FORECASTING THE MARINE BIOLOGICAL ENVIRONMENT

EXPLORING THE SPATIAL DISTRIBUTION OF A NORTH ATLANTIC FISH SPECIES AT THE EXAMPLE OF BLUE WHITING

DISSERTATION

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ABSTRACT

This dissertation contributes towards forecasting the marine biological environment. The overall aim of this contribution is to better understand, model, and forecast changes in the spatial distribution of marine organisms, at the example of the North East Atlantic fish species blue whiting. Climate-driven distributional shifts of marine organisms pose challenges to both monitoring and management of the species. Anticipating such spatial shifts would enhance the climate-resilience of marine resource management practices and motivated this dissertation.

A central and novel aspect of this dissertation is the quantification of the relationship between blue whiting and its marine environment, which for the first time allows us to explore the potential of forecasting spatial variations of this species distribution. Using blue whiting as a case study, I illustrate how spatial variations of the potential spawning region of blue whiting are connected to oceanographic variability. Based on an extensive set of blue whiting larval observations I create statistical species distribution models. These models show an expansion of the potential spawning region over Rockall Plateau during warm and saline conditions and a contraction towards the continental shelf when conditions are colder and fresher, supporting previous studies. Going beyond, my work enables a quantification of the species-environment relationship that highlights that spawning commonly occurs within a specific range of salinity.

This quantification of the species-environment relationship enables me to translate forecasts of the physical marine environment into biological forecasts. In particular, I explore the potential of forecasting spatial variations of the suitable spawning habitat of blue whiting at inter- to multiannual timescales based on a state-of-the-art Earth System Model (ESM). I find that the ESM skilfully predicts temperature and in particular, salinity within the spatial and temporal domain relevant for spawning blue whiting, making biological forecasts feasible. Forecasts of the marine environment and the suitable spawning habitat perform particularly well in the area of Rockall-Hatton Plateau. Here, distributional changes of the suitable spawning habitat can be predicted skilfully with the ESM around a year in advance. A clear benefit of modelling and forecasting the suitable spawning habitat with the dynamic ESM lies in its dynamic consistency that enables the ESM to represent hydrodynamic processes, specifically in the bathymetrically distinct region Rockall-Hatton Plateau. By exposing these benefits, this dissertation emphasises that ESMs can be well suited for creating distributional forecasts of marine organisms in the North East Atlantic. Operational distributional forecasts of marine organisms have until now, only been delivered on seasonal timescales. Therefore, the creation of skilful inter-annual forecasts, as presented in this dissertation, marks an innovation in the field of biological forecasting. This longer management lead-time increases the capacity of biological forecast to contribute to the pro-active and dynamic management of our common marine resources.

ZUSAMMENFASSUNG

Diese Dissertation leistet einen Beitrag zur Vorhersage der biologischen Meeresumwelt. Das übergeordnete Ziel dieser Dissertation besteht darin, Veränderungen in der räumlichen Verteilung von Meeresorganismen besser zu verstehen, zu modellieren und vorherzusagen, am Beispiel der nordostatlantischen Fischart Blauer Wittling. Klimabedingte Verschiebungen in der Verteilung von Meeresorganismen stellen eine Herausforderung sowohl für ihre Überwachung als auch für ihre Bewirtschaftung dar. Die Vorhersage solcher räumlichen Verschiebungen würde die Klimaresilienz der Bewirtschaftungspraktiken für Meeresressourcen verbessern und motiviert diese Dissertation.

Ein zentraler und neuartiger Aspekt dieser Dissertation ist die Quantifizierung der Beziehung zwischen dem Blauen Wittling und seiner Meeresumwelt, die es uns zum ersten Mal ermöglicht, dass Potenzial der Vorhersage räumlicher Variationen der Verbreitung dieser Art zu untersuchen. Am Beispiel des Blauen Wittling zeige ich, wie räumliche Variationen des potenziellen Laichgebiets des Blauen Wittling mit lokalen ozeanografischen Schwankungen zusammenhängen. Auf der Grundlage umfangreicher Beobachtungen der Larven des Blauen Wittling erstelle ich statistische Modelle der Artenverteilung. Diese Modelle zeigen eine Ausdehnung des potenziellen Laichgebiets über dem Rockall Plateau bei eher warmen und salzhaltigen Bedingungen und eine Kontraktion in Richtung Kontinentalschelf, wenn die Bedingungen kälter und frischer sind, was frühere Studien bestätigt. Darüber hinaus ermöglicht meine Arbeit, die Beziehung zwischen der Art und seiner Umwelt zu quantifizieren, und verdeutlicht, dass das Laichen vorzugsweise in einem bestimmten Salzgehaltbereich stattfindet.

Diese Quantifizierung der Beziehung zwischen dem Blauen Wittling und seiner Umwelt ermöglicht es mir, Vorhersagen über die physikalische Meeresumwelt in biologische Vorhersagen zu übersetzen. Insbesondere untersuche ich das Potenzial räumliche Schwankungen des geeigneten Laichhabitats des Blauen Wittling mit einem Erdsystemmodel (ESM) mehrere Jahre im Voraus vorherzusagen. Ich stelle fest, dass das ESM die Temperatur und insbesondere den Salzgehalt in dem für den laichenden Blauen Wittling relevanten räumlichen und zeitlichen Bereich gut vorhersagen kann, so dass biologische Vorhersagen möglich sind. Die Vorhersage des Meeresklimas und des geeigneten Laichhabitats funktioniert besonders gut im Bereich des Rockall-Hatton Plateaus. Hier können mit dem ESM Verteilungsänderungen des geeigneten Laichhabitats etwa ein Jahr im Voraus zuverlässig vorhergesagt werden. Ein klarer Vorteil der Modellierung und Vorhersage des geeigneten Laichhabitats mit dem dynamischen ESM liegt in dessen dynamischer Natur, die es befähigt hydrodynamische Prozesse abzubilden, insbesondere in der bathymetrisch ausgeprägten Region Rockall-Hatton Plateau. Durch die Entdeckung dieser Vorteile unterstreicht die vorliegende Dissertation, dass sich ESMs gut eignen, um Vorhersagen über die Verteilung von Meeresorganismen im Nordostatlantik zu erstellen. Operative Vorhersagen über die Verteilung von Meeresorganismen wurden bisher nur auf saisonalen Zeitskalen erstellt. Daher stellt die Erstellung zuverlässiger Prognosen ein Jahr im Voraus, wie sie in dieser Dissertation vorgestellt werden, eine Innovation auf dem Gebiet der biologischen Vorhersage dar. Diese längere Vorlaufzeit verbessert die Fähigkeit biologischer Vorhersagen, zu einer proaktiven und dynamischen Bewirtschaftung unserer gemeinsamen Meeresressourcen beizutragen.

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PUBLICATIONS RELATED TO THIS DISSERTATION

APPENDIX A

Miesner, Anna K., and Mark R. Payne, 2018. Oceanographic variability shapes the spawning distribution of blue whiting (*Micromesistius poutassou*). Fisheries Oceanography 27(6): 1–16. doi:10.1111/fog.12382.

APPENDIX B

Miesner, Anna K., Sebastian Brune, Patrick Pieper, Vimal Koul, Johanna Baehr, and Corinna Schrum (*under review*). Exploring the potential of forecasting fish distributions in the North East Atlantic with a dynamic Earth System Model, exemplified by the suitable spawning habitat of blue whiting. Frontiers in Marine Science.

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FORECASTING THE SPATIAL DISTRIBUTION OF FISH IN THE NORTH EAST ATLANTIC

This dissertation contains highly interdisciplinary research that is based, among others, on methods from atmospheric science, physical oceanography, biogeography, and ecology. Building on the advances of observing, modelling and forecasting the marine environment, this dissertation aims at providing a solid understanding of the processes that shape the spawning distribution of a pelagic fish species in the North East Atlantic, namely blue whiting. Building on this knowledge, this dissertation explores the potential of forecasting spatial variations of the suitable spawning habitat of this species. While blue whiting serves as a case study, many of the lessons learned are also common to modelling and forecasting the distribution of other marine living organisms. As such, this dissertation is a contribution towards advancing forecasts of the marine biological environment. Moreover, this dissertation is a tribute to interdisciplinary science and in particular to all the scientists, even if not mentioned explicitly, that have contributed towards shaping this underlying body of knowledge.

1 INTRODUCTION

"The present investigation is in part to be regarded as a pioneer attempt towards a service of information to the [Fishing] *industry which may be realized in the future - a service like that of weather forecasting"*

Sir Alistair C. Hardy (1939)

Just like migratory birds fly into warmer regions with a more plentiful food supply when winter arrives, fish may respond to changes in their surrounding marine environment by migrating into areas where environmental conditions are more favourable (Neill 1984; Neill et al. 1994). A major endeavour in fisheries oceanography has always been to explain the relationship between the abundance and distribution of fish and their surrounding marine environment and spans back to the seminal works of Bjørn Helland-Hansen and Fridtjof Nansen (1909) and Johan Hjort (1914) published a century ago. At that time, fluctuations in the fishery were mainly thought to be caused by changes in fish migration. Helland-Hansen and Nansen (1909), two pioneers in the field of physical oceanography, suggested a link between Atlantic water properties (in particular temperature) and the growth, onset of spawning and number of fish caught in the following year. Hjort (1914), however, proposed that the biological and physical conditions *after* spawning affected the survival of early larval stages and hence fluctuations in the abundance of fish. This hypothesis became a prime focus of fisheries oceanography in the last century (Houde 2008). After 100 years of fisheries oceanography, we know that these hypotheses are not contradictory. On the opposite, each explains a facet of the complex biological interactions between fish and their marine environment that shape the dynamics of their abundance and distribution on various spatial and temporal scales (Houde 2008; Hare 2014; Kjesbu et al. 2021).

Already at the beginning of the 20th century researchers thought about the possibility of forecasting the abundance and distribution of fish based on the physical and biological properties of the water (Helland-Hansen and Nansen 1909; Hardy 1930). However, their observational time series were too short and regionally restricted to allow for robust analyses, let alone forecasts. The idea that plankton (i.e. phyto- and zooplankton) could be an indicator for the presence of fish in the water sparked the invention of the Continuous Plankton Recorder (CPR) by Sir Alistair C. Hardy (Hardy 1925; 1926). The CPR is a passive plankton sampling device that was first intended to be used by fishermen as a simple indicator of plankton and hence fish abundance (Hardy 1925). However, its main purpose became to study the abundance and spatial distribution of plankton in the oceans (Hardy 1926). After its first applications, the CPR was modified so it could be towed behind non-research vessels, so-called ships-of-opportunity, and has remained relatively unchanged until today (Reid et al. 2003). This ingeniously farsighted improvement facilitated the large spatial coverage of the survey and its continuation over decades[1] that made the CPR survey the most extensive and longest-running survey of marine organisms in the world (Planque and Reid 2002; Reid et al. 2003).

The CPR's inventor Sir Alistair Hardy (1939), envisioned that information from CPR could form the basis of forecasting changes in the abundance and distribution of fish and turn into *"a service like that of weather forecasting*". He hypothesised that forecasts could be based either on the direct link between plankton and fish or on an indirect link whereby plankton was merely a proxy for hydrological changes that would affect the abundance and distribution of fish. However, until today plankton-based forecasts of fish have not succeeded. Conversely, Hardy's (1939) second hypothesis that changes in the physical marine environment could be used to anticipate changes in the distribution and abundance of fish has proven to be more fruitful for creating marine biological forecasts in the years to come.

One prerequisite for creating biological forecasts of marine organisms is a sound understanding of the link between the local physical marine environment and the species' response, such as its distribution. Many living organisms are indirectly, e.g. through food availability, or directly, e.g. through physiological responses, affected by variations in the environment they live in. The underlying idea of distributional biological forecasts today is that changes in the physical marine environment, such as changing temperatures, alter the geographic distribution of a species' suitable environmental habitat, which results in changes in the species' actual distribution (Payne et al. 2017). Thereby biological forecasts are related to the concept of the ecological niche.

Joseph Grinnell (1917) first coined the term *"niche"* when he found a specific range of abiotic environmental conditions (i.e. temperature) that delineated the distribution of a bird species. Charles Elton (1927) presented an opposing theory that focused on biotic interactions, such as predation, competition or food availability, as defining factors of the distribution of a species. Grinnell (1917) and Elton (1927) both ascribed niches to environments. In a new approach George Evelyn Hutchinson (1957), however, combined these approaches and attributed niches to species, which formed a crucial innovation of the niche concept (Colwell and Rangel 2009). In the Hutchinsonian niche concept, the presence of an organism is limited by the abiotic environment *and* by biotic interactions. Accordingly, the ecological niche *sensu* Hutchinson (1957), represents a multidimensional volume consisting of a range of biotic and abiotic factors that permit a species to thrive, i.e. to reproduce, feed, grow and survive (Colwell and Rangel 2009). Jorge Soberón and

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[1] The CPR survey was initiated in 1931 and runs continuously until today, with the exemption of 8 years from 1939 to 1946 due to the Second World War and its aftermath when there were no ships of opportunity available (Henderson 1953; Reid et al. 2003).

Andrew Townsend Peterson (2005) proposed a further addition to the niche framework, namely dispersal abilities since many organisms are also limited by their ability to move or migrate into suitable habitats (see also Soberón and Nakamura 2009; Soberón 2007). Thereby, today the ecological niche is an essential framework to explore patterns and mechanisms behind spatial variations of marine organisms (Figure 1a). Since not all processes that shape the realized spatial distribution of a species, such as biotic interactions like predation and competition or dispersal abilities, can be known or measured, biological forecasts today are mainly based on abiotic environmental niche components, in the marine realm mainly temperature. However, with growing knowledge on species-environment interactions and our increasing ability to describe and predict the marine environment, we will likely see more realistic niche descriptions and biological forecasts in the future.

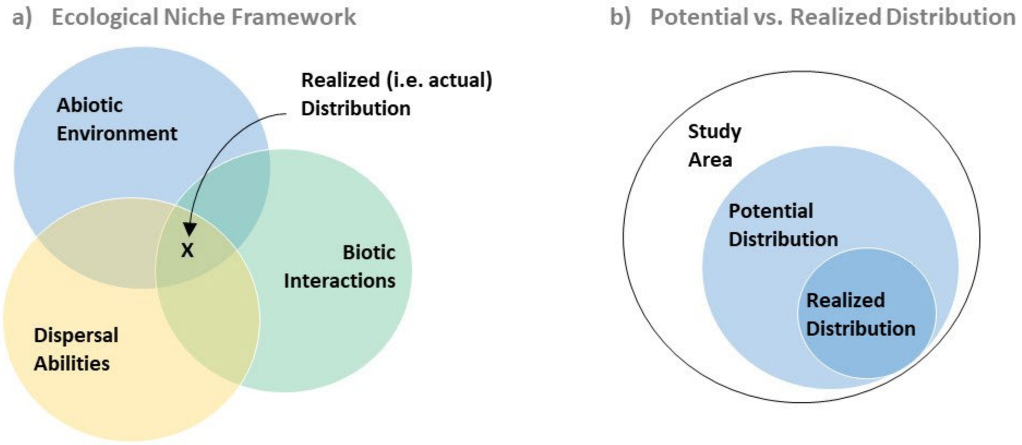

Figure 1 a) Within the modern ecological niche framework the realized spatial distribution of an organism (x, where it is actually observed in geographic space) is a function of favourable environmental conditions (the abiotic environment, blue) and biotic interactions (green) as well as dispersal abilities (yellow). Figure adapted from Soberón and Peterson (2005); Soberón (2007); Melo-Merino et al. (2020).
b) Illustrating the difference between the potential and the realized distribution of a species within the geographic space of the study area. The potential distribution of a species indicates regions where the abiotic environment is suitable for the species at a certain point of time and thereby indicates where the species might potentially occur. The potential distribution of a species is generally larger than the realized distribution, which is affected (made smaller) by the species' dispersal or migratory abilities and biotic interactions such predation and competition (Soberón 2007).

The establishment of long time series of the biological and physical environment is among the prime advances in fisheries oceanography that facilitated exploring the connection between fish and their surrounding marine environment (Bograd et al. 2014). Understanding and quantifying the species-environment relationship, however, requires observations of the species and corresponding observations of its surrounding physical marine environment in the same spatio-temporal resolution. In many cases, we do have both physical and biological observations, however not sampled synchronously. Therefore, statistical methods are needed to combine observations of a species of interest with environmental observations at the same point in time and space. In this respect, one commonly used statistical tool is species distribution modelling (Elith and Leathwick 2009; Guisan and Zimmermann 2000). Species Distribution Models (SDMs[2]) use the concept of the ecological niche to bridge the gap between physical and biological processes (Wiens et al. 2009). Thereby, SDMs are efficient tools for translating projections of the physical environment into ecological consequences (Wiens et al. 2009). By correlating occurrence observations of an organism with co-occurring environmental conditions, SDMs can be used to approximate the suitable environmental niche of the organism (Elith and Leathwick 2009; Guisan and Zimmermann 2000). Regions, where the abiotic environment is suitable for a species, are also commonly referred to as potential niche (Jackson and Overpeck 2000) or potential distribution (e.g. Guisan and Zimmermann 2000; and Figure 1b). This simple yet powerful approach enables SDMs to indicate drivers of species distributions, quantify species-environment relationships and project spatial changes in the potential distribution of a species (Wiens et al. 2009; Elith and Leathwick 2009). As such, SDMs are commonly applied to explore past and current distributional patterns of marine organisms, in particular, fish and their response to environmental variation (Melo-Merino et al., 2020, and references therein). Moreover, SDMs are powerful tools to project distributional changes associated with climate change (Melo-Merino et al., 2020, and references therein). Additionally, a range of marine biological forecasts products today employ SDMs as a tool to translate physical forecasts into biological forecasts to anticipate climate-driven habitat shifts of a variety of fish species, turtles and sea lions (Hazen et al. 2018; 2017; Malick et al. 2020).

For many marine organisms, specifically fish, variations in the marine environment, predominantly temperature, have caused substantial shifts in their spatial distribution (Pinsky et al. 2013; Poloczanska et al. 2016). Since one country might perceive the distributional shift of a commercially important fish stock[3] as a "gain" and the other as a "loss", changes in the spatial distribution of fish can be politically loaded and in some cases may require a careful (re-) assessment of the stock (Link, Nye, and Hare 2011). The poleward shift of Northeast Atlantic mackerel in response to ocean warming (Jansen et al. 2016), for example, sparked an intense political dispute about the allocation of fishing quotas (Spijkers and Boonstra 2017). Other

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[2] *"What we term SDMs have also been called (sometimes with different emphases and meanings): bioclimatic models, climate envelopes, ecological niche models (ENMs), habitat models, resource selection functions (RSFs), range maps, and—more loosely—correlative models or spatial models"* (Elith and Leathwick 2009).

