lehmann, A., Mérigot, B., Otto, S. A., Sguotti, C., *et al.* 2018. A three-dimensional view on biodiversity changes: spatial, temporal, and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, 75: 2463–2475.

Funk, S., Krumme, U., Temming, A., and Möllmann, C. 2020. Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (Gadus morhua) in the Western Baltic Sea. ICES Journal of Marine Science, 77: 1816–1829.

Funk, S., Funk, N., Herrmann, J., Hinrichsen, H., Krumme, U., Möllmann, C., and Temming, A. 2023. Tracing growth patterns in cod (Gadus morhua L.) using bioenergetic modelling. Ecology and Evolution, 13: e10751.

Galparsoro, I., Menchaca, I., Garmendia, J. M., Borja, Á., Maldonado, A. D., Iglesias, G., and Bald, J. 2022. Reviewing the ecological impacts of offshore wind farms. npj Ocean Sustainability, 1: 1.

Gilman, E., Kaiser, M. J., and Chaloupka, M. 2019. Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives? Ecosphere, 10: e02968.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., *et al.* 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PLOS ONE.

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., and Genner, M. J. 2020. Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species. Current Biology, 30: 1572-1577.e2.

Hedman, J. E., Rüdel, H., Gercken, J., Bergek, S., Strand, J., Quack, M., Appelberg, M., *et al.* 2011. Eelpout (Zoarces viviparus) in marine environmental monitoring. Marine Pollution Bulletin, 62: 2015–2029.

Heessen, H. J. L., Daan, N., and Ellis, J. R. (Eds). 2015. Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys. Brill | Wageningen Academic. https://brill.com/view/title/68532 (Accessed 2 January 2024).

HELCOM. 2023. State of the Baltic Sea. Third HELCOM holistic assessment 2016-2021. Baltic Sea Environment Proceedings n°194.

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G., *et al.* 2013. Projected impacts of climate change on marine fish and fisheries. ICES Journal of Marine Science, 70: 1023–1037.

Horta E Costa, B., Assis, J., Franco, G., Erzini, K., Henriques, M., Gonçalves, E., and Caselle, J. 2014. Tropicalization of fish assemblages in temperate biogeographic transition zones. Marine Ecology Progress Series, 504: 241–252.

ICES. 2024a. Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice: Recurrent Advice. https://ices-library.figshare.com/articles/report/Herring_i_Clupea_harengus_i_in_subdivisions_20_24_spring_spawners_Skagerrak_Kattegat_and_western_Baltic_/25019273 (Accessed 16 January 2025).

ICES. 2024b. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports. https://ices-library.figshare.com/articles/report/Baltic_Fisheries_Assessment_Working_Group_WGBFAS_/25764978 (Accessed 9 October 2024).

ICES. 2024c. Sprat (Sprattus sprattus) in subdivisions 22–32 (Baltic Sea). ICES Advice: Recurrent Advice. https://ices-

library.figshare.com/articles/report/Sprat_i_Sprattus_sprattus_i_in_subdivisions_22_32_Baltic_Sea_/25019687 (Accessed 15 November 2024).

Illing, B., Moyano, M., Hufnagl, M., and Peck, M. A. 2016. Projected habitat loss for Atlantic herring in the Baltic Sea. Marine Environmental Research, 113: 164–173.

Jepsen, N., Koed, A., and ØKland, F. 1999. The movements of pikeperch in a shallow reservoir. Journal of Fish Biology, 54: 1083–1093.

Jones, M. C., Dye, S. R., Fernandes, J. A., Frölicher, T. L., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. 2013. Predicting the Impact of Climate Change on Threatened Species in UK Waters. PLoS ONE, 8: e54216. Public Library of Science (PLoS).

Kershner, J., Samhouri, J. F., James, C. A., and Levin, P. S. 2011. Selecting Indicator Portfolios for Marine Species and Food Webs: A Puget Sound Case Study. PLoS ONE, 6: e25248.

Knorrn, A. H., Teder, T., Kaasik, A., and Kreitsberg, R. 2024. Beneath the blades: Marine wind farms support parts of local biodiversity - a systematic review. Science of The Total Environment, 935: 173241.