[3] The management unit of a fishery is the fish stock, which is defined as a "*group of individuals in a species occupying a well defined spatial range independent of and more or less genetically isolated from other stocks of the same species*" (Cochrane and Garcia 2009).

commercially important North Atlantic fish stocks with observed climate-driven distributional shifts include bluefin tuna (MacKenzie et al. 2014; Jansen et al. 2021) and blue whiting (Hátún, Payne, and Jacobsen 2009; Miesner and Payne 2018). Biological forecasts that provide information at time scales relevant to stakeholders and managers, e.g. several months or even years in advance (Tommasi, Stock, Hobday, et al. 2017; Payne et al. 2017), can be valuable for preparing ocean governance and marine spatial management for climate-driven distributional shifts (Pinsky et al. 2018; Tommasi, Stock, Hobday, et al. 2017).

Blue whiting[4] (Figure 2) is a North East Atlantic fish species with an extraordinary long observational time series that revealed a close connection between its spawning distribution and the surrounding marine environment (Bainbridge and Cooper 1973; Hátún, Payne, and Jacobsen 2009; Schmidt 1909). Already at the beginning of the 20th century Johannes Schmidt, a scientist leading the first research cruises of the newly founded International Council for the Exploration of the Sea (ICES), noted that blue whiting is sensitive to the ambient temperatures and salinities the fish experienced during spawning (Schmidt 1909). His observations of adult and larval blue whiting in the North East Atlantic, coupled with ship-based measurements of temperatures and salinity, contributed to *"new evidence* […] *that a species is frequently more bound to definite external conditions at the spawning time than at any other parts of its life!"* (Schmidt 1909).

Figure 2. Blue whiting depicted on a Faroes stamp from 2002 by Martin Mörck to celebrate the 100th anniversary of ICES.

Until now, the hypothesis that early-life stages and spawning fish are more susceptible to unfavourable environmental conditions than other life stages holds. Fish have complex life cycles

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[4] In older literature (e.g. Schmidt (1909); Henderson (1953, 1964)), blue whiting is referred to as *Gadus poutassou,* while now *Micromesistius poutassou* (1827 Risso) is the accepted scientific name of this species.

and may respond differently to changes in the ambient marine environment, depending on the life stage (Rijnsdorp et al. 2009). Specifically, juveniles have narrower tolerable ranges to varying environmental conditions and are less capable of actively swimming towards habitats that are more suitable than adult fish (Houde 2002; Pörtner and Peck 2010 and references therein). Therefore, in fish with distinct habitat requirements for spawning, such as blue whiting, juveniles and spawning fish show greater susceptibility to oceanographic variability than non-spawning adults.

Around the centre of the 20th century, blue whiting regained importance when it (unintentionally) was captured by the CPR survey west of the British Isles (Henderson 1953). The focus of the CPR survey was to sample phyto- and zooplankton, however, the device also captured eggs and larvae of some fish species (Richardson et al. 2006). One of the most commonly occurring fish species found in CPR samples is blue whiting, which accounts for 10 % of all the fish larvae identified in the CPR and even over 75% of larvae encountered west off Scotland (Bainbridge and Cooper 1973). Based on CPR observations, a great abundance of blue whiting larvae was discovered during spring in the deep waters west of the British Isles (Henderson 1964; 1953), extending from the European Continental Shelf onto Rockall Plateau (Figure 3) and thereby confirming the early observations of Schmidt (1909). The high number of blue whiting larvae observed west of the British Isles suggested a large spawning stock of the species (Bailey 1970; Raitt 1968a). This discovery sparked economic interests in blue whiting since this species had not been previously exploited commercially in that region (Bailey 1970; Raitt 1968b). As a result, in the early 70's the industrial fishery of blue whiting commenced and the stock is now considered to be fully exploited (FAO 2012). Thereby, the CPR survey has played a significant role in the discovery and exploration of blue whiting.

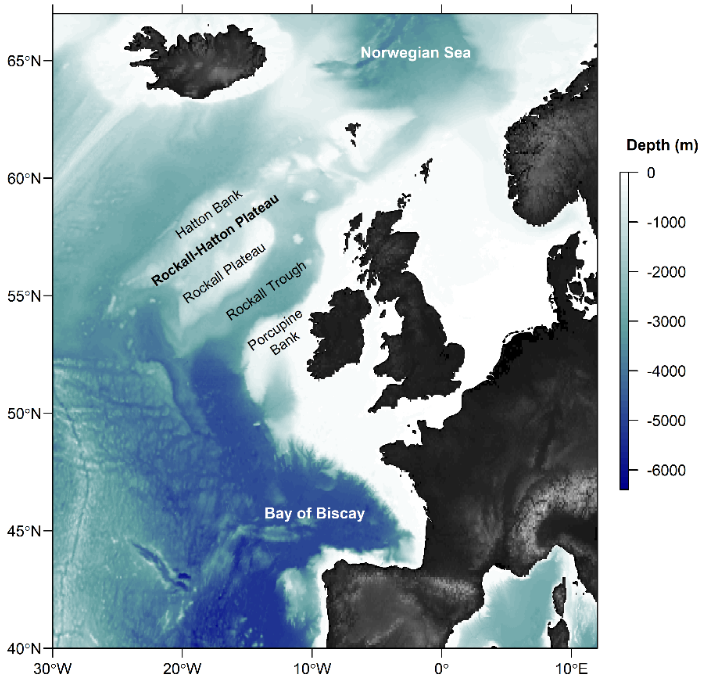

Figure 3. Bathymetric relief map of the study region, indicating geographic features mentioned in the text.

A major challenge for the scientific monitoring, assessment and management of blue whiting are extensive fluctuations of the spawning distribution. Even though blue whiting are widely distributed in the North East Atlantic, most fish are caught west of the British Isles during early spring, when blue whiting aggregate in this area for spawning (NEAFC 2013; Figure 4). The International Blue Whiting Spawning Stock (IBWSS) survey, which aims at annually sampling the core spawning region of blue whiting within two to three weeks in spring, also targets the spawning aggregation of blue whiting (ICES 2015a). While the spawning distribution mainly stretches alongside the European Continental Shelf west of the British Isles, during some years, the spawning region stretches further westwards towards Rockall-Hatton Plateau (Bailey 1982; ICES 2019; Bainbridge and Cooper 1973). Sampling the spawning distribution of blue whiting can be challenging. Sampling is particularly challenging further off-shore on Rockall-Hatton Plateau due to bad weather conditions and the great distance to ports (ICES 2015a). Insufficient survey coverage on Rockall-Hatton Plateau can result in underestimating the abundance of blue whiting during years when the stock shows an expanded distribution (ICES 2010b; 2011). These uncertainties and biases in the survey propagate into stock assessment and can potentially lead to misleading fisheries advice. Skilfully forecasting these distributional changes of blue whiting would benefit the species' management and ensure its sustainable exploitation, which motivated this dissertation.

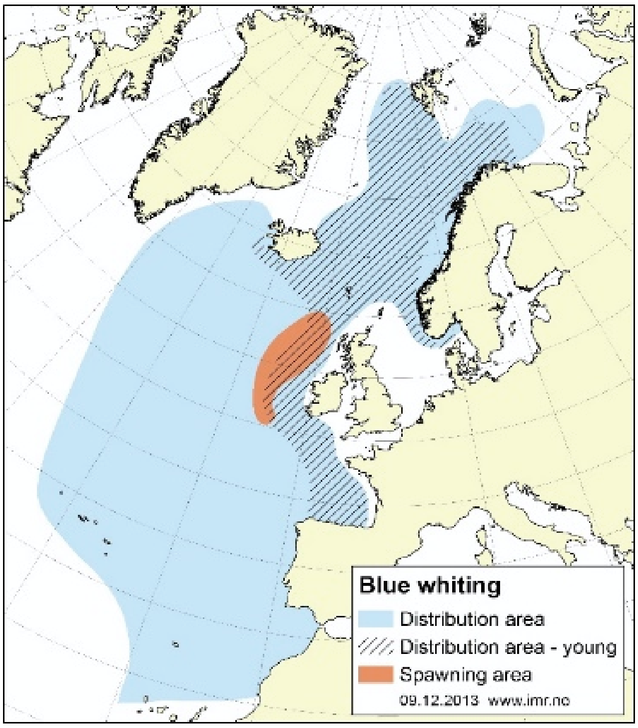

Figure 4. The overall distribution of blue whiting in the North East Atlantic (blue), the main spawning distribution west of the British Isles (orange) and the distributional area of the juvenile fish (dashed). Figure provided by the Institute of Marine Research, Norway.

Besides a sound understanding of the species-environment relationship, another essential ingredient to successfully developing biological forecasts is skilful predictions of the physical environment. Accordingly, forecasting the biological environment would not have been possible without the advances in weather and climate prediction along with progress in observational and computational technology.

Vilhelm Bjerknes (1904) revolutionary idea that a mathematical model based on the laws of mechanics and physics could be used to model atmospheric dynamics was a milestone for weather prediction. However, due to the quantity and complexity of calculations involved and the lack of sufficient observational records, the first meteorological forecast originated only in 1950 with the help of an *"electronic computer"* (Charney, Fjörtoft, and Neumann 1950). Based on ever-improving weather forecasts, pioneering operational ecological forecasts emerged in the field of epidemiology. In 1977, the first hay fever forecast became operational by switching from pollen counts to weather information as the determining factor driving the forecast (Spieksma 1980). Moreover, today meteorological data is used to forecast ticks and fleas (Beugnet, Chalvet-Monfray, and Loukos 2009). In 1983, the first successful "ocean weather" or mesoscale forecasts (Treguier et al. 2017) was created by Allan R. Robinson et al. (1984; 1986) but forecasts could only be run on a global scale when computational efficiency increased in the late 1990s (Pinardi et al. 2017). Since then, forecasts of the atmospheric and the marine climate have greatly improved.

The increase in quality and quantity of observations of the physical marine environment has considerably improved our ability to describe and predict the ocean and the climate. In that respect, the continuous development of Earth System Models (ESMs) has been of central importance. ESMs are global climate models that simulate all relevant elements of the Earth system by integrating interactions between the ocean, atmosphere and land (e.g. Flato 2011; Hasselmann 1976). Besides providing spatially complete data sets to approximate the observed state of the ocean or the atmosphere, dynamic ESMs are able to produce skilful predictions. Thereby, ESMs simulate the Earth's climate of the past, present and future. A great source of predictability in climate predictions stems from the inertia of the ocean, which allows predictions of the marine climate, e.g. temperature and salinity, to be skilful over longer time scales than atmospheric climate predictions (e.g. Merryfield et al. 2020). Thereby, today ESMs are able to skilfully predict the marine climate several years in advance, and in some regions like the North Atlantic, even a decade in advance (Shaffrey et al. 2017; Matei et al. 2012; Tommasi, Stock, Pegion, et al. 2017; Meehl et al. 2014).

Building on these advances of observing and forecasting the physical marine environment, together with the ever-increasing amount and quality of biological observations that enhance characterizing the species-environment relationship, marine biological forecast products have been developed (Payne et al. 2017; Tommasi, Stock, Pegion, et al. 2017; Jacox et al. 2020). The first operationalized marine biological forecast originated in Australia in 2006 for forecasting the suitable habitat of southern bluefin tuna in near-real-time (Hobday and Hartmann 2006). Since then, several operational forecasts of the marine biological environment have been created and are mainly delivered at near-real-time to seasonal scales (Figure 5; Payne et al. 2017; Tommasi, Stock, Pegion, et al. 2017). While the North Atlantic is one of the more predictable oceans of the world with skill on inter-annual to decadal timescales (Shaffrey et al. 2017; Matei et al. 2012; Tommasi, Stock, Pegion, et al. 2017), operational biological forecasts are virtually absent here (Figure 5). Moreover, biological forecast products do not yet exploit the long predictive horizon of the marine climate (Payne et al. 2017). Currently, all operational, distributional forecasts of marine organisms are provided at near-real-time to seasonal timescales (Figure 5). Examples include distributional forecasts of tuna in south Australian waters (Hobday et al. 2011; Eveson et al. 2015), as well as Pacific sardines (Kaplan et al. 2016; Siedlecki et al. 2016) and hake in Californian waters (Malick et al. 2020).

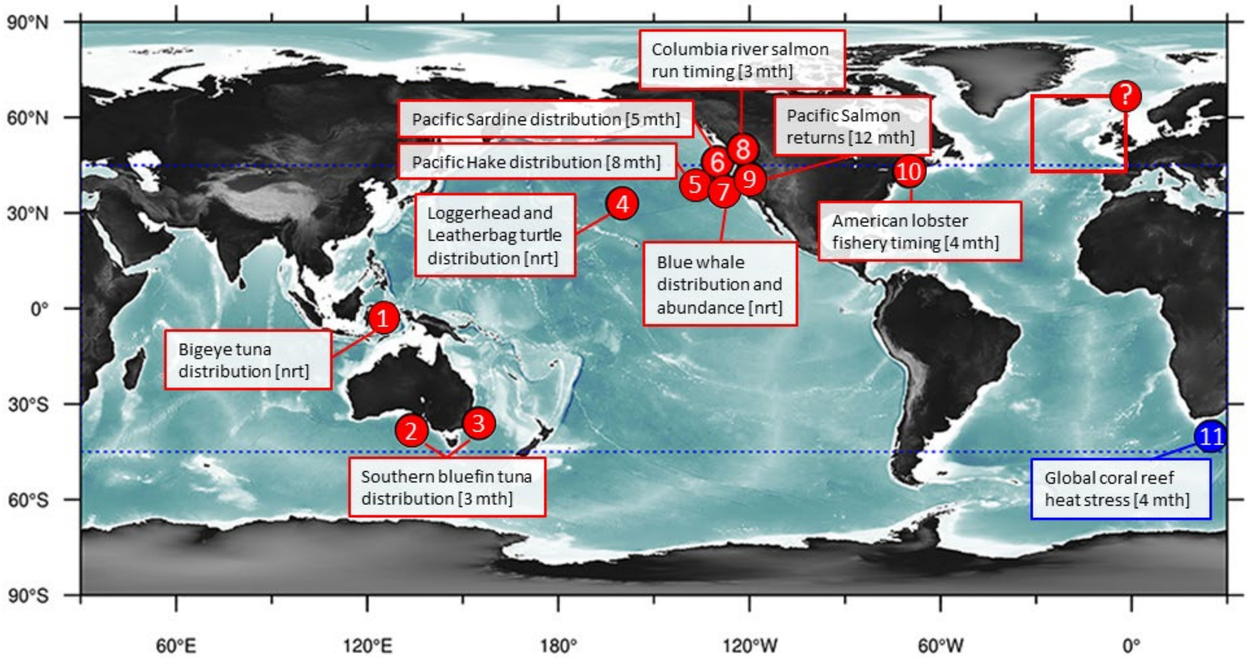

Figure 5. Operational marine ecological forecast products presented in Payne et al. (2017) and updated by the author. The lead time for which forecasts are provided is indicated in months [mth] or by near-real-time [nrt]. The operational forecasts (1-11) presented here include 1) *SEAPODYM*, Lehodey et al. (2018); 2) Eveson et al. (2015); 3) Hobday et al. (2011); 4) *TurtleWatch*, Howell et al. (2008, 2015); 5) Malick et al. (2020); 6) Kaplan et al. (2016), Siedlecki et al. (2016); 7) *WhaleWatch*, Hazen et al. (2016); 8) Anderson and Beer (2009); 9) Burke et al. (2013), Pacific Fishery Management Council (2020); 10) Mills et al. (2017); 11) *Coral Reef Watch*, Liu et al. (2018). Forecast product names, if applicable, are indicated in italics. Additionally, the approximate study region in this dissertation is indicated and attached with a question mark. Here, several operational forecasts are under development in collaboration with the ICES working group on seasonal-to-decadal prediction of marine ecosystem (ICES 2018). Figure adapted from Payne et al. (2017).

Distributional forecasts provided at seasonal timescales can be valuable to inform operational fisheries decisions (e.g. port and gear selection, labour allocation etc.) or for short-term adjustment of fishing area closures (Hobday et al. 2016a; Tommasi, Stock, Hobday, et al. 2017). Moreover, these distributional biological forecasts facilitate improving the sustainability and efficiency of the target species' fisheries by reducing non-target bycatch (Hobday et al. 2011; Hobday and Hartmann 2006) and enhance management and survey planning (Malick et al. 2020), e.g. by providing an early warning of climate-driven distributional shifts (Kaplan et al. 2016). Forecasts provided at longer inter- to multi-annual time scales, however, would provide a longer planning horizon and allow for longer-term climate-informed decision-making.

Forecasting the distribution of commercial fish species like blue whiting at inter-annual to multi-year time scales could be used to anticipate geographic shifts across political or management boundaries, which are already taking place in the North Atlantic (Peck and Pinnegar 2018) and might occur more frequently under climate change (Pinsky et al. 2018). Time is a crucial factor in international negotiations. Therefore, maximizing the forecast lead time can be beneficial for the fishing industry, resource managers and politicians alike to initiate discussions on quota allocations and long-term management strategies in response to climate variability (Tommasi, Stock, Hobday, et al. 2017). Additionally, long-term fishing industry decisions such as resource capitalization, i.e. whether or not to buy new fishing equipment, require biological forecasts provided at multi-year lead times (Tommasi, Stock, Hobday, et al. 2017).

The North Atlantic, with its highly predictable marine climate, is an ideal candidate region for exploring the potential of forecasting the spatial distribution of fish beyond seasonal timescales, and is at the core of this dissertation. In particular, this dissertation explores the potential of forecasting spatial variations in the spawning distribution of blue whiting. Distributional shifts in the spawning distribution of blue whiting were repeatedly associated with variations in the North Atlantic marine climate (Schmidt 1909; Bainbridge and Cooper 1973; Hátún et al. 2009; Hátún, Payne, and Jacobsen 2009). The long observational records of blue whiting larvae from the CPR that, contain half a century of spatially and temporally resolved information, are particularly valuable for analysing the species-environment relationship. For these reasons, blue whiting serves as an ideal species to explore the potential of modelling and forecasting changes of the species' suitable spawning habitat.

As mentioned earlier, there are two main ingredients to successfully creating a biological forecast. One is a sound understanding and quantification of the species-environment relationship. Secondly, the physical environment that shapes the suitable habitat of the species needs to be skilfully predictable. Therefore, in the following, I first assess which mechanisms control spatial variations in the spawning distribution of blue whiting and establish a quantifiable link between the marine climate and the potential spawning region based on species distribution modelling

(Chapter 2 & Appendix A). Subsequently, I analyse whether the marine climate is skilfully predictable within blue whiting's spawning region and spawning depth and during the main spawning period (Chapter 3.1 & Appendix B). Based on the quantified species-environment relationship and the proven skill of predicting the marine climate in the spawning region, I finally explore the potential of forecasting changes of the suitable spawning habitat of blue whiting at inter-annual to multi-annual lead times with a dynamic ESM (Chapter 3.2 & Appendix B). Thereby, this dissertation might serve as a general framework for future studies of coupled physical-biological forecasts.

2 OCEANOGRAPHIC VARIABILITY SHAPES THE SPAWNING DISTRIBUTION OF BLUE WHITING

> *“The key to prediction and understanding*
> *lies in the elucidation of mechanisms underlying observed patterns*”
> Simon A. Levin (1992)

Every year, adult blue whiting undertake long migrations between their feeding areas in the Norwegian Sea and the Bay of Biscay to their main spawning grounds west of the British Isles and Ireland (Bailey 1982). Scientists, aiming at monitoring the stock, and fisheries alike, target these dense spawning aggregations. However, while most spawning occurs from March to April at depths between 250 and 600 m along the edges of the European Continental Shelf, in some years, the spawning region expands further westwards over Rockall-Hatton Plateau (Bailey 1982; ICES 2019; Bainbridge and Cooper 1973).

In the past century, repeated suggestions point towards a connection between spatial variations in the spawning distribution of blue whiting and oceanographic variability (Bainbridge and Cooper 1973; Hátún, Payne, and Jacobsen 2009; Schmidt 1909). Most notably, Hátún, Payne, and Jacobsen (2009) connected changes in the spawning distribution of blue whiting to the basin-scale dynamics of the North Atlantic Subpolar Gyre. The gyre influences the flow trajectory of the North Atlantic Current and thereby affects the marine climate in the spawning region of blue whiting in terms of temperature and salinity (Figure 6). A qualitative assessment highlighted that when the gyre was strong and conditions mainly fresh and cold within the spawning region, most spawning blue whiting were observed along the European Continental Shelf edge west of Ireland, in particular on Porcupine Bank (Figure 6a). In contrast, a weak gyre promoted an expansion of the spawning distribution further westward onto Rockall Plateau and further northward along the European Continental Shelf (Figure 6b).

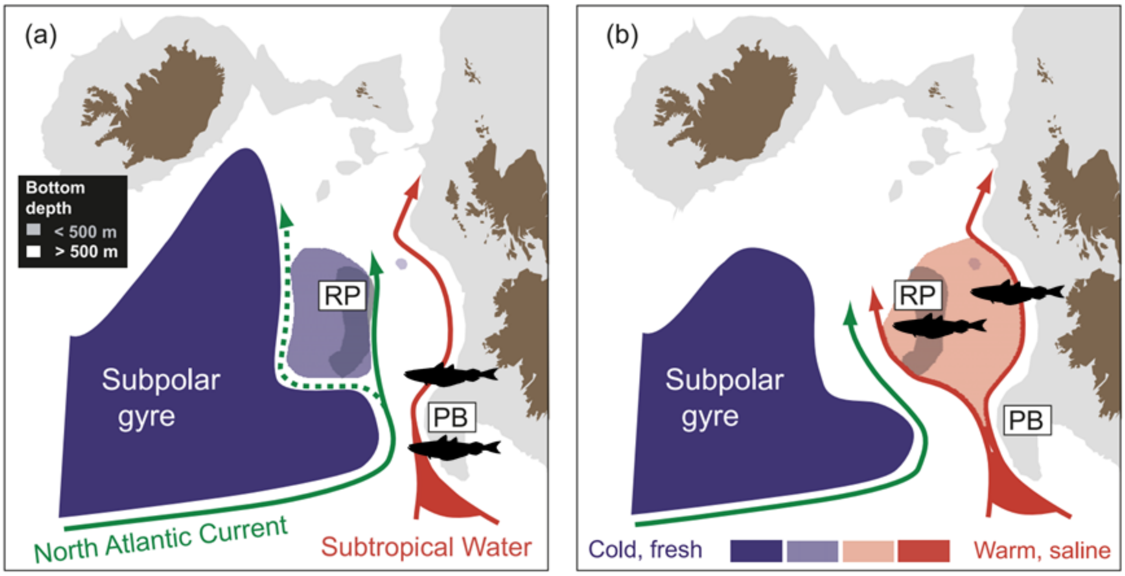

Figure 6. Schematic of the different water masses that influence the spawning region of blue whiting under a strong North Atlantic Subpolar Gyre (SPG; a) and under a weak SPG (b). The bathymetric features Rockall Plateau (RP) and Porcupine Bank (PB) as well as the main spawning locations of blue whiting (fish) are indicated. The marine climate in the spawning region of blue whiting is characterized by a combination of subpolar (fresh, blue) Western North Atlantic Waters residing within SPG and subtropical (saline, red) Eastern North Atlantic Waters from the Subtropical Gyre that enters the spawning region via the northward-flowing shelf-edge current (Holliday et al. 2000; Hátún et al. 2009). Through changes in the flow trajectory of the North Atlantic Current, the SPG affects the relative combinations of these water masses (Hátún et al. 2009; Hátún et al. 2005).
a) During a strong SPG, cold and fresh water masses dominate in the spawning region and most blue whiting spawn along the European Continental Shelf and on Porcupine Bank. **b)** During a weak SPG, conditions become more warm and saline and spawning extends westwards onto Rockall Plateau and takes place further north along the Continental Shelf. Figure adapted from Hátún, Payne, and Jacobsen (2009).

Thereby, Hátún, Payne, and Jacobsen (2009) provided a qualitative description of the connection between basin-scale physical processes driven by the SPG and the spatial distribution of spawning blue whiting. While this knowledge is beneficial for understanding past changes in the spawning distribution, its qualitative nature precludes quantitative predictions of the spawning distribution. Skilfully forecasting climate-driven distributional shifts of blue whiting could, however, be of great value for the scientific monitoring, assessment and management of the species' and motivated this dissertation. A first precondition towards creating distributional forecasts lies in the development of a quantitative understanding of the species-environment relationship and therefore raises the following questions:

I.I **What is the role of the marine climate in determining the spawning distribution of blue whiting relative to other processes, such as migration dynamics or bathymetric features?**

I.II **Can we develop a quantitative understanding of these processes?**

I answer[5] the questions outlined above, by combining blue whiting larval observations from the CPR survey (Reid et al. 2003) with geographic and oceanographic information using statistical modelling techniques. Here, the likelihood of observing larvae is a proxy for the spawning distribution of blue whiting. Elaborating on previous work (e.g. Hátún, Payne, and Jacobsen 2009), I employ an extended CPR data set comprising of 55 years of blue whiting larval observations, which provides a unique opportunity to understand and model spatial variations in the spawning distribution of blue whiting. However, due to the opportunistic sampling design of the CPR, CPR observations are distributed highly unevenly in time and space (Batten et al. 2003). Additionally, the narrow device opening of the CPR (Batten et al. 2003) and the uneven and temporally varying distribution of blue whiting larvae in the water column (Ådlandsvik et al. 2001; Hillgruber and Kloppmann 1999) pose further challenges to the analysis. Focussing on the presence-absence aspect of the CPR data and applying statistical models enables me to circumvent many of the above-mentioned caveats while retaining the valuable spatio-temporal information of the data set.

Individual fish are affected by the local marine climate and respond to changes in their ambient oceanographic environment. Therefore, correlating co-located CPR larval observations to oceanographic variables through SDMs enables analysing and quantifying the species-environment relationship. When SDMs employ the species-environment relationship to map the suitable (spawning) habitat of a species in geographic space, the resulting distribution is commonly referred to as potential (spawning) distribution (e.g. Guisan and Zimmermann 2000). Thereby, SDMs estimate suitable habitats and spatial distributions from unevenly distributed pointwise observations, such as the CPR data set. These remarkable strengths of SDMs make them ideally suited to investigate processes that shape the spawning distribution of blue whiting.

I create correlative SDMs in two consecutive steps. First, I connect observations of blue whiting larvae to inter-annually constant "geographic" features. Subsequently, larval observations are linked to the inter-annually varying marine climate (i.e. temperature and salinity) to develop the full SDM. The results from this analysis reveal that geographic variables, specifically the temporal aspect of migration and bathymetry are essential features for constraining the SDMs. Moreover, these variables show biologically meaningful results that confirm previous findings. For example, that spawning commences in the south in early spring and progresses northward (e.g. Bailey 1982), and that spawning unlikely occurs in waters shallower than 300 m depth (ICES 2020; Coombs, Pipe, and Mitchell 1981; Hillgruber and Kloppmann 1999; Ådlandsvik et al. 2001).

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[5] See Appendix A: Miesner, A.K., and Payne, M.R. 2018. Oceanographic variability shapes the spawning distribution of blue whiting (*Micromesistius poutassou*). Fisheries Oceanography 27(6): 1–16.

Most striking is, however, the substantial improvement in model parsimony (i.e. model skill) when adding information on the marine climate. Accordingly, oceanographic variability predominantly shapes the spawning distribution of blue whiting. The SDM with the highest overall predictive performance includes the salinity encountered by the spawning fish, i.e. the salinity at the spawning depth of 250-600 m during the time of spawning. This result provides an answer to the first question posed (I.I): **Inter-annual variations in the spawning distribution of blue whiting are driven by variations in the marine climate the fish experience upon spawning, in particular salinity.** The importance of salinity in defining the suitable spawning habitat and explaining distributional variations is a unique feature of this work since distributional studies of marine organisms generally focus on temperature as the prime oceanographic variable to explore current and future species distributional patterns (e.g. Pinsky et al. 2013; Poloczanska et al. 2016; Melo-Merino, Reyes-Bonilla, and Lira-Noriega 2020).

The SDM captures previously reported shifts in the spatial distribution of spawning blue whiting in response to the dominant marine climatic regime. In agreement with earlier work (Bailey 1970; Bainbridge and Cooper 1973; Hátún, Payne, and Jacobsen 2009; Hátún et al. 2009), blue whiting show an expanded north- and westward potential spawning distribution covering Rockall Plateau under warm and saline conditions and a more contracted potential distribution along the European Continental Shelf edge under cold and fresh conditions. Moreover, there is a good spatial agreement between the potential spawning distribution of blue whiting estimated from the SDM and independent observations from fisheries and scientific surveys targeting spawning adults.

Besides confirming that the marine climate influences the spawning distribution of blue whiting, my study permits *for the first time* to quantify this species-environment relationship. The SDM with the highest overall predictive performance shows that blue whiting larvae are typically encountered at a salinity between 35.3 and 35.5, which can be understood as the suitable salinity for spawning. The suitable salinity for spawning agrees well with independent observations of adult blue whiting from fishery and scientific surveys. Moreover, it is in rough agreement with observations of blue whiting larvae from two individual surveys. Johannes Schmidt (1909) already noted that spawning is unlikely to occur in waters with salinity less than 35.25 - 35.3. Moreover, during a survey in 1994, Bailey and Heath (1996) found most larvae in warm water with salinities of 35.25 to 35.4. Thereby, this analysis provides an answer to the second question posed (I.II): Variations in the spawning distribution of blue whiting are driven by variations in the marine climate the fish experience upon spawning, in particular salinity, where **spawning is limited to salinities in the range of 35.3 and 35.5.** In the following, I will refer to this salinity range as suitable salinity for spawning.

Admittedly, salinity might be a proxy for other processes that might affect where the fish deliver their eggs, such as suitable feeding conditions (Hátún et al. 2009). However, the strong connection between the potential spawning region and the local salinity marks a substantial and novel contribution towards understanding and quantifying the processes that shape the spawning distribution of blue whiting. Moreover, based on this quantification of the species-environment relationship, it is now possible to explore the potential of forecasting climate-driven changes in the potential spawning distribution of blue whiting.

3 EXPLORING THE POTENTIAL OF FORECASTING FISH DISTRIBUTIONS IN THE NORTH EAST ATLANTIC WITH A DYNAMIC EARTH SYSTEM MODEL: THE CASE OF BLUE WHITING

> *"These varying movements of fish must have a definite ascertainable cause, and once ascertained, forecasting cannot be difficult "*
>
> Sir Alister C. Hardy (1930)

Based on the species-environment relationship developed in the previous chapter, this chapter explores the potential for forecasting the suitable spawning habitat of blue whiting at inter-annual to multi-annual timescales. In collaboration with the ICES Working Group on Seasonal to Decadal Prediction of Marine Ecosystems, first endeavours have been undertaken to create an operational forecast product of blue whiting's suitable spawning habitat (Payne and Lehodey 2019; ICES 2018) based on the SDM developed in the previous chapter (Chapter 2; Miesner and Payne (2018)). However, until now the forecast was provided only two months before the IBWSS survey and was solely based on the persistence of the marine environment (Payne 2021). Persistence forecasts are the simplest form of generating a forecast. They are based on the assumption of stationarity, meaning that future conditions are assumed the same as past conditions. Therefore, persistence forecasts might function well in regions of low variability and for forecasts with short lead times of a few months (e.g. Hobday et al. 2018). In contrast, forecasts with longer lead times, beyond seasonal timescales, that can anticipate changes from one climatic regime to the next would be more appropriate to support climate-informed decision-making and environmental risk management. Such dynamic forecasts require dynamical predictions based on ESMs (Tommasi, Stock, Hobday, et al. 2017). For that reason, the following chapter will explore the potential of forecasting the suitable spawning habitat of blue whiting on inter-annual to multi-annual timescales with a dynamic ESM, namely the Max Planck Institute Earth System Model at low resolution (MPI-ESM; Giorgetta et al. 2013; Brune and Baehr 2020).

3.1 FORECASTING THE PHYSICAL MARINE ENVIRONMENT

Decadal predictions with MPI-ESM perform particularly well at capturing the warming and cooling periods within the SPG region (Polkova et al. 2019) and show good predictive skill of North Atlantic sea surface temperature and upper ocean heat content (0-700 m) on multi-annual to decadal times scales (Brune and Baehr 2020). These studies analysed predictive skill averaged over large-scale oceanic regions and several lead years. However, these broad averages do not allow analysing the predictive potential for biological applications that often act on finer spatio-temporal scales.

Since distributional forecasts of fish are commonly based on forecasting the species suitable (environmental) habitat locally, i.e. the niche, they require skilful predictions of environmental variables that characterize the species' niche at relevant spatial and temporal scales. Assessing the predictability of the marine climate within the particular part of the water column that blue whiting inhabits upon spawning, namely 250 to 600 m, is therefore pivotal to the creation of forecasts of the suitable spawning habitat of this species. Since predictability analyses are non-existent for this particular depth range, I first set out to evaluate whether the marine climate is skilfully predictable with MPI-ESM at spatial and temporal scales relevant for spawning blue whiting. Thus, I ask:

II.I Is the marine climate, i.e. temperature and salinity, skilfully predictable at inter-annual or multi-annual lead times with MPI-ESM within the region and depth at which blue whiting spawn and during the main spawning period?

I answer[6] this question by employing MPI-ESM to generate retrospective forecasts (i.e. hindcasts) of the marine climate and subsequently of the suitable spawning habitat of blue whiting for lead times of up to five years. In terms of the marine climate, I consider the average temperature and salinity over the species' spawning depth and over the peak months of spawning (February to April) within the core spawning region of blue whiting west of the British Isles. The quality of the hindcast is judged by comparing it to two observational reference products, which differ by their spatio-temporal distribution of observed temperature and salinity profiles: the EN4 objective analysis (Good, Martin, and Rayner 2013) and the MPI-ESM ensemble Kalman filter assimilation (Brune and Baehr 2020; Polkova et al. 2019). This comparison of two oceanographic reference products enables me to account for their uncertainty.

I find that both observational reference products resolve the major oceanographic features in the North Atlantic, such as the SPG carrying cold and fresh water masses and the subtropical gyre with its warmer and more saline waters. In the vicinity of bathymetric features, like seamounts or ridges, however, the observational data sets behave differently. EN4 statistically interpolates between observed profiles resulting in relatively smooth contours of temperature and salinity that appear disconnected from bathymetric features. This behaviour of EN4 is in stark contrast to MPI-

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[6] See Appendix B: Miesner, A.K., Brune, S., Pieper, P., Koul, V., Baehr, J., and Schrum, C. (*under review*) Exploring the potential of forecasting fish distributions in the North East Atlantic with a dynamic Earth System Model, exemplified by the suitable spawning habitat of blue whiting. Frontiers in Marine Science.

ESM. MPI-ESM assimilates observational profiles into a dynamic ESM that inherently accounts for hydrodynamic processes. Thereby, MPI-ESM competently considers bathymetric features by distributing oceanic properties such as temperature and salinity dynamically consistent around seamounts like Rockall Plateau or along the European Continental Shelf. Accordingly, MPI-ESM provides a more realistic hydrodynamic representation than EN4 in the bathymetrically diverse spawning region of blue whiting.

When comparing the predictive quality and forecast horizon of the MPI-ESM hindcast to the two observational reference products, I find substantially larger differences for salinity compared to temperature. Due to these higher salinity uncertainties between both observational reference products, the prediction skill of salinity also exhibits higher uncertainties than the skill of temperature. These differences between the MPI-ESM assimilation and EN4 might be attributed to the principally higher observational uncertainty of salinity. In general, observations of salinity are sparser compared to temperature (MacIntosh, Merchant, and von Schuckmann 2017) especially at depth and before the onset of Argo sampling (Tesdal et al. 2018). Therefore, the large range of predictive skill of salinity can in part be attributed to the sparsity of salinity observations and the different methods that are used in MPI-ESM and EN4 to close observational gaps further amplify the differences.