Kornis, M. S., Mercado-Silva, N., and Vander Zanden, M. J. 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology, 80: 235–285.

Korpinen, S., and Andersen, J. H. 2016. A Global Review of Cumulative Pressure and Impact Assessments in Marine Environments. Frontiers in Marine Science, 3. http://journal.frontiersin.org/Article/10.3389/fmars.2016.00153/abstract (Accessed 3 December 2025).

Lappalainen, J., Dörner, H., and Wysujack, K. 2003. Reproduction biology of pikeperch (Sander lucioperca (L.)) – a review. Ecology of Freshwater Fish, 12: 95–106.

Lee-Yaw, J. A., McCune, J. L., Pironon, S., and Sheth, S. N. 2022. Species distribution models rarely predict the biology of real populations. Ecography, 2022: e05877.

Lefébure, R., Larsson, S., and Byström, P. 2014. Temperature and size-dependent attack rates of the three-spined stickleback (Gasterosteus aculeatus); are sticklebacks in the Baltic Sea resource-limited? Journal of Experimental Marine Biology and Ecology, 451: 82–90.

Ling, S. D., Johnson, C. R., Frusher, S. D., and Ridgway, K. R. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences, 106: 22341–22345.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology, 85: 784–794.

MacKenzie, B. R., Horbowy, J., and Köster, F. W. 2008. Incorporating environmental variability in stock assessment: predicting recruitment, spawner biomass, and landings of sprat (Sprattus sprattus) in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1334–1341.

MacNeil, L., Madiraca, F., Otto, S., and Scotti, M. 2025. Spatial Change of Dominant Baltic Sea Demersal Fish Across Two Decades. Ecology and Evolution, 15: e71309.

Manica, A., and Johnstone, R. A. 2004. The Evolution of Paternal Care with Overlapping Broods. The American Naturalist, 164.

Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., *et al.* 2015. Dynamic ocean management: Defining and conceptualizing real-time management of the ocean. Marine Policy, 58: 42–50.

McLean, M. J., Mouillot, D., Goascoz, N., Schlaich, I., and Auber, A. 2019. Functional reorganization of marine fish nurseries under climate warming. Global Change Biology, 25: 660–674.

Meier, H. E. M., Dieterich, C., and Gröger, M. 2021. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. Communications Earth & Environment, 2: 50.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Möllmann, C., Cormon, X., Funk, S., Otto, S. A., Schmidt, J. O., Schwermer, H., Sguotti, C., *et al.* 2021. Tipping point realized in cod fishery. Scientific Reports, 11: 14259.

Mori, A. S., Furukawa, T., and Sasaki, T. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews, 88: 349–364.

Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Hattab, T., Peck, M. A., and Shin, Y.-J. 2022. Using species distribution models only may underestimate climate change impacts on future marine biodiversity. Ecological Modelling, 464: 109826. Elsevier.

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., Müller-Karulis, B., *et al.* 2013. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. Global Change Biology, 19: 3327–3342.

Nissling, A., and Westin, L. 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. Marine Ecology Progress Series, 152: 261–271.

Oestreich, W. K., Chapman, M. S., and Crowder, L. B. 2020. A comparative analysis of dynamic management in marine and terrestrial systems. Frontiers in Ecology and the Environment, 18: 496–504.

Ojaveer, E., and Kalejs, M. 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Reviews in Fish Biology and Fisheries, 20: 203–217.

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., and Bergström, U. 2022. Increases of opportunistic species in response to ecosystem change: the case of the Baltic Sea three-spined stickleback. ICES Journal of Marine Science, 79: 1419–1434.

O'Regan, S. M., Archer, S. K., Friesen, S. K., and Hunter, K. L. 2021. A Global Assessment of Climate Change Adaptation in Marine Protected Area Management Plans. Frontiers in Marine Science, 8: 711085.

Orio, A., Bergström, U., Florin, A., Lehmann, A., Šics, I., and Casini, M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46: 633–645.

Orio, A., Bergström, U., Florin, A.-B., Šics, I., and Casini, M. 2020. Long-term changes in spatial overlap between interacting cod and flounder in the Baltic Sea. Hydrobiologia, 847: 2541–2553.