Evaluating against both observational reference products, I find that the MPI-ESM hindcast is significantly more skilful than persistence-based forecasts after lead year three for salinity. For temperature, the hindcast is only more skilful than persistence in predicting the amplitude, but not the phase of observed variations. Specifically, I find that hindcasts of salinity have a higher predictive skill than temperature in particular at longer lead times (>2 years). The higher predictive skill of salinity, especially over longer lead times, might be ascribed to the property of salinity to act as a passive tracer and thereby as an indicator for circulation changes in the subpolar North Atlantic (Mauritzen, Hjøllo, and Sandø 2006). Few studies directly compare the predictability of salinity and temperature (e.g. perfect model studies of Mignot et al. 2016; Koenigk and Mikolajewicz 2009). Therefore, the higher predictability of salinity compared to temperature provides a novel facet to the predictability of the North Atlantic marine climate.

The MPI-ESM hindcast performs best at forecasting the marine climate in the area around Rockall Plateau. This region is considered to have a rather low oceanographic variability (Holliday et al. 2015) and frequently shows extended periods of anomalously high or low salinity (Holliday et al. 2000; Koul et al. 2019). This low oceanographic variability is likely contributing to the higher predictability of the marine climate encountered here. These findings present the first detailed account for the predictability of the mesopelagic marine climate in the spawning region of blue whiting.

In summary, I find that **temperature and especially salinity is skilfully predictable by MPI-ESM with significant skill within the spatial and temporal scales relevant for spawning blue whiting. While persistence forecasts perform well at shorter lead times of less than two years, the MPI-ESM hindcast clearly shows more skill than persistence in forecasting salinity at longer multi-annual lead times.** Accordingly, these results provide an answer to question II.I and indicate that MPI-ESM bears promising potentials for developing a coupled physical-biological forecast in this region.

3.2 FORECASTING THE MARINE BIOLOGICAL ENVIRONMENT

Now the stage is set for the final endeavour of this dissertation: Building on the previously established species-environment relationship of blue whiting and the ability of MPI-ESM to skilfully predict the marine climate, specifically salinity, I now combine this knowledge to translate forecasts of the marine climate into forecasts of the marine biological environment, and ask:

II.II Is the suitable spawning habitat of blue whiting skilfully predictable at inter-annual or multi-annual time scales with MPI-ESM?

First, I compare two alternative approaches to define the suitable spawning habitat of blue whiting. I find that the suitable salinity for spawning shows better agreement with independent observations of spawning adults than applying full SDMs calibrated with temperature and salinity from either MPI-ESM or EN4 and fixed geographic information. Moreover, in terms of suitable salinity for spawning, MPI-ESM shows better observational agreement than EN4. Therefore, in the following, forecasts of the suitable habitat of blue whiting are based on forecasting the suitable salinity for spawning. Here, the suitable spawning habitat of blue whiting serves as a proxy for the species' spawning distribution and can be understood as the geographic space where the environment is suitable for spawning. Due to non-resolved processes such as competition or predation, the actual distribution of the species (where we observe fish) might be smaller than the suitable habitat. Accordingly, the presence of suitable habitat is no guarantee for the presence of fish, however the absence of suitable habitat guarantees the absence of fish (Payne et al. 2021). Thereby, distributional forecasts based on forecasting the suitable habitat of fish generally have a higher predictive skill for predicting absences than presences (Payne et al. 2021). This is also the case for predictions of the suitable spawning habitat of blue whiting with MPI-ESM.

Predictions of the suitable spawning habitat based on the MPI-ESM hindcast yield good skill at inter-annual time scales, particularly over Rockall-Hatton Plateau. A clear benefit of predicting the suitable spawning habitat of blue whiting with MPI-ESM is its ability to differentiate between the presence and absence of suitable spawning habitat over Rockall Plateau. In contrast, predictions based on EN4 persistence constantly show suitable spawning habitat on Rockall

Plateau, which renders them unsuitable for distributional forecasts here. As a result, during years where most spawning takes place along the Continental Shelf and less on Rockall-Hatton Plateau, such as in the rather cold and fresh 1990s, predictions based on MPI-ESM hindcast perform considerably better than predictions based on EN4 persistence. This better ability of MPI-ESM to show both presence and absence of suitable habitat on Rockall Plateau is at least in part attributed to the ESMs better ability to represent hydrodynamic processes. Accordingly, the more differentiated representation of the marine climate around bathymetric features in MPI-ESM leads to more reliable results in the area of Rockall-Hatton Plateau in predictions based on MPI-ESM (in particular MPI-ESM hindcast) than in predictions based on EN4 persistence. Notably, the **MPI-ESM hindcast skilfully predicts distributional changes over Rockall-Hatton Plateau around a year in advance. For longer, multi-annual lead times forecast skill drops, and there is no clear advantage of the MPI-ESM hindcast.** These results provide an answer to question II.II.

In summary, a unique feature of this work is the thorough analysis of both physical and biological forecast skill, which revealed *for the first time:*

i. A higher predictive skill of mesopelagic (250-600 m) salinity compared to temperature in the North East Atlantic.
ii. A more realistic representation of the marine climate and more skilful predictions of the suitable spawning habitat of blue whiting based on MPI-ESM compared to EN4, in particular over Rockall-Hatton Plateau.
iii. A high predictive skill of both the marine climate and the suitable spawning habitat of blue whiting on Rockall-Hatton Plateau around a year in advance, indicating that this region is particularly promising for creating of coupled physical-biological forecast.

The multi-annual forecast skill of the marine climate in the spawning region did not translate into a multi-annual predictive skill of the suitable habitat of blue whiting. The shorter biological forecast horizon might be related to limitations in defining and verifying the suitable spawning habitat. A major obstacle in spatially verifying distributional biological forecasts of fish, or any other mobile marine organism, are uncertainties in observing the species of interest. Because observations of freely moving animals only provide a snapshot of their distribution.

However, the high predictive skill of both the marine climate and the suitable spawning habitat around Rockall-Hatton Plateau at inter-annual lead times with MPI-ESM marks a success. Skilful inter-annual forecasts in the area of Rockall-Hatton Plateau are of particular value since distributional changes are most pronounced here (Hátún, Payne, and Jacobsen 2009; Miesner and Payne 2018) and insufficient sampling coverage can lead to an underestimation of the stock's biomass and thereby to misleading fisheries management advice (ICES 2010b; 2011). Since distributional forecasts are currently only provided at *seasonal* timescales (Figure 5; Payne et al.

2017), turning the research of this dissertation into an operational forecast to anticipate distributional changes of the spawning distribution at *inter-annual* timescales would present a new frontier in the field of marine biological forecasts.

4 CONCLUSIONS

I opened this dissertation with a quote from a pioneer in marine biology and the inventor of the Continuous Plankton Recorder (CPR), Sir Alister Clavering Hardy, who envisioned that one day we might provide forecasts of fish in a similar fashion as weather forecasts (Hardy 1939). The serendipitous sampling of blue whiting larvae by the CPR enabled analysing and quantifying the species-environment relationship. In particular, the strong connection between blue whiting larval observations and salinity formed the basis for forecasting climate-induced changes of the species suitable spawning habitat. Thereby, Hardy's vision of forecasting the distribution of fish based on the CPR survey became at least in part true through this dissertation. Consequently, this dissertation is a continuation and modest contribution to this *"pioneer attempt"* of forecasting the distribution of fish, at the example of blue whiting.

In this dissertation, I demonstrate the viability of forecasting climate-driven habitat shifts of blue whiting using a dynamic ESM at inter-annual timescales. Skilful biological forecasts at inter-annual time scales, as presented in this dissertation, are beyond the prediction horizon of the first generation of biological forecast products (Payne et al. 2017) and thereby present a new frontier in marine biological forecasting. In contrast to the common practice of using temperature to delineate the species' suitable habitat and to anticipate climate-driven habitat shifts of fish (Siedlecki et al. 2016; Kaplan et al. 2016; Malick et al. 2020; Eveson et al. 2015; Hobday and Hartmann 2006), I illustrate that for blue whiting, salinity is better suited to model and forecast the species' suitable spawning habitat. Another unique feature of this dissertation is the thorough analysis of both physical and biological forecast skill. The predictability analysis reveals a higher predictive skill of mesopelagic salinity compared to temperature in the North East Atlantic for the first time. Accordingly, the skill of MPI-ESM in predicting salinity bears the promising potential to anticipate distributional shifts of further marine organisms in the North East Atlantic.

Many economically important fish species inhabit the North East Atlantic and environmental effects on their spatial distribution and phenology of spawning are in many cases well documented (Trenkel et al. 2014; and references therein). Though blue whiting is as a case study in this dissertation, the approach employed here is readily transferable to other species. Creating forecasts for a range of different fish species with overlapping distributions will mark an important contribution towards ecosystem-based fisheries management (Schmidt et al. 2019). Moreover, the North Atlantic climate variability affects not only the distribution of blue whiting but also affects the distribution, production, abundance and species composition of various trophic levels of the marine ecosystem, ranging from phyto- and zooplankton, to fish, whales and seabirds (Hátún et al. 2009; Drinkwater et al. 2003). Therefore, the creation of marine biological forecasts in the North Atlantic could also be extended to other groups of organisms, for example with the aim of enhancing the management and conservation of large marine mammals and other endangered species, as currently employed in the North Pacific (Hazen et al. 2017; Howell et al. 2008; Hazen et al. 2018).

Predictions of the marine climate with MPI-ESM show significant skill in the SPG region and thereby introduce predictability in the North East Atlantic (Brune et al. 2018). SPG-driven changes of temperature and salinity travel downstream into the North and Barents Sea and thereby affect the abundance and productivity of some fish species there, while introducing predictability via adjective delays (Akimova et al. 2016; Koul et al. 2021). In a novel approach, Koul et al. (2021) created skilful decadal predictions of the Barents Sea cod stock based on MPI-ESM by integrating lagged correlations of SPG temperature and stock biomass. Moreover, Post et al. (2020) found a lagged response between the marine climate southwest of Iceland and the abundance of blue whiting and other boreal fish species in Greenlandic waters. Accordingly, there is a high potential for developing further biological forecasts of fish abundance and distribution based on dynamical ESMs such as MPI-ESM in the North Atlantic and its adjacent seas. Additionally, considering multiple species within the same forecasting framework could enable biological forecasts to enhance ecosystem-based and dynamic ocean management.

Distinct habitat requirements for spawning, as seen for blue whiting, represent bottlenecks in the life cycles of the affected fish species (Petitgas et al. 2013). As such, adverse habitat conditions for spawning, and thus for eggs and larvae, can negatively affect the entire population (with a lag). Recruitment[7] dynamics of blue whiting are not yet fully understood (Payne et al. 2012). Still, various mechanisms have been proposed on how variability of the spawning distribution in the area of Rockall-Hatton Plateau could be related to recruitment variability (Hátún, Payne, and Jacobsen 2009). For instance, spawning on Rockall-Hatton Plateau might lead to improved feeding and growth conditions of the larvae and decreased predation pressure from mackerel resulting in better larval survival (Hátún, Payne, and Jacobsen 2009; Payne et al. 2012). Assuming that the occurrence of spawning on Rockall-Hatton Plateau, indeed, indicates higher recruitment of blue whiting (Hátún, Payne, and Jacobsen 2009), skilful inter-annual forecasts of the suitable spawning habitat on Rockall-Hatton Plateau, as those presented in this dissertation, might pave the way for forecasting trends in recruitment variability of blue whiting.

In even broader terms, this dissertation highlights that ESMs are essential for anticipating climate-driven habitat shifts in the North East Atlantic. ESMs are particularly well suited to forecast unprecedented conditions and therefore can potentially provide early warnings on sudden climate-

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[7] Definition of recruitment according to Cochrane and Garcia (2009): *"The number of fish added to the exploitable stock, in the fishing area, each year, through a process of growth (i.e. the fish grows to a size where it becomes catchable) or migration (i.e. the fish moves into the fishing area)"*.

driven habitat shifts of marine organisms (Tommasi et al. 2016). A central point that emerged from this research is the superior ability of MPI-ESM to both represent and forecast the marine climate in the bathymetrically diverse spawning region of blue whiting, relative to the statistical observational product EN4. On the one hand, this highlights the need to evaluate the observational products used for defining and forecasting the suitable habitat of a species carefully. On the other hand, it indicates that the creation of coupled physical-biological forecasts based on ESMs have a great potential in bathymetrically diverse regions and for species whose distribution is linked to bathymetric features, as observed for blue whiting. These findings present a novel insight in the context of marine biological forecasts. Accordingly, it is important to examine differences in the way oceanographic reference products represent the observed marine climate spatially. However, this aspect is often neglected in biological, distributional forecast studies. One way to account for this source of uncertainty is to employ a suite of observational products and possibly ensemble of different ESMs.

Since the North Atlantic marine climate is skilfully predictable at multiyear to decadal timescales (Shaffrey et al. 2017; Matei et al. 2012; Tommasi, Stock, Pegion, et al. 2017; Yeager and Robson 2017), there is a high and undisclosed potential for further extending the forecast horizon of biological forecasts in this region. In this context, the employment of multi-ESM-ensembles bears promising potentials (Jacox et al. 2020; Payne et al. 2021). The predictability of the marine climate is generally higher in averaged multi-ESM-ensembles than in individual ESMs (Jolliffe and Stephenson 2012; Weigel, Liniger, and Appenzeller 2008), as exemplified for the North American Multimodel Ensemble by Kirtman et al. (2014). And indeed, Payne et al. (2021) show that biological forecast based on multi-ESM-ensembles perform better than biological forecasts based on individual ESMs in forecasting the area of suitable habitat for blue whiting, bluefin tuna and mackerel (Payne et al. 2021). Moreover, their study revealed that the size of the suitable habitat for these species is skilfully predictable on multi-annual to decadal time scales (Payne et al. 2021). Accordingly, there appears to be a great potential for improving the predictive horizon of biological forecasts by combining multiple ESMs into a multi-ESM-ensemble.

Besides examining different ensembles of physical models to drive the biological forecast, various options exist to create multi-model-ensembles for forecasting species distributions (Araújo and New 2007). In particular, creating an ensemble of SDMs based on different SDM algorithms could minimise structural uncertainty from different model formulations (Jones et al. 2012) and enhance SDM-based reconstructions into the past (Svenning et al. 2011) and projections into the future (Araújo and New 2007; Brun et al. 2020). Akin to multi-ESM ensembles, which improve physical forecasts (Jolliffe and Stephenson 2012; Weigel, Liniger, and Appenzeller 2008), there is the hope that combining multiple SDMs into one multi-SDM ensemble could improve biological forecasts. However, this has not been demonstrated as thoroughly for biological forecasts as for physical forecasts. Yet, in some cases multi-SDM ensembles showed better performance than individual SDMs (e.g. Abrahms et al. 2019; Malick et al. 2020). Therefore, the next frontier in biological forecasting is the exploration of different biological and physical forecast ensembles, thus, entering the realm of probabilistic predictions.

The added value of using ensembles, such as the potential increase in skill or possibility to use probabilistic forecast metrics (Jolliffe and Stephenson 2012; Murphy 1973; Wilks 2011), needs to be carefully gauged against additional computational cost and the challenges of appropriately communicating forecast output and uncertainty to the end-users (Taylor, Dessai, and de Bruin 2015). Therefore, a close collaboration between potential users and the developers of the biological forecasts is essential (Tommasi, Stock, Hobday, et al. 2017; Payne et al. 2017; Hobday et al. 2011). Ultimately, the development of successful marine biological forecasts will require "*Striking the balance between what is feasible and what is useful*" (Payne et al. 2017).

In summary, this dissertation provides a framework for the creation of biological forecasts of marine organisms. Analysing the species-environment relationship is the first prerequisite for developing quantitative predictions. Secondly, we need to ensure that the marine climate is skilfully predictable at spatial and temporal scales relevant to the species of interest. Finally, we can use the species-environment relationship to translate physical forecasts of the marine climate into biological forecasts for our species of interest and analyse their predictive skill. This translational step is not trivial and requires careful consideration and thorough analysis. Moreover, all steps require observations of the physical and the biological marine environment at relevant spatio-temporal scales and over a range of environmental gradients. While this dissertation has shown that ESMs are very well suited for representing the observed marine climate and creating dynamical forecasts, further efforts are needed to improve biological data availability and the willingness of institutions to share survey data (Maureaud et al. 2021). Thereby, this dissertation highlights the value of employing an ESM for developing distributional forecasts of marine organisms in the North East Atlantic. In this manner, the framework presented in this dissertation contributes towards advancing biological forecasts to facilitate dynamic ocean management and enhance the sustainable management of our common marine living resources.

Appendix A

OCEANOGRAPHIC VARIABILITY SHAPES THE SPAWNING DISTRIBUTION OF BLUE WHITING (*MICROMESISTIUS POUTASSOU*)

This appendix contains the following article:

Miesner, A.K., and Payne, M.R. 2018. Oceanographic variability shapes the spawning distribution of blue whiting (*Micromesistius poutassou*). Fisheries Oceanography. 27(6): 1–16. doi:10.1111/fog.12382.

The contribution of Anna Miesner (A.M.) and Mark Payne (M.P.) to this paper is as follows: A.M. performed the analysis and wrote the paper. A.M., and M.P. conceived the work, discussed the results and reviewed the manuscript. M.P. provided guidance on the overall direction of the work.

Oceanographic variability shapes the spawning distribution of blue whiting (*Micromesistius poutassou*)

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ABSTRACT

The spawning distribution of blue whiting (*Micromesistius poutassou*) has varied considerably between years, but quantitative understanding of the processes driving this change is lacking. Using 55 years of larval-observations from the wide-ranging Continuous Plankton Recorder (CPR) survey, we show that changes in the spawning distribution of blue whiting are associated with variations in the marine environment and particularly salinity. We first corroborated previously reported associations between variations in the spawning distribution and environmental regimes in the spawning region based on space-time interpolation models. We then applied species distribution models to quantify the linkage between the environment and the distribution of blue whiting larvae and verified these model results against independent fisheries and scientific survey data. Models incorporating salinity in the spawning region gave the best agreement with data, with observations of larvae in the CPR being limited to a window of salinities between 35.3 and 35.5. Changes in the area of suitable spawning habitat (estimated here to be up to 2.5 times) can therefore be understood as arising from the spread of saline subtropical water masses throughout the spawning region due to a weak North Atlantic subpolar gyre. We postulate that blue whiting actively select optimum oceanographic conditions to deliver their eggs to enhance their offsprings likelihood of survival and thereby their fitness. The knowledge derived here, together with the high predictability of salinity at depth in the North-East Atlantic, can potentially form the basis for forecasting the spawning distribution of this species.

A1 INTRODUCTION

Blue whiting *Micromesistius poutassou* (Risso, 1827) is a commercially important gadoid found throughout the North-East Atlantic. This species migrates annually between its feeding grounds in the Norwegian Sea to its spawning region west of Great Britain and (Figure A 1; Bailey, 1982; ICES, 2016a; ICES, 2016b). While there are indications of limited spawning activity outside of the main spawning area (Bainbridge and Cooper 1973; Bailey 1982), most spawning takes place from March to April along the European Continental Shelf edge and over banks to the west of Great Britain and Ireland (Pointin and Payne 2014; Bailey 1982).

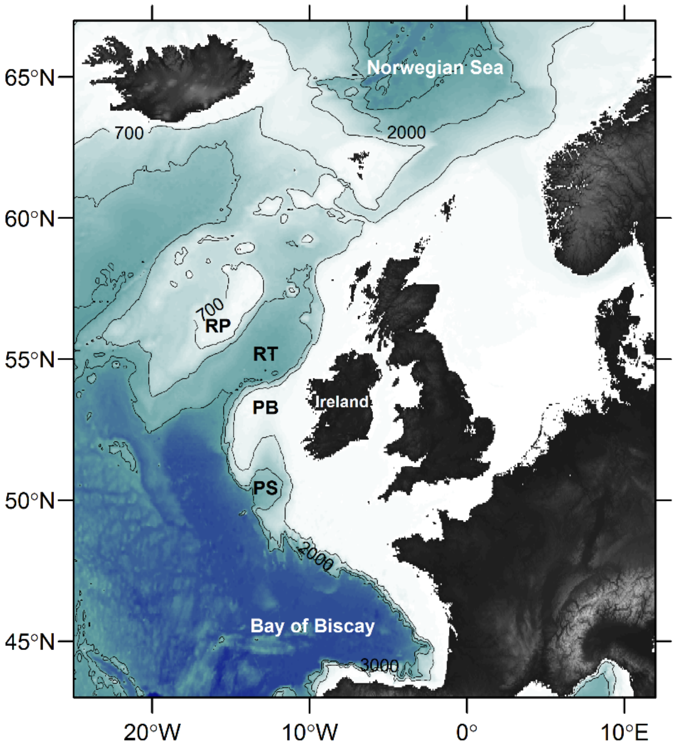

Figure A 1. Bathymetric relief map of the study region. Contour lines indicate the water depth in meters (showing the isobaths of 700, 2000 and 3000 m). Geographic features mentioned in the text are labelled Rockall Plateau (RP), Rockall Trough (RT) Porcupine Bank (PB) and Porcupine Seabight (PS).

However, the spatial distribution of blue whiting spawning has been shown to vary substantially between years. Scientific surveys have shown that in some years the distribution extends all the way from Rockall Trough to Rockall Plateau and Hatton Bank (ICES 2007), while in other years it is compacted close to the Continental Shelf edge (ICES 2015b). These shifts in distribution are typically attributed to the variability of the marine environment: already in 1909, Schmidt noted that blue whiting were sensitive to temperatures and salinities during spawning (Schmidt 1909). A century later, Hátún, Payne, and Jacobsen (2009) suggested that under fresher and colder conditions in the spawning region, blue whiting mainly spawn along the European Continental Shelf edge west of Ireland, in particular on Porcupine Bank, while during more saline and warmer conditions, spawning expands further westward across Rockall Trough onto Rockall Plateau and shifts northward along the European Continental Shelf (Figure A1). Unfortunately, the current understanding of these dynamics is largely qualitative in nature: it is not currently possible, for example, to make quantitative predictions of the spawning distribution. Such knowledge, however, could be potentially of great value in the scientific monitoring of the stock, its assessment and management, and even in optimising the performance of the fishery.

A key line of evidence supporting the current understanding stems from the Continuous Plankton Recorder (CPR) survey. The CPR survey is one of the most wide-ranging long term monitoring programmes of marine organisms in the world (Batten et al. 2003), and has been influential in the history of the blue whiting fishery. The first records of blue whiting larvae in CPR samples were reported in the early 1950s (Henderson 1953). Further CPR data revealed a great abundance and broad spatial distribution of blue whiting larvae in the North-East Atlantic, causing Raitt (1968) to conclude that the spawning stock would be sufficiently large for commercial exploitation and resulting in fisheries biologists becoming interested in the species (Polonsky 1968; Bainbridge and Cooper 1973). Since the subsequent development of the fishery in the late 1970s, CPR larval data has also been used to resolve the population structure of blue whiting (Pointin and Payne 2014). In addition, Hátún, Payne, and Jacobsen (2009) used a spatial subset of CPR data from 1951 to 1970 along a narrow axis across the Rockall Trough to support their hypothesised link between the marine environment and blue whiting spawning. Since much of this work was performed, the use of species distribution models (SDMs) to characterise the linkage between environmental variables and the distribution of organisms has become commonplace (Elith and Leathwick 2009; Guisan and Zimmermann 2000). SDMs correlate species observations with environmental variables to characterize a set of environmental conditions (the “niche”) where the species can occur. Once the relationship between distribution and the environment is appropriately parameterized, spatially resolved fields of environmental variables can then be used with the SDM to produce predictions of the potential habitat and/or geographical distributions of the species (Araújo and Guisan 2006; Araújo and Peterson 2012; Kearney and Porter 2009). A strength of SDMs is their ability to estimate spatial distributions and habitat from pointwise observations, a particularly valuable attribute that can add value to data that is unevenly distributed in time and/or space (e.g., CPR data). Furthermore, SDMs can be used to both predict and project environmental conditions beyond the conditions where they were developed, which is useful when considering the responses of an organism to climate change or climate variability.

In this work, we use SDMs to elucidate the mechanisms that are important for regulating spawning distribution of blue whiting. Our analysis is based on the unique and underutilised data set of blue whiting larvae obtained from the CPR survey. Building on previous work (e.g. Hátún, Payne, and Jacobsen 2009)(Hátún, Payne, and Jacobsen 2009) we use an expanded set of blue whiting CPR observations with an additional 35 years of data together with modern SDM modelling techniques to develop a quantitative model of the distribution. We first investigate the spawning distribution of blue whiting in time and space with the aim of developing a better picture of the modes of variability seen in the distribution and confirming previous results. Then we examine the role played by the marine environment in determining the spawning distribution of blue whiting relative to other processes, such as migration dynamics or bathymetric features. Finally, we validate our model results by comparing them to completely independent observations from fisheries and scientific surveys of the spawning distribution.

A2 MATERIALS AND METHODS

A2.1 ANALYSIS STRATEGY

Our analysis of the dynamics of blue whiting spawning distribution, and the factors controlling them, is based primarily on data obtained from the Continuous Plankton Recorder (CPR). We first applied space-time interpolation models (STI) to estimate average spawning distributions from this data, and how the distribution relates to marine climatic regimes. Species distribution models (SDM) were then developed to allow quantitative characterisation of the key environmental processes driving variability in the spawning distribution. The factors identified as important by the SDM were examined in detail using a standard suite of model checking tools. Finally, the CPR-based results were verified against independent data sources from fisheries and scientific surveys.

A2.2 CONTINUOUS PLANKTON RECORDER (CPR) DATA

Blue whiting larval data from the Continuous Plankton Recorder (CPR) survey (Reid et al. 2003; Bainbridge and Cooper 1973) from 1951 to 2005 were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), Plymouth, UK. The CPR is a plankton sampling device that is towed behind vessels of opportunity at 7 to 10 m depth, allowing for continuous sampling of the upper mixed water column across major commercial shipping routes (Richardson et al. 2006; Reid et al. 2003). Water enters the device through a small (12.7 mm) square opening in the front of the recorder, and is subsequently filtered through a 270 µm silk screen that is continuously replaced and preserved in formalin (Richardson et al. 2006). On shore, the silk is divided into samples corresponding to 10 nautical miles of towing and analysed under a microscope by taxonomists (Richardson et al. 2006). The position in space and time of CPR measurements are characterized by the spatial and temporal mid-points (Richardson et al. 2006).

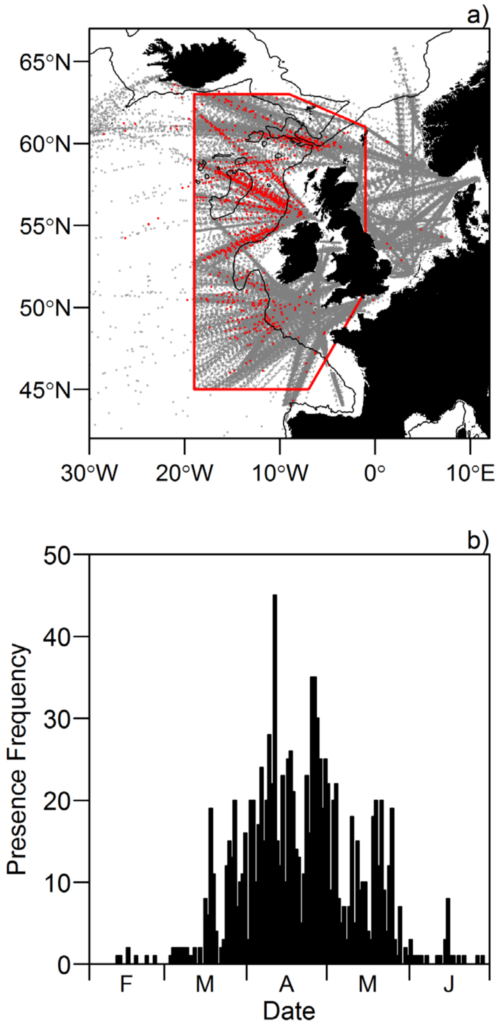

Figure A 2. a) Spatial distribution of CPR samples from 1951 to 2005. Grey points indicate CPR sampling stations where blue whiting larvae were absent. Red points indicate CPR sampling stations where blue whiting larvae were present. The red polygon delineates the study region used in further model-based analysis. The black lines indicate the 700 m isobath. **b)** Temporal distribution of larval-presences (counts) within the study region shown in panel a), as a function of day in the year from February (F) to June (J). Each bar corresponds to a day.

For the purposes of this analysis and following previous work (Pointin and Payne 2014) the CPR data was geographically restricted to the region where blue whiting larvae were most commonly observed (Figure A 2a), and to the period between February and June, covering more than 99% of all larval-presences (Figure A 2b; Pointin and Payne 2014). The CPR data consisted of 34,422 CPR observations over 54 years (1951 - 2005) including 1,122 presences of blue whiting larvae between February to June (Figure A 2b).

A2.3 PHYSICAL AND OCEANOGRAPHIC DATA

The UK Met Office Hadley Centre's EN4 ocean analysis product (version EN4.1.1) was used as the primary source of oceanographic data in the analysis (Good, Martin, and Rayner 2013). EN4 is based solely on observational data, and provides monthly, quality controlled objective analyses with a 1° spatial resolution and associated estimates of uncertainty.

A key feature of this data set, in the context of this analysis, is that it is also depth resolved, consisting of estimates of conditions at 42 vertical levels: blue whiting adults and larvae utilise a range of vertical habitats, however, and the appropriate choice of depth layer requires careful consideration. Spawning blue whiting adults are typically observed at depth ranges from 300 m to 500 or 600 m (ICES 2014; 1996), with the majority of eggs and non-feeding larvae reported at depths between 300 - 400 m (Hillgruber and Kloppmann 1999); 300 - 600 m (Ådlandsvik et al. 2001) or 250 - 600 m (eggs: 250 - 450 and larvae $\leq$ 2.5mm length: 300 - 600; according to Coombs et al., 1981). After spawning, the larvae require around 20 - 25 days to complete the ascent from the depth at which they are spawned to the sea surface (Ådlandsvik et al. 2001), where they can first be detected in the CPR. The majority of larvae found in the CPR samples are smaller than 6 mm in length (Bainbridge and Cooper 1973): from an average growth rate of > 0.3 mm per day (Bailey and Heath 2001) and hatching length of $\leq$ 2.5 mm (Ådlandsvik et al. 2001; Coombs, Pipe, and Mitchell 1981), it is very likely that larvae captured by the CPR were spawned in the 3 weeks prior to capture.

This understanding can then be used as the basis for extracting relevant environmental data from EN4. Temperature (T) and salinity (S) variables representative of the spawning conditions experienced by adults and eggs (hereafter referred to as T_{SPAWN} and S_{SPAWN}) were extracted from the EN4 data set for the spatial location of each CPR observation (both presence and absence) over the depth bounds between 252 and 596 m (inclusive) and averaged vertically. However, the environmental data used were that one calendar month prior to the timing of the CPR observation to allow for the lag time between spawning and observation of larvae in the CPR (within the restrictions imposed by the monthly temporal resolution of EN4). While drift of eggs and larvae during this one month may blur the relationship between the actual environmental conditions in which they were spawned and those used in the model, the error introduced is not expected to be worse than that due to the coarse scale (1 degree) of the EN4 product and will be dampened by the strong spatial correlation present in these fields. Furthermore, preliminary analyses showed that the T and S at spawning depth within the month of the CPR observation were highly correlated with T_{SPAWN} and S_{SPAWN} (correlation coefficient = 0.98) indicative of the slow dynamics of these sub-surface water masses. This approach to extracting environmental conditions therefore appears appropriate. Finally, in cases where the water depth at the location of a CPR observation was shallower than 252 m, T and S closest to the sea floor were extracted.

As a proxy for the environmental conditions experienced by blue whiting larvae at the time of capture in the CPR, sea surface temperature (SST) and salinity (SSS) were extracted from the EN4 data set, corresponding to the average T and S between the sea surface and 10 m depth (Good, Martin, and Rayner 2013). In this case, the data extracted from EN4 corresponded directly to the month of the CPR observation (i.e. with no time lag).

Oceanographic data for each CPR haul was complemented with geographic-based variables. The water depth corresponding to each CPR observation was extracted by means of bilinear interpolation from NOAAs ETOPO1 product (Amante and Eakins 2009). The associated slope (in degrees) was computed according to Horn (1981) based on 8 neighbouring cells located adjacent to each grid point using the `terrain`() function of the raster package (version 2.5.8; Hijmans, 2016) in R (version 3.3.2; R Core Team, 2016).

It is hypothesised that blue whiting larvae perform diel vertical migrations by ascending to the surface waters during dusk and dawn (Hillgruber and Kloppmann 2000), which could affect the CPR's capture efficiency as pointed out by Pointin and Payne (2014). To quantify light conditions in the upper water column at the time of capture, the angle of the sun measured from the horizon upwards at the time and point of observation was calculated using the `solarpos`() function in the maptools package (version 0.8.39; Bivand and Lewin-Koh 2015) in R.

A2.4 MARINE ENVIRONMENT OF THE STUDY REGION

We calculated a time series indicative of the state of the marine environment in the spawning region of blue whiting from 1951 to 2016 (red box, Figure A 2a) by area-weighted averages of T and S over spawning depth of blue whiting (~250 - 600m) in regions with water depths ≥ 600 m for each year during the main spawning period of blue whiting (March - May). We then calculated the 33rd and 67th percentile of these values over the 65 year period and partitioned the time-series into three environmental regimes to represent the broad forms of variability present in the system (Figure A 3).

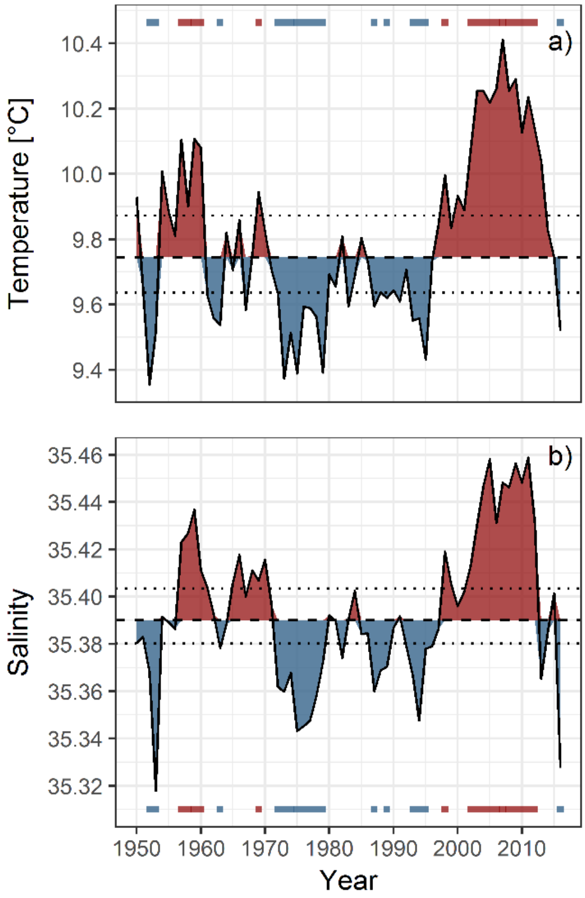

Figure A 3. Mean spring (March - May) (a) temperature and (b) salinity averaged over spawning depth of blue whiting (250 - 600 m) within the study region (red box in Figure A 2a). Dashed horizontal lines indicate the median spring temperature and salinity within the study region from 1951 to 2016 ($\overline{\boldsymbol{T}}$= 9.74 °C, $\overline{\boldsymbol{S}}$ = 35.39) and dotted lines the 33rd and 67th percentiles. Red colour indicates warmer/more saline conditions ($T > \overline{\boldsymbol{T}}$, $S > \overline{\boldsymbol{S}}$) and blue colder/fresher conditions ($T < \overline{\boldsymbol{T}}$, $S < \overline{\boldsymbol{S}}$). Horizontal bars indicate years defined by one of the two regimes: the saline and warm regime (red bar) with T and S above the 67th percentile, and the fresh and cold regime (blue bar) with T and S below the 33rd percentile.

A2.5 SPACE-TIME AND SPECIES DISTRIBUTION MODELLING

A.2.5.1 Basic model structure

Continuous Plankton Recorder data is provided as abundance categories (Richardson et al. 2006) with the majority (ca. 60 %) of the reported blue whiting abundance data comprising of one, two or three larvae. Initial explorations examined this data using a spatial model similar to Pointin and Payne (2014) with an ordered categorical response variable (Wood, Pya, and Säfken 2016): however, this analysis suggested that there was little further information in the abundance categories and the data is therefore treated as presence-absence for the remainder of the study.

Observations of blue whiting larvae were modelled using a Generalized Additive Model (GAM) with a binomial distribution and logit link structure:

$$P(X_i = \text{PRESENT}|\pi_i) \sim \text{Bernoulli}(\pi_i)\ ;\ \text{with}\ \ \text{logit}(\pi_i) = f() \qquad (1)$$

where X_i is the presence/absence of observation i and π_i is the probability (P) that blue whiting larvae are observed. The explanatory variables, regardless of whether they are spatial or environmental, are indicated by the function *f()*. All models were fitted using the `mgcv()` package (version 1.8.16) in R with a "gamma" parameter of 1.4 to avoid overfitting (Wood 2006). Light conditions in the upper water column, as represented by the elevation of the sun, θ, was included as a cubic spline smoother in all models.