Ory, N. C., Gröger, J. P., Lehmann, A., Mittermayer, F., and Clemmesen, C. 2022. Early Arrival of Spring-Spawner Atlantic Herring at Their Spawning Ground in the Kiel Fjord, Western Baltic, Relates to Increasing Sea Water Temperature. SSRN Electronic Journal. https://www.ssrn.com/abstract=4164412 (Accessed 16 February 2024).

Otto, S. A., Kadin, M., Casini, M., Torres, M. A., and Blenckner, T. 2018. A quantitative framework for selecting and validating food web indicators. Ecological Indicators, 84: 619–631.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana, 10: 29–59.

Pecl, G. T., Ward, T. M., Doubleday, Z. A., Clarke, S., Day, J., Dixon, C., Frusher, S., *et al.* 2014. Rapid assessment of fisheries species sensitivity to climate change. Climatic Change, 127: 505–520.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., *et al.* 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science, 355: eaai9214.

Pecuchet, L., Lindegren, M., Kortsch, S., Całkiewicz, J., Jurgensone, I., Margonski, P., Otto, S. A., *et al.* 2020. Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization. Ecography, 43: 197–208.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308: 1912–1915.

Petereit, C., Haslob, H., Kraus, G., and Clemmesen, C. 2008. The influence of temperature on the development of Baltic Sea sprat (Sprattus sprattus) eggs and yolk sac larvae. Marine Biology, 154: 295–306.

Pinsky, M. L., and Fogarty, M. 2012. Lagged social-ecological responses to climate and range shifts in fisheries. Climatic Change, 115: 883–891.

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung, W. W. L. 2018. Preparing ocean governance for species on the move. Science, 360: 1189–1191.

Pinsky, M. L., Selden, R. L., and Kitchel, Z. J. 2020. Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science, 12: 153–179.

Pollom, R. A., Cheok, J., Pacoureau, N., Gledhill, K. S., Kyne, P. M., Ebert, D. A., Jabado, R. W., *et al.* 2024. Overfishing and climate change elevate extinction risk of endemic sharks and rays in the southwest Indian Ocean hotspot. PLOS ONE, 19: e0306813.

Polte, P., Gröhsler, T., Kotterba, P., Von Nordheim, L., Moll, D., Santos, J., Rodriguez-Tress, P., *et al.* 2021. Reduced Reproductive Success of Western Baltic Herring (Clupea harengus) as a Response to Warming Winters. Frontiers in Marine Science, 8: 589242.

Queirós, A. M., Strong, J. A., Mazik, K., Carstensen, J., Bruun, J., Somerfield, P. J., Bruhn, A., *et al.* 2016. An Objective Framework to Test the Quality of Candidate Indicators of Good Environmental Status. Frontiers in Marine Science, 3. http://journal.frontiersin.org/Article/10.3389/fmars.2016.00073/abstract (Accessed 3 December 2025).

Ramos, J. E., Tam, J., Aramayo, V., Briceño, F. A., Bandin, R., Buitron, B., Cuba, A., *et al.* 2022. Climate vulnerability assessment of key fishery resources in the Northern Humboldt Current System. Scientific Reports, 12: 4800.

Rau, A., Lewin, W.-C., Zettler, M. L., Gogina, M., and Von Dorrien, C. 2019. Abiotic and biotic drivers of flatfish abundance within distinct demersal fish assemblages in a brackish ecosystem (western Baltic Sea). Estuarine, Coastal and Shelf Science, 220: 38–47.

Receveur, A., Bleil, M., Funk, S., Stötera, S., Gräwe, U., Naumann, M., Dutheil, C., *et al.* 2022. Western Baltic cod in distress: decline in energy reserves since

1977. ICES Journal of Marine Science, 79: 1187–1201. Oxford University Press (OUP).

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. Science Advances, 4: eaar8195.

Rosciszewski-Dodgson, M. J., and Cirella, G. T. 2024. Environmental drivers affecting the status of top commercial fish stocks in the Baltic Sea: review. Frontiers in Marine Science, 11: 1399707.