A.2.5.2 Space-time interpolation (STI)

In order to allow a simple characterisation of the spawning distribution in relation to the state of the marine environment, a model of the CPR data over space (latitude and longitude) and time (i.e. the day of the year, DOY) was employed, termed the "space-time interpolation" model (STI), which is similar to the model of Pointin and Payne (2014). A three-dimensional tensor-product smoother (Wood 2006), with latitude, longitude and day-of-year as the dimensions was employed to characterise the space-time variability. In order to investigate whether the previously reported shifts in the distribution of spawning blue whiting in response to the climatic regime in the spawning region is also apparent in the larval CPR data, separate space-time models were also fitted for individual climatic regimes, and compared to a single baseline model using all data.

A.2.5.3 Species distribution models (SDMs)

Species distribution models (SDMs) were used to examine the processes driving the spatial and temporal distribution of spawning. Due to the relatively large number of potential variables that could be considered, the development of the SDM took place in two steps: first, the effect of constant geographical features was considered in a model set termed geographical model set (GEO) and the "best" model identified. Environmental variables were then added to this model to develop the full SDM.

As blue whiting are typically found between 250 and 600 m, their distribution can be expected to be shaped, at least in part, by oceanic bathymetry. There is little evidence to support spawning in shallow waters and we therefore considered a depth term in our models to account for this effect. Similarly, spawning blue whiting are commonly associated with the Continental Shelf edge (ICES 2016a) and we therefore considered the bottom-slope as an additional term in the model.

A particular challenge in developing SDMs for this species stems from the large migrations that blue whiting undertake. While the feeding (and overwintering) grounds for this species are mainly in the Norwegian Sea, spawning occurs to the west of Great Britain and Ireland (Bailey 1982; ICES 2016b). After spawning, the species returns quickly to the Norwegian Sea feeding grounds in time to take advantage of the productivity in this region in late-spring and summer. The need to return to the feeding grounds therefore can be expected to introduce an additional consideration regarding where to spawn: migrating far from the feeding grounds in search of optimal spawning habitat incurs a penalty due to both the extra migration distance required and the risk of missing part or all of the feeding season. Such behavioural considerations are potentially problematic for the standard species distribution modelling approach, however, which assumes that the environmental niche is the only factor determining distribution (e.g. Wiens et al., 2009), rather than, in this case, additional constraints imposed by migration and life-history considerations. Here we have circumvented this problem by incorporating the potential costs of migration-distance explicitly into our species distributions models. We represent this process with a two-dimensional interaction term (tensor-product smoother) between latitude and day-of-year, as the cost and feasibility of returning to the feeding grounds will clearly depend on both distance and time: spawning further south, for example, could be a feasible proposition if it were to happen earlier in the year, allowing sufficient time to return. The form of this term, however, is left unspecified and is fitted as part of the modelling procedure. In addition, this term also allows for changes in the timing of spawning with latitude to be incorporated, in line with previous results (Pointin and Payne 2014).

In many fish species, spawning fish as well as eggs and larvae are particularly sensitive to ambient environmental conditions since their tolerable ranges are more restrictive than those of other life-history stages (Pörtner and Peck, 2010; and references therein). In particular, salinity has also been proposed as being critical via its effect on water density and therefore the buoyancy of marine fish eggs, including those of blue whiting (Sundby and Kristiansen 2015) and has shown to be important for blue whiting larvae (Ådlandsvik et al. 2001). An ensemble of different temperature and salinity structures was therefore considered as explanatory variables and incorporated into the model structure based on this *a priori* reasoning (Anderson 2008).

A2.6 MODEL VALIDATION AND ASSESSMENT

A2.6.1 Model validation metrics

To assess a model's goodness of fit, several standard measures were employed. In generalized linear and generalised additive models the "explained deviance" (Dev. Expl.) is an analogue to the coefficient of determination (R^2) and was used here as an overall indicator of model quality. The Akaike Information Criterion (AIC), which measures the trade-off between model fit and model complexity (Burnham, Anderson, and Huyvaert 2011), was used as the primary tool for model selection: in a set of models, the model with the smallest AIC has the smallest information loss and is therefore defined as the "best" (most parsimonious) model within the set (Burnham, Anderson, and Huyvaert 2011; Anderson 2008). The difference in AIC relative to the smallest AIC value in the model set (ΔAIC), provides an easy way to compare and rank models (Anderson 2008; Burnham, Anderson, and Huyvaert 2011): the "best" model within a set has by definition $\Delta AIC \equiv 0$. However, evaluating models based on the same data set used for calibration has been proposed to be a poor approach (Guisan and Zimmermann 2000). Therefore, for the purpose of evaluation, 5-fold cross validation (CV) was employed, where the models were trained with 80% of the data and predictions subsequently made and validated against for the remaining 20%. Data partitioning was performed based on years, with every 5th year being incorporated into the same fold. The prediction-based model validation metrics were derived for each of the five iterations and their mean calculated.

The ability of the models to discriminate between the presence and absence of larvae were derived from a confusion matrix, summarizing the four possible outcomes between modelled presence/absence predictions and the validation data set (Table A 1).

Table A 1. Confusion matrix used to evaluate the predictive accuracy of presence/absence models. TP (true positives): correctly predicted presences; FP (false positives): erroneously predicted presences; FN (false negatives): erroneously predicted absences; TN (true negatives): correctly predicted absences.

		Validation data set	
		Presence	**Absence**
Model	**Presence**	TP	FP
	Absence	FN	TN

The threshold used for translating the predicted probability of blue whiting larval-occurrence into presences and absences was chosen for each model so that the total number of presences in the prediction data set was equal to the number of presences in the observed dataset, in accordance with Freeman and Moisen (2008). The positive predictive value (PPV) is the proportion of hauls where the presence of larvae is predicted and was in fact a larval-presence:

$$\text{PPV} = \frac{TP}{TP+FP} \qquad (2)$$

where TP (true positive) and FP (false positive) are the elements of the confusion matrix (Table A 1). The negative predictive value (NPV) is the proportion of sites where no larvae are predicted that are actually an absence:

$$\text{NPV} = \frac{TN}{FN+TN} \qquad (3)$$

where TN are the true negatives and FN the false negatives. The true skill statistic (TSS) is the average of the net prediction success rate for presences and absences (Liu, White, and Newell 2011) and independent of prevalence (Allouche, Tsoar, and Kadmon 2006) and calculated by:

$$\text{TSS} = \text{sensitivity} + \text{specificity} - 1, \qquad (4)$$

where sensitivity is the probability that the model correctly predicts a presence at a site

$$\text{Sensitivity} = \frac{TP}{TP+FN} \qquad (5)$$

and specificity is probability that a known absence site is correctly predicted

$$\text{Specificity} = \frac{TN}{TN+FP} \qquad (6)$$

Accordingly, when the TSS is 1 it indicates that the model accuracy is perfect, while a TSS of zero is associated with a purely random model. The best performing models within the set were also validated using standard model diagnostic tools appropriate to generalised additive models e.g. the use of simulation-based quantile-quantile plots (Augustin, Sauleau, and Wood 2012).

The relative importance of each variable was evaluated using permutation importance. Data for each explanatory variable was randomly reassigned to a different CPR observation from that which it was originally associated with: in this way, any potential relationship between larval-presence/absence and the environmental variable is broken, while the statistical properties of the data remain unchanged. The model was then refitted and the predictive performance in terms of TSS and PPV calculated, as described before. The process was repeated for each variable and the difference between the original model and the TSS and PPV for each of the randomised models was calculated. A strong reduction in the performance metrics indicates a greater sensitivity of the model to the variable that has been randomized.

A2.6.2 Model visualisation

Estimated larval distributions were visualised by applying models based on the full CPR data set (i.e. not based on the cross-validation data sets) on a regular grid in space and time. The data used for model predictions was extracted by means of bilinear interpolation onto a regularly spaced grid of 0.25 x 0.25 ° resolution within the study region (Figure A 2a). For spatial maps, and due to the monthly resolution of the EN4 data, the 15th of each month was used as the day-of-year (DOY), while solar elevation angle (θ) was fixed to 0°, representing the time of sunrise or sunset. To show the progression of spawning over time with respect to latitude, predictions were made for each DOY from February to June. Afterwards, the predicted larval-observation probabilities were averaged over longitude for each DOY.

A2.6.3 Comparison to fisheries & survey data

The SDM results were also validated by comparison with entirely independent data sources from fisheries and scientific surveys. This comparison took place by comparing the relative distributions of each of these data sources with respect to the key environmental variables identified by the SDMs to check for agreement between data sets: observations from fisheries and scientific surveys were matched-up with the corresponding environmental data derived from the EN4 data. Comparisons of spatial distribution were also made between outputs from the best SDM and the individual data sources.

Spatially and temporally resolved catch statistics of adult blue whiting fished between 1977 - 2012 have been prepared by the North East Atlantic Fisheries Commission (NEAFC 2013). This data is available gridded onto 0.5° latitude x 1° longitude pixels with monthly resolution: data from March, the peak timing of spawning, was used in this analysis.

Acoustic biomass survey data of blue whiting spawning aggregations from 1981 to 2013 was also available. Data prior to 2004 originate from Norwegian surveys on the spawning grounds of blue whiting, while data from 2004 onwards stem from the International Blue Whiting Spawning Stock (IBWSS) Survey that is carried out annually for two weeks from late March to early April (ICES 2016b). The acoustic survey records data continuously along its cruise track and provides biomass estimated of blue whiting per 0.5° latitude x 1° longitude rectangle.

A3 RESULTS

A3.1 MARINE CLIMATE IN SPAWNING REGION OF BLUE WHITING

The mean temperature and salinity in the spawning area of blue whiting has varied greatly between years. However a distinct pattern is noticeable: the marine climate was typically either both saline and warm or to the contrary fresh (i.e. of low-salinity) and cold (Figure A 3, correlation between temperature and salinity (r) = 0.82). Years where salinity and temperature both exceeded the 67th percentile (S > 35.40 and T > 9.87 °C) were defined as belonging to the "saline and warm" regime (17 years, indicated by the red horizontal bars in Figure A 3), while years with mean salinity and temperature below the 33rd percentile (S < 35.38 and T < 9.64 °C) were defined as "fresh and cold" regime (17, indicated by the blue horizontal bars in Figure A 3).

The spatial distribution of temperature and salinity within the study region varies between regimes (Figure A 4). During the saline and warm regime water masses of subtropical origin with high salinity and temperature spread along Rockall Trough towards Rockall Plateau, with mean salinities during March at spawning depth of blue whiting reaching ≥ 35.35 and temperatures ≥ 10 °C within Rockall Plateau region (Figure A 4a). Conversely, during the fresh and cold regime such high salinities are constrained within Rockall Trough and onto Porcupine Bank with more waters of North Atlantic origin pushing in from the west (Figure A 4b) due to the influence of a strong subpolar gyre (Hátún et al. 2005).

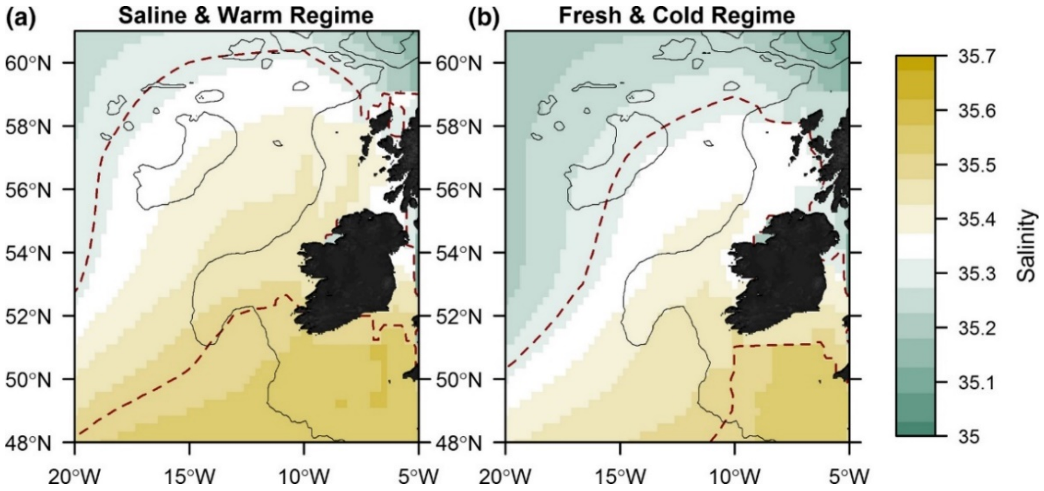

Figure A 4. Salinity averaged over spawning depth (250–600 m) of blue whiting during the (a) saline and warm and (b) fresh and cold regimes in March. The black solid lines indicate the 700 m isobaths and the red dashed lines the isoline of 35.3 and 35.5 psu averaged over spawning depth of blue whiting, indicative of the optimum salinity range for spawning in blue whiting (Figure 6d). In regions where water depth is <250 m, bottom salinity is plotted.

A3.2 SPACE-TIME INTERPOLATION OF CPR DATA

Simple interpolation of the CPR data, using a statistical model with a space-time smoother, revealed substantial differences in distribution associated with the different marine climate regimes (Table A 2).

Table A 2. Model fitting result of the space-time interpolation.
Model formulation (*f()* in Equation 1) is expressed as an equation where each term is implemented in the model using a either a 1D spline smoother (single terms) or a 2D tensor-product smoother (multiplied terms) and |regime indicates the term is conditional on the oceanographic regime (3 regimes: fresh & cold, saline & warm, and neutral regime). Lat: Latitude; Lon: Longitude; θ : solar elevation angle; DOY: day of the year; DevExpl: Explained Deviance; AIC: Akaike Information Criteria; ΔAIC: difference in AIC relative to the smallest AIC value within the model set; TSS: True Skill Statistic; PPV = Positive predictive value; NPV = Negative predictive value.

Model	Formulation, f()	DevExpl	AIC	ΔAIC	TSS	PPV	NPV
STI1	Lon x Lat x DOY + θ	0.419	5977	105	0.356	0.374	0.858
STI2	Lon x Lat x DOY |regime + θ	0.451	5861	0	0.342	0.36	0.849

A large decrease in AIC was seen when adding regime as a conditional term (STI2), indicating an improved model over that which is not conditional on regime (STI1, Table A 2), although the predictive skill of STI2 was marginally worse, indicated by slightly lower TSS, PPV and NPV. Comparison of the larval-observation probability during the two most extreme regimes revealed clear differences in distribution (Figure 5). A map of the interpolated larval distribution for April (the peak of larval-presence probability, corresponding to March spawning) highlights a greater westward and northward larval distribution during saline and warm conditions, peaking at the Continental Shelf edge with high probabilities extending from the shelf edge through the Rockall Trough and along the north-eastern edge of the Rockall Plateau (Figure A 5a): the peak at 45 °N is likely to be erroneous, since GAMs perform worse on the edges as opposed to the centre of the modelling domain (Wood 2006). In contrast, during the fresh and cold regime, the larvae are more concentrated within Rockall Trough and along the shelf edge (Figure A 5b). The probability difference plot (Figure A 5c) highlights regions that are most dissimilar between the regimes: during the saline and warm regime the probability of larval-presence is higher in the vicinity of Rockall Plateau, in particular towards its west and north up to 63 ºN, in contrast to the fresh and cold regime, when larvae are encountered with a higher probability along the shelf edge, on Porcupine Bank and extending into Rockall Trough. Also of note is the absence of larvae in the Porcupine Seabight during warm and saline years.

These differences are also reflected in the temporal changes in the distribution of larvae between the regimes. While a northward progression of spawning over time was apparent during both regimes, the onset and latitudinal distribution of larval appearance differed (Figure A 5d,f). During the fresh and cold regime, significant amounts of larvae are first seen in mid- to late-March at latitudes of around 50 °N, associated with of Porcupine Seabight spawning area (Figure A 5e). Conversely, larval appearance generally commences later at higher latitudes during the saline and warm regime when the Porcupine Seabight spawning area is not used (Figure A 5d), as highlighted by the probability difference plot (Figure A 5f). Furthermore, while the peak of larval occurrence probably occurs at approximately the same latitude and day-of-year in both regimes, larval-observation probabilities are generally higher during the warm and saline regime, peak probabilities ($p \geq 0.225$) persist over a longer period and are found at higher latitudes compared to the fresh and cold regime.

While we have focused primarily on the extremes of the distribution as a way to understand the modes of variability, it is important to note that the intermediate regime also occurs approximately one-third of the time. Comparison of the distributions of spawning in this regime in time and space reveal that it is, as the name suggests, intermediate between the two extremes, with a more northerly distribution and reduced (although not eliminated) spawning in Porcupine Seabight. Westward extension, however, is limited, and the distribution does not extend much beyond the Rockall trough. (Figure A S2 and S3).