Schaber, M., Marohn, L., Petereit, C., Schroeder, J. P., Zumholz, K., and Hanel, R. 2011. Newcomers in the Baltic Sea: an attempt to trace the origins and whereabouts of thicklip grey mullet Chelon labrosus. Fisheries Science, 77: 757–764.

Schade, F. M., Weist, P., Dierking, J., and Krumme, U. 2022. Living apart together: Long-term coexistence of Baltic cod stocks associated with depth-specific habitat use. PLOS ONE, 17: e0274476.

Smialek, N., Pander, J., and Geist, J. 2021. Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. Fisheries Management and Ecology, 28: 437–467.

Smit, K. P., Bernard, A. T. F., Lombard, A. T., and Sink, K. J. 2021. Assessing marine ecosystem condition: A review to support indicator choice and framework development. Ecological Indicators, 121: 107148.

Somodi, I., Lepesi, N., and Botta-Dukát, Z. 2017. Prevalence dependence in model goodness measures with special emphasis on true skill statistics. Ecology and Evolution, 7: 863–872.

Souza, A. T., Dias, E., Antunes, C., and Ilarri, M. 2023. Disruptions caused by invasive species and climate change on the functional diversity of a fish community. NeoBiota, 88: 211–244.

Sparholt, H. 1994. Fish species interactions in the Baltic Sea. Dana, 10: 131–162.

Spencer, P. D., Hollowed, A. B., Sigler, M. F., Hermann, A. J., and Nelson, M. W. 2019. Trait-based climate vulnerability assessments in data-rich systems: An application to eastern Bering Sea fish and invertebrate stocks.

Sternecker, K., Denic, M., and Geist, J. 2014. Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. Ecology and Evolution, 4: 2749–2758.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., *et al.* 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature, 501: 539–542.

Sumaila, U. R., and Tai, T. C. 2020. End Overfishing and Increase the Resilience of the Ocean to Climate Change. Frontiers in Marine Science, 7: 523.

Thompson, P. L., Rooper, C. N., Nephin, J., Park, A. E., Christian, J. R., Davies, S. C., Hunter, K., *et al.* 2023. Response of Pacific halibut (Hippoglossus stenolepis) to future climate scenarios in the Northeast Pacific Ocean. Fisheries Research, 258: 106540.

Thorson, J. T., Pinsky, M. L., and Ward, E. J. 2016. Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods in Ecology and Evolution, 7: 990–1002.

Tomczak, M. T., and Sapota, M. R. 2006. The fecundity and gonad development cycle of the round goby (Neogobius melanostomus Pallas 1811) from the Gulf of Gdańsk. International Journal of Oceanography and Hydrobiology, 35: 353–367.

Veneranta, L., and Urho, L. 2021. Reproduction range of garfish, Belone belone (L.), in the northern Baltic Sea.

Verges, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Jr, K. L. H., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., *et al.* 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings of the Royal Society B: Biological Sciences, 281: 20140846.

Von Nordheim, L., Kotterba, P., Moll, D., and Polte, P. 2018. Impact of Spawning Substrate Complexity on Egg Survival of Atlantic Herring (Clupea harengus, L.) in the Baltic Sea. Estuaries and Coasts, 41: 549–559.

Walters, C. J., and Holling, C. S. 1990. Large-Scale Management Experiments and Learning by Doing. Ecology, 71: 2060–2068.

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., *et al.* 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Science of The Total Environment, 733: 137782.

Zhao, K., Gaines, S. D., García Molinos, J., Zhang, M., and Xu, J. 2022. Climate change and fishing are pulling the functional diversity of the world's largest marine fisheries to opposite extremes. Global Ecology and Biogeography, 31: 1616–1629.

FUNDING



I was supported through the balt_ADAPT (Adaptation of the Western Baltic Coastal Fishery to Climate Change) project. The balt_ADAPT project has received funding from the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung, BMBF) grant 03F0863.