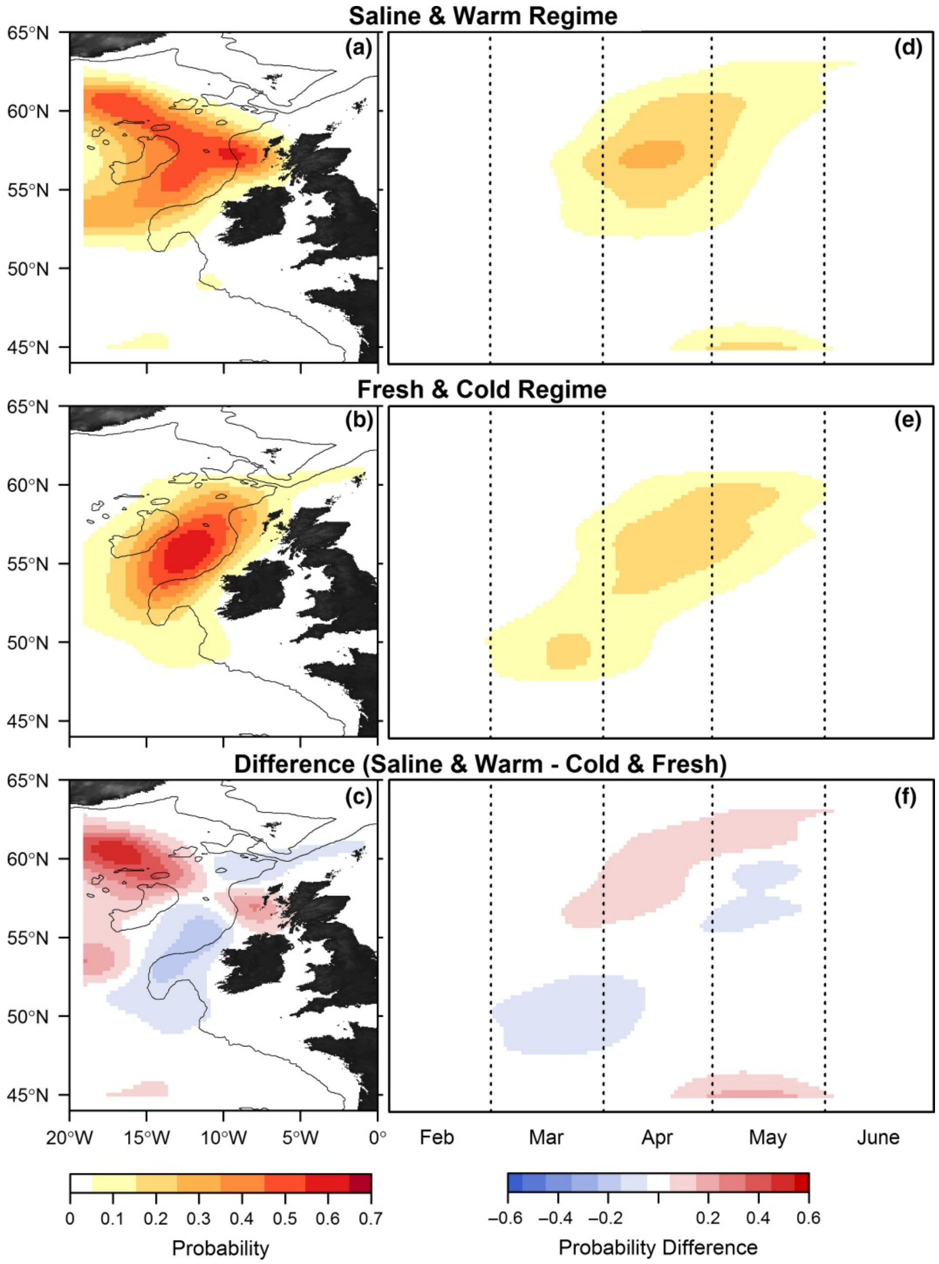

Figure A 5. Larval-observation probabilites, a proxy for blue whiting spawning distribution, based on space-time interpolation (STI2, Table A 2), mapped for April (a-c) and as latitude-time plot from February to June (d-f), during the saline and warm a & d), and fresh and cold b & e) regimes (1951 - 2005); Figure c & f) depict the probability difference of larval-presence between the two regimes, i.e. the difference in larval observation probability between the saline & warm regime (a/d) and fresh & cold regime (b/e); with red colours corresponding to higher larval-observation probabilities during the saline and warm regime compared to the fresh and cold regime, while blue colours indicate the opposite, i.e. higher larval-observation probabilities during the fresh and cold regime. The black lines in a-c indicate the 700 m isobaths.

A3.3 SPECIES DISTRIBUTION MODELLING

A3.3.1 Model selection

Species distribution modelling proceeded in two steps, first considering the optimal structure for geographical predictors, and then further considering environmental predictors on top of the best geographical model. Including depth into the geographical model (GEO2, Table A 3) enhanced model skill compared to the starting model (GEO1, Table A 3). Improvements were seen in terms of AIC, explained deviance, and enhanced predictive ability compared to the baseline model (Table A 3). However, the addition of seabed slope did not increase model skill further, either alone (GEO3) or in combination with depth (GEO4, Table A 3). For further analysis, the simpler geographical model structure GEO2 was as chosen as a refined baseline model for incorporating environmental variability.

Table A 3. Model fitting result of the geographic models.
Model formulation, *f()*, where abbreviations are defined in Table 2. Models GEO2 – GEO4 use the baseline structure of GEO1, plus addition modifications of their own.

Model	Formulation, f()	DevExpl	AIC	ΔAIC	TSS	PPV	NPV
GEO1	Lat x DOY + θ	0.251	7465	1160	0.222	0.243	0.825
GEO2	GEO1 + Depth	0.369	6305	0	0.331	0.35	0.849
GEO3	GEO1 + Slope	0.318	6812	507	0.311	0.33	0.847
GEO4	GEO1 + Depth + Slope	0.369	6305	0	0.332	0.351	0.853

The addition of environmental variables to the geographical baseline model further improved the fit and slightly increased the predictive performance (Table A 4). Extending the baseline model to incorporate inter-annual variation of T and S reduced the AIC up to nearly 150 units, indicating a great improvement in model parsimony (Table A 4): models with a difference in AIC above about 15 to 20 are judged as being strongly different (Anderson 2008), meaning that this is strong evidence that inter-annual variation in environmental conditions plays a key role in shaping the spawning distribution of blue whiting.

However, the choice of the best environmental model is not immediately clear. The best three models (SDMs 3, 6, 7) are within 1 AIC unit of each other, and the fourth (SDM 8) is 8 AIC units different. Furthermore, while the predictive skill of these models varies, the differences are generally minor: any of these four models could potentially be chosen as the "best model" (for the sake of simplicity of interpretation we have chosen not to employ an ensemble approach or model averaging). Upon closer examination, we can see that the best of these models, SDM 7, gets good results using two-dimensional interactions between surface variables (SSS and SST) as it's explanatory variables, even though neither of these terms show much skill individually (i.e. SDMs 1 and 2). Examination of the form of this smoother indicates dependencies that are hard to reconcile biologically and it is furthermore difficult to understand why surface variables would be determining for a species that lives primarily at depth. Conversely, all of the three remaining top models (SDMs 3, 6, 8) include spawning salinity (S_{SPAWN}) as a predictor. The addition of spawning temperature to the model (i.e. from SDM 3 to 6) only makes for a very minor improvement, and a more-complex two-dimensional interaction between spawning salinity and temperature (SDM 8) has less support than salinity on its own (SDM 3). The biological interpretability of these models is an important feature and we therefore choose the simplest of them, SDM 3 (spawning salinity) as the "best" model for further analysis. However, it is important to bear in mind that this is a subjective choice, and that other models show comparable explanatory and predictive skill.

Table A 4. Model fitting results for models incorporating environment variables.
Model formulation, *f()*, where abbreviations are defined in Table A 2. *GEO2* is the best fitting geographical model (Table A 3): the details of this model are duplicated here from Table A 3 for reference.

Model	Formulation, f()	DevExpl	AIC	ΔAIC	TSS	PPV	NPV
GEO2	Lat x DOY + θ + Depth	0.369	6305	146	0.331	0.350	0.849
SDM1	GEO2 + SSS	0.369	6304	145	0.332	0.350	0.849
SDM2	GEO2 + SST	0.380	6213	54	0.344	0.362	0.851
SDM3	GEO2 + S_{SPAWN}	0.385	6160	1	0.356	0.373	0.850
SDM4	GEO2 + T_{SPAWN}	0.376	6243	84	0.337	0.355	0.849
SDM5	GEO2 + SSS + SST	0.382	6195	36	0.337	0.356	0.852
SDM6	GEO2 + S_{SPAWN} + T_{SPAWN}	0.385	6159	0	0.351	0.368	0.851
SDM7	GEO2 + SSS x SST	0.385	6159	0	0.348	0.366	0.856
SDM8	GEO2 + S_{SPAWN} x T_{SPAWN}	0.384	6167	8	0.343	0.361	0.847

A3.3.2 SDM visualisation

Examining the individual terms in the SDM gives insight into the processes that it views as being important in shaping the distribution of blue whiting larvae. The 2D tensor-product smoother on latitude and day-of-year shows a clear relationship between the two variables, with peak larval-observation probabilities occurring later at higher latitudes (Figure A 6a). There are two centres of high larval-observation probability, one during mid-March at around 50 °N latitude (approximately the Porcupine Seabight area) and a greater region during mid-April to mid-May, reaching a peak observation probability between 57 °N and 59 °N (Figure A 6a). The smoother of the solar elevation angle (θ) took positive values from -20° to 40° and assigned the greatest probability of observing larvae at around 10°, corresponding to the period shortly before sunset and/or after sunrise (Figure A 6b). The probability of observing larvae decreased and effectively vanishes in waters shallower than 300m, while is constant above this value (Figure A 6c). The larval-observation probability with respect to S_{SPAWN} showed a clear window of high observation probability where the smooth took positive values between 35.3 and 35.5 (Figure A 6d), later referred to as the optimum salinity window.

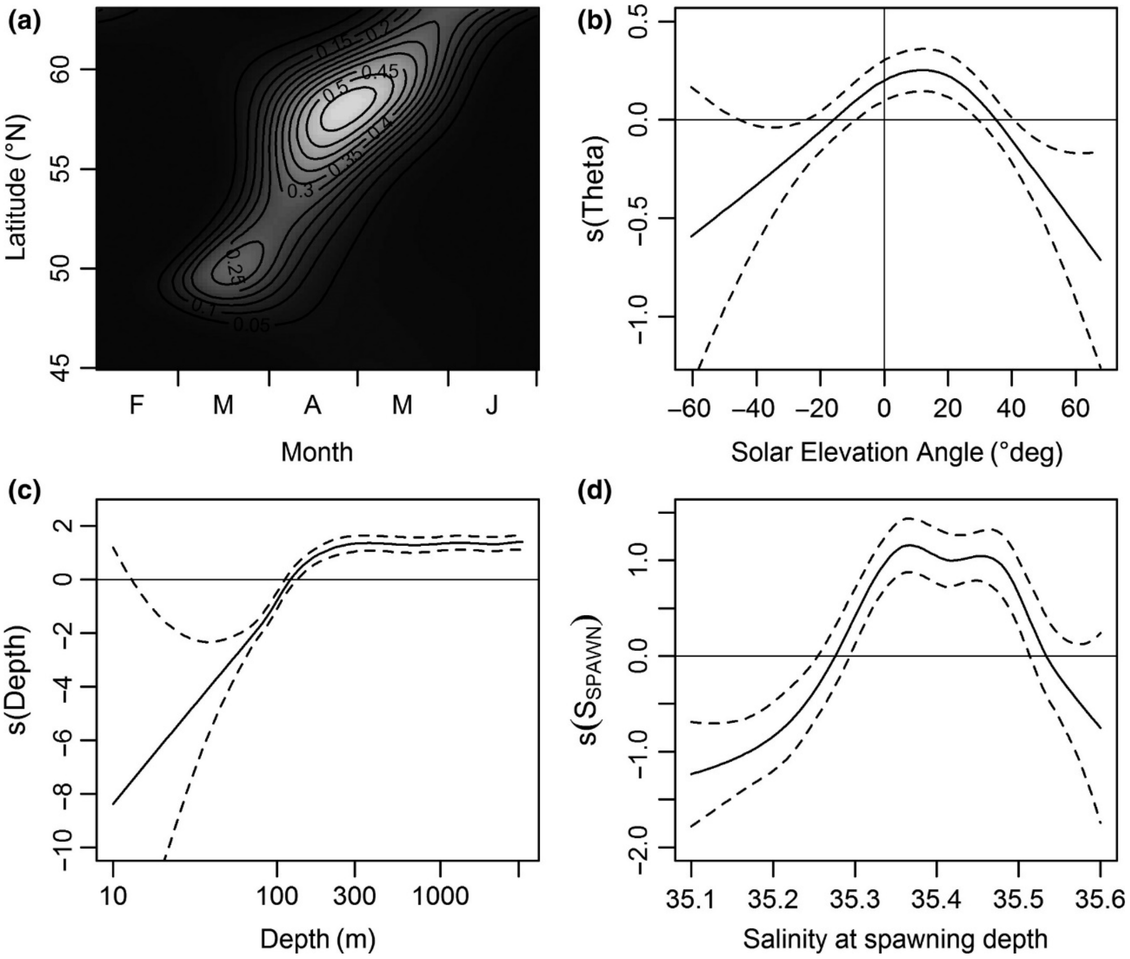

Figure A 6. SDM components. a) Contour plot of the larval-observation probability as a function of latitude [in °N] and the day of the year (DOY, here shown as month). b-d) Smooth functions of the SDM with b) the solar elevation angle (θ in degrees), c) the depth [m], and d) the salinity at spawning depth during the spawning time of blue whiting (S_{SPAWN}). In Figures b-d) the solid non-linear lines indicates the estimate of the smooth s() and the dashed lines indicate the 95% confidence interval. The vertical line in b) indicates sunrise/sunset, with positive values indicating that the sun is above the horizon, i.e. that there is light.

Permutation importance experiments can be used to gain insight into the relative importance of each variable in the model fit. Permutation importance was calculated here as the relative loss in TSS upon scrambling of the variable(s) in question. Latitude and DOY, and in particular DOY, appeared to be the most important of these variables followed by depth (Figure A 7).

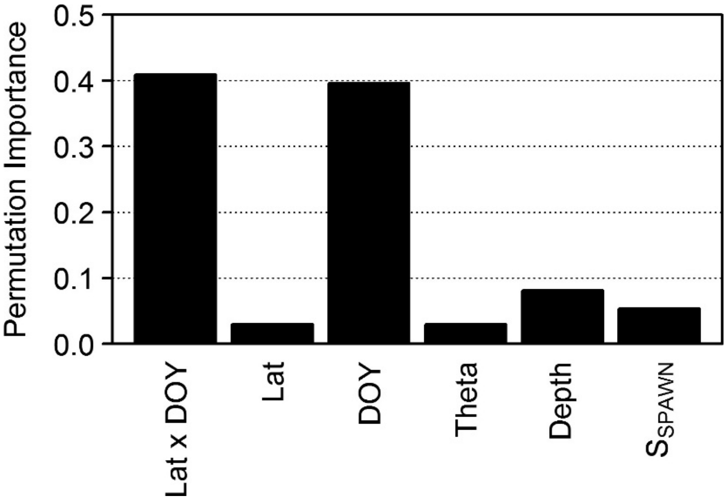

Figure A 7. Permutation importance of variables. The difference in true skill statistics (TSS) between the original model and models with randomized explanatory variables is used as an indicator of the importance of each explanatory variable in the model fit: Latitude (Lat), day-of-year (DOY), solar elevation angle (Theta), log-transformed depth (Depth) and the salinity at spawning depth during the spawning time of blue whiting (S_{SPAWN}). The "x" indicates that both Latitude and DOY variables within the 2D smoother were randomized at the same time. The permutation importance in terms of positive predictive prevalence (PPV) was very similar to TSS and is therefore not shown.

Model-based estimates of larval-presence probability were visualised for both regimes during April, the month with observed peak larval-presence, corresponding to March spawning (Figure A 2b). During the saline and warm regime, the main region of predicted high larval-observation probability extends from Rockall Plateau over Rockall Trough up to the European Continental Shelf between latitudes of 55 and 59 °N, in particular along Rockall Plateau's eastern slope and within Rockall Trough (Figure A 8a). During fresh and cold conditions the main region of larval-observation probability is more contracted, spanning across Rockall Trough between 55 and 58 °N, with peak probabilities of observation along the Continental Shelf at 57 °N (Figure A 8b). Overall, the projected area of high observation probability (i.e. greater than 0.45) is 2.5 times larger during the saline and warm regime (147 000 km^2), compared to the fresh and cold regime (59 000 km^2).

A map of the differences in distribution between the two extreme regimes clearly highlights these changes. Areas of high larval-observation probability have the greatest west- and northward extent during saline and warm conditions and are especially high on Rockall Plateau, while during fresher and colder conditions they are more constricted towards the Continental Shelf and found slightly further south (Figure A 8c). In particular, more larvae are observed on Porcupine Bank and Seabight during fresher and colder conditions while they are virtually absent from Porcupine Seabight during the saline and warm regime (Figure A 8c).

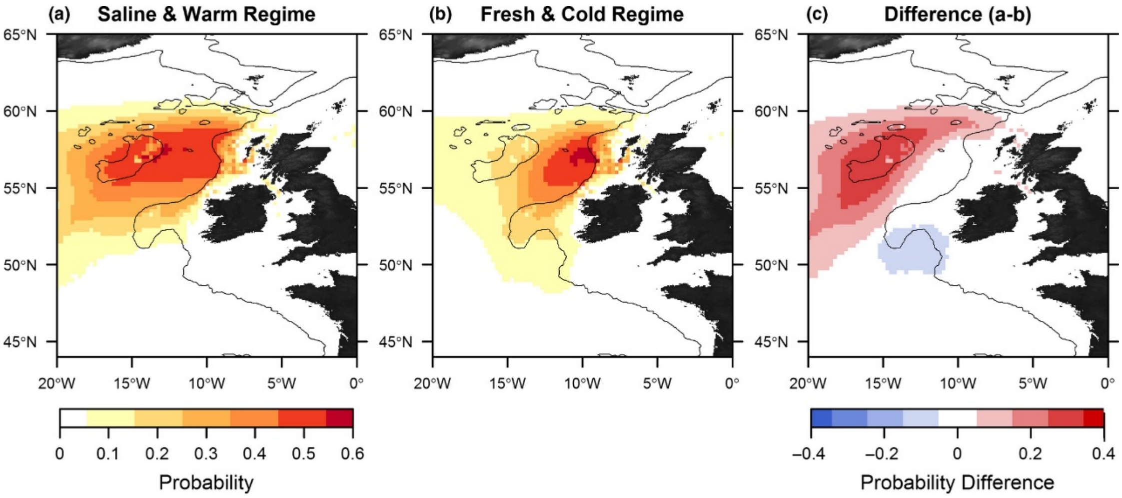

Figure A 8. Map of CPR larval-presence probabilities (a proxy for blue whiting spawning distributions) estimated by the SDM in April during a) the more saline and warmer and b) and fresher and colder regime and c) the probability difference between the two regimes. The probability difference was calculated by subtracting the CPR larval-presence probability encountered during the saline & warm regime by that during fresh & cold regime. Accordingly, positive values (red) correspond to higher probability of larval observation during a saline & warm regime compared to the fresher & colder regime. The black lines indicate the 700 m isobaths.