EIDESSTATTLICHE VERSICHERUNG

Hiermit versichere ich an Eides statt, die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen benutzt zu haben. Sofern im Zuge der Erstellung der vorliegenden Dissertationsschrift generative Künstliche Intelligenz (gKI) basierte elektronische Hilfsmittel verwendet wurden, versichere ich, dass meine eigene Leistung im Vordergrund stand und dass eine vollständige Dokumentation aller verwendeten Hilfsmittel gemäß der Guten wissenschaftlichen Praxis vorliegt. Ich trage die Verantwortung für eventuell durch die gKI generierte fehlerhafte oder verzerrte Inhalte, fehlerhafte Referenzen, Verstöße gegen das Datenschutz- und Urheberrecht oder Plagiate.

Affidavit:

I hereby declare and affirm that this doctoral dissertation is my own work and that I have not used any aids and sources other than those indicated. If electronic resources based on generative artificial intelligence (gAI) were used in the course of writing this dissertation, I confirm that my own work was the main and value-adding contribution and that complete documentation of all resources used is available in accordance with good scientific practice. I am responsible for any erroneous or distorted content, incorrect references, violations of data protection and copyright law or plagiarism that may have been generated by the gAI.

Hamburg, 5.1.2026

Ort, den | City, date Unterschrift | Signature

ACKNOWLEDGEMENTS

Completing one's doctoral studies is no simple task and I wish to express my gratitude to all the kind people who supported and helped me in seeing it through. Firstly, I want to thank my supervisors Saskia Otto and Christian Möllmann. Thank you for giving me the chance to undertake my doctoral journey, a wish I had for many years, for your guidance and for allowing me the flexibility to explore my own research interests.

A big thank you goes to all the kind people with whom I had the chance to collaborate with through shared projects and otherwise – Marco Scotti, Liam MacNeil, Cyril Dutheil, Markus Meier and many others. An especially big thank you goes to Guilherme Pinto for all the advice, shared laughs and friendship.

I always felt at home at the IMF thanks to all the good people I had the chance to meet there. A huge thank you goes to the friends with whom I shared our office – Alexandra Blöcker, Helene Gutte, and Elvis Kamberi. Thank you for all the laughs, interesting discussions, and taking care of my house plants while I was away.

I am forever grateful to Vedran, Gabriela, Marijeta, and Kate for their continued support over the years. Furthermore, I wish to thank my brother Vinko for his calming words when they were needed and for helping me see the world from a more optimistic perspective when it didn't feel like that. Also, while I was writing this thesis, there were times when I felt overwhelmed and lacked motivation. Because of this, I am thankful to my sister Lucija for her advice as it helped me persevere and overcome this challenge. I am also grateful to their families for their kindness and support.

It is hard to put in the words the gratitude that I feel towards my parents, Branka and Pavle. My mother, who read countless stories about giant squids and descriptions of fish to me while I was still a child, and my father, who always stressed that being a

good person is far more important than being a good academic, instilled in me all the curiosity for the world and a wish to find my own purpose in life that eventually led me to pursue my scientific journey.

While it is true that only one person can hold their doctoral degree, at the center of this achievement lie the support and love that were given to them by others. Thus, it is only fitting that I end this text with a Thank you to a person I owe the world to – my wife Ita. In the darkest of moments, you were the light that helped me find my way and wherever in the world we found ourselves, your smile always made me feel at home. Thank you for your love, your kindness, and a healthy dose of loving disagreement.

ERKLÄRUNG ZUR IDENTITÄT DER GEDRUCKTEN DISSERTATION

Ich versichere, dass dieses gebundene Exemplar der Dissertation und das in elektronischer Form eingereichte Dissertationsexemplar (über den Docata-Upload) und das bei der Fakultät (Studienbüro des Fachbereichs Biologie der Universität Hamburg) zur Archivierung eingereichte gedruckte gebundene Exemplar der Dissertationsschrift identisch sind.

Hamburg, 6.1.2026 Frane Madiraca

I, the undersigned, declare that this bound copy of the dissertation and the dissertation submitted in electronic form (via the Docata upload) and the printed bound copy of the dissertation submitted to the faculty (Academic Office of the Department of Biology at the University of Hamburg) for archiving are identical.

Hamburg, 6.1.2026 Frane Madiraca