A3.3.3 Validation against independent data

We found good agreement between the SDM’s response to salinities based on CPR observations of blue whiting larvae, and that inferred for adult fish, based on observations from fisheries and scientific surveys. The majority of adult blue whiting were encountered between salinities of 35.3 and 35.5 (Figure A 9). This result is in good agreement with the smooth function of S_{SPAWN} of the SDM, which predicts the highest larval-observation probability at this salinity range. The low abundance of blue whiting at salinities < 35.3 is, however, not in reflected the SDM and may arise due to the capture of fish that are migrating to or from their spawning location.

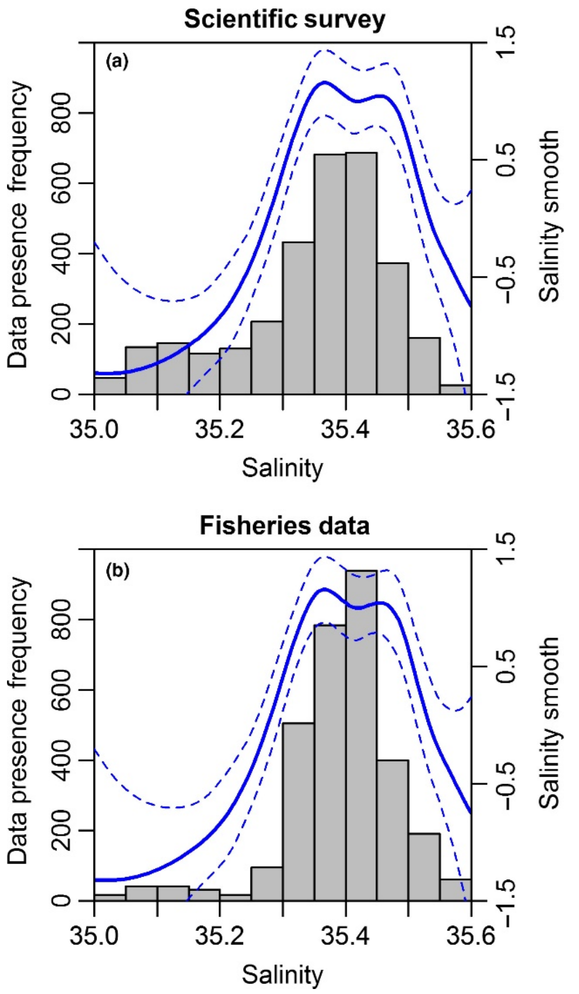

Figure A 9. Presence frequency of spawning blue whiting (number of pixels with presences) observed in a) scientific surveys and b) caught in fisheries during March compared to the salinity at which these observations were made (bars). The solid (blue) line indicates the modelled smooth function of blue whiting larval-presence obtained from the SDM (Figure A 6d), with dashed lines indicating the 95% confidence interval.

Good spatial agreement is also seen between the estimated distribution of larvae from the SDM and independent observations from fisheries and scientific surveys targeting spawning adults (Figure A 10). In particular, the expanded, westward distribution of larvae during saline and warm conditions in 2007, and the contracted distribution during fresh and cold conditions in 1993 resemble observations from independent fisheries and scientific surveys targeting spawning adults well (Figure A 10). The optimum salinity window encompasses the majority of observations and delineates the maximum westwards extent specifically in 2007 (Figure A 10). However, observations of adult blue whiting reach further north and south than predicted by the SDM or expected from the optimum salinity window and observed catches from 1993 fail to match the predicted peak occurrence (Figure A 10): again, these may be due to fish on their way to or from the spawning grounds.

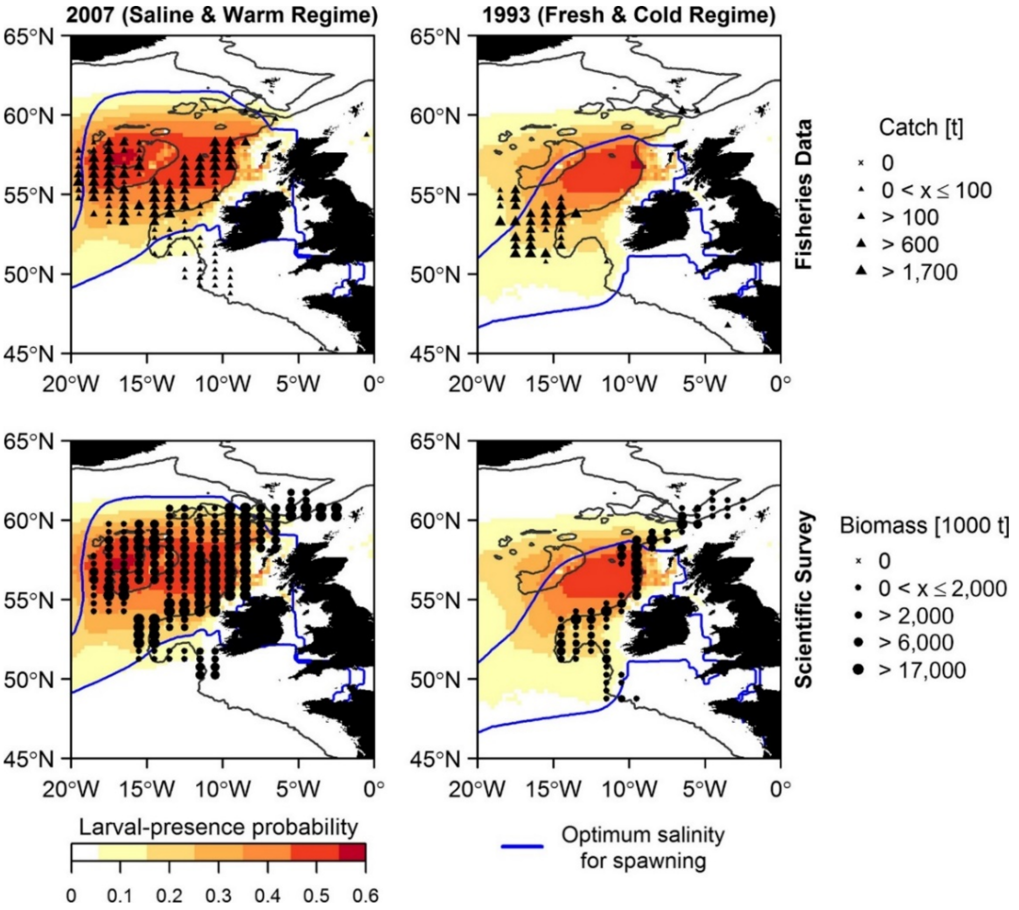

Figure A 10. Distribution of blue whiting in March 2007 during the saline and warm regime (left) and in March 1993 during the fresh and cold regime (right) obtained from the fisheries catch data (top, triangles) and the scientific surveys (bottom, circles). The blue isolines indicate the window of optimum salinity for spawning of blue whiting ($35.3 < S < 35.0$), averaged over the spawning depth (250 to 600 m) of blue whiting in March. The black lines indicate the 700 m isobaths and the grey shading the bathymetry. Colours correspond to the larval presence probability predicted to be observed in the CPR in the following month of the year in question (April).

A4 DISCUSSION

This study provides a quantitative insight into the processes determining the spatial distribution of blue whiting spawning for the first time. By combining the wide ranging observations of blue whiting presence and absence from the CPR with species distribution modelling tools and ocean observation products, it is possible to characterise the processes driving the observed distributional shifts. Here we place these conclusions in a broader context.

A4.1 THE MARINE ENVIRONMENT IMPACTS THE SPAWNING DISTRIBUTION

Firstly, the distributional shifts reported here agree with previously published work. The north- and westward expansion of the region with high probability of observing blue whiting larvae in the CPR (i.e. the potential spawning region) during saline and warm conditions, and its contraction towards the Continental Shelf during fresher and colder conditions (e.g. Figure A 5) has been observed previously (Bailey 1970; Bainbridge and Cooper 1973). Distributional changes of larvae (Hátún, Payne, and Jacobsen 2009) and spawning adults (Hátún et al. 2009) have previously been linked to variations in the North Atlantic subpolar gyre (SPG). However, in view of the fact that the SPG is a basin-scale process, while individual fish respond to their local environment, our analysis offers a more nuanced perspective. Furthermore, our use of a statistical model and the focus on the presence-absence aspect of the CPR data circumvents many of the problems hidden in previous analyses such as the information content associated with CPR abundance values used by Hátún, Payne, and Jacobsen (2009) and biases resulting from the CPR's opportunistic sampling design, it's small sampling volume (Batten et al. 2003), and the uneven and temporally varying distribution of blue whiting larvae within the water column (Hillgruber and Kloppmann 1999; Ådlandsvik et al. 2001; Pointin and Payne 2014).

Our results confirm that blue whiting spawning distribution appears to be following inter-annual variations in the marine environment during spawning. The highest probability of observing larvae in the CPR was found between salinities of 35.3 to 35.5: this possibly resembles the optimum salinity window for spawning in blue whiting, since independent observations from scientific and fisheries surveys targeting spawning adults also encountered the majority of adult blue whiting at this salinity range (Figure A10 and 11). Moreover, these results are in rough agreement with ichthyoplankton surveys that demonstrated peak spawning above salinities of 35.3 (Schmidt 1909) and between 35.2 to 35.4 (Bailey and Heath 2001). Our results therefore suggest that spawning is constrained by fresh and cold water masses in the spawning region associated with a strong SPG.

The apparent selection for this salinity range by spawning blue whiting may have a number of explanations. Blue whiting eggs are positively buoyant initially and their density increases during egg development enabling them to maintain a stable bathypelagic distribution (Ådlandsvik et al. 2001). Subsequently, blue whiting larvae ascend passively through the water column towards the surface where they feed (Ådlandsvik et al. 2001). Since variations in water density affect the buoyancy of eggs and larvae and thus their vertical distribution, changes in salinity can alter the ascent of larvae from their spawning depth towards the food-rich surface waters, which is critical for their survival (Ådlandsvik et al. 2001).

Additionally, changes in the marine environment also affect the plankton community and thus the food conditions for blue whiting. Hátún et al. (2009) have found that during a weak SPG, when the spawning region is influenced by saline, subtropical water masses, the zooplankton community switches from a dominance of *Calanus finmarchicus* to a greater abundance of smaller copepod species such as *Pseudocalanus, Acartia* and *Oithona.* These species represent the main food items of blue whiting larvae (Bailey 1982) and it is therefore possible that shifts in the spawning distribution may in fact be a result of spawning adults choosing regions to spawn where there is abundant and suitable prey for the larvae, thereby maximising larval survival probabilities.

The strong relationship between the potential spawning region and the ambient salinities found here may therefore arise in part as a response to the correlation between salinity and the planktonic community in this region. Alternatively, spawning blue whiting may be using salinity (which they most likely can sense) as a proxy for the planktonic community to be encountered by the larvae (which they most likely cannot sense). Based on this analysis alone it is not possible to determine which, if any, of these mechanisms is causative in nature, and further research is required to clarify this issue.

An interesting, although subtle, result from this analysis concerns the presence of blue whiting larvae in the Porcupine Seabight region. In a previous paper (Pointin and Payne 2014) it has been suggested that these observations may represent a southern spawning population. However, the results gathered here show that there is essentially no spawning in this region during more saline and warmer regions (Figure A 5) (although larvae are present in this region in both the fresher and colder regime and the intermediate regime). The absence of larvae during this regime can be explained by the distribution of regions of suitable salinity (Figure A 4 and 10) and is a result that is replicated in the species distribution model (Figure A 8). The consequences of this result for the interpretation of a southern spawning component are unclear but suggest that more analysis and particularly more observations in this region are required.

A second important question raised by these results is how the shifts in spawning distribution relate to the large changes in recruitment seen in this stock. It has been proposed, for example, that the overlap between the distribution of blue whiting larvae and the distribution of mackerel in this area is a key factor determining recruitment success (Payne et al. 2012). The hypothesis arises from the observation that mackerel distributions are typically restricted to close to the Continental Shelf edge: in years where the blue whiting distribution expands far to the west, beyond Rockall Plateau, the larvae spawned in these regions would be free from predation by mackerel. There is some empirical evidence to support this hypothesis: large year classes of blue whiting in the mid-late 1990s are associated with the collapse of the SPG and therefore an expanded spawning distribution. However, understanding the processes driving recruitment is notoriously tricky and much more work is required to resolve this issue: nevertheless, the model and the results developed here can be expected to make a valuable contribution to understanding the recruitment dynamics of this stock in the future.

A4.2 LIMITATIONS

The approach employed here to estimate the spatial distribution of blue whiting and the processes driving it has a number of limitations. In particular, our approach is limited by processes that are not included in the modelling approach, which can affect how the potential niche in environmental space is realized as a distribution in geographical space.

Firstly, it is unlikely that all factors determining the niche of blue whiting has been captured by this approach. Due to the complexity of nature, one can never find all factors that determine a species niche (Wiens et al. 2009), and even if one could, some relevant processes are difficult to observe and quantify, such as biotic interactions (i.e. competition and predation) or dispersal limitation (Elith and Leathwick 2009; Colwell and Rangel 2009). For example, our study cannot rule out that changes in the spawning distribution of blue whiting are caused by secondary processes resulting from changes in the marine environment that we have not characterised in our model, such as variations in the phyto- and zooplankton composition and abundance and thus in the food conditions for blue whiting (Payne et al., 2012; Hátún et al., 2009). Migration behaviour and other aspects of the life-history (such as the need to return to the feeding grounds) are also particularly problematic (although we have attempted to compensate for them in our model structure). These and other processes can prevent the species from being in full equilibrium with the current climate, thereby violating a critical assumption of SDMs (Araújo and Peterson 2012; Guisan and Zimmermann 2000).

Furthermore, larval-presences are assumed to be recorded within physiologically suitable (environmental) conditions: in practice however, larvae might have drifted away from their initial spawning location into regions beyond suitable environmental conditions for spawning. Nonetheless, it is possible that blue whiting (instinctively or consciously) chose a region to spawn, where eggs and larvae are likely to be retained in a suitable environment or conversely where they drift within suitable water masses, as already hypothesised by Bailey (1982).

Another requirement of SDMs is that the environmental variables have appropriate temporal and spatial scales. The rather coarse spatial and temporal resolution of the temperature and salinity data might have overestimated potentially suitable spawning areas (i.e. the realised niche) and thus inaccurately amplified the area of high larval-observation probability. An extension of this work would take into account multiple ocean analysis and reanalysis products, with the goal of assessing the relative importance of this source of uncertainty.

Observations of adult blue whiting during spawning from both scientific surveys and fisheries data, however, also struggle to characterize their spawning habitat properly. The species distribution model developed here is based on larval-observations, and is therefore a very direct proxy for spawning distribution. However, while data obtained from fisheries and scientific surveys provide a snapshot of the adult distribution, it is ambiguous whether observed individuals are spawning or migrating. The lack of distinction between these two processes creates uncertainty in the correct geographic representation of the spawning adults, and also explains the partial mismatch in places between the modelled suitable habitat (from CPR observations) and observations from scientific surveys/fisheries (e.g. Figure A 10). Nevertheless, the general agreement between the model and the adult observations is satisfying, and increases our confidence in the results.

A5 CONCLUSION

A5.1 OUTLOOK

In this study, the observed changes of the spawning distribution of blue whiting have been clearly linked to inter-annual variations in the marine environment. The North Atlantic subpolar gyre region is one of the most predictable marine regions worldwide (Matei et al. 2012; Meehl et al. 2014), and therefore opens the door to forecasting this distribution. In particular, the switch from one marine climatic regime to another could be a key starting point: modelling studies have shown the ability to retrospectively predict the mid-1990s contraction of the SPG (Wouters et al. 2013; Msadek et al. 2014), and the associated increase in the upper 500 m heat content up to five years in advance (Robson et al. 2017). Consequently, the onset of warmer and more saline conditions in the spawning region of blue whiting and an expanded spawning distribution of this species could potentially be predicted. The high predictive potential of the marine environment in the spawning region of blue whiting, coupled with the persistence of salinity at depth, might therefore enable us to forecast the extent of spawning distribution of blue whiting at timescales relevant for the monitoring and management of this stock.

A6 ACKNOWLEDGMENTS

We wish to thank Sophie Pitois (Cefas) and David Johns (SAHFOS) for providing the CPR data. Moreover we wish to thank Georg H. Engelhard (Cefas) and a second, anonymous, reviewer whose comments at the review stage greatly improved the manuscript. The order of authors is determined following the “First-last-author-emphasis” norm.

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A8 SUPPORTING INFORMATION

The geographical model was adapted to incorporate abundance as an ordered categorical variable by including the family argument “ocat” within the mgcv package including 7 categories in R (version 3.3.2; R Core Team, 2016). The first six categories corresponded to the abundance classes in which zooplankton and fish larvae are classified within the CPR data, consisting of larval abundances of : 0, 1, 2, 3, 4-11, 12-25 (Richardson et al. 2006), while all abundance classes containing more than 25 larvae were grouped into one abundance class, since these consisted of less than 5% of the entire presence data. A generalized additive model of the abundance categories of blue whiting larvae with ordered categorical (ocat) family was set up (dev.expl. = 45.9 %) applying the same model formulation as STI 1 (Table A 2).

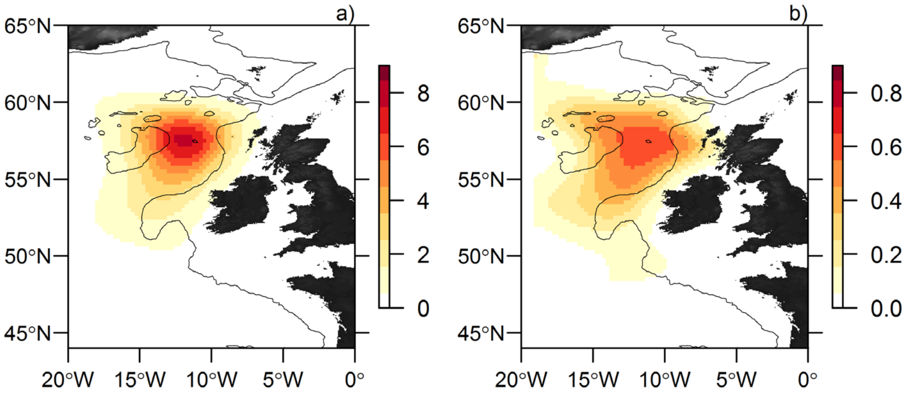


Figure A S1. Map of the overall expected abundance [number] a) and presence probability b) of blue whiting larvae in April as modelled by STI 1 (Table A 2). The expected abundance is the product of the predicted probability and the accepted value in each pixel summed up for each abundance class (Richardson et al. 2006).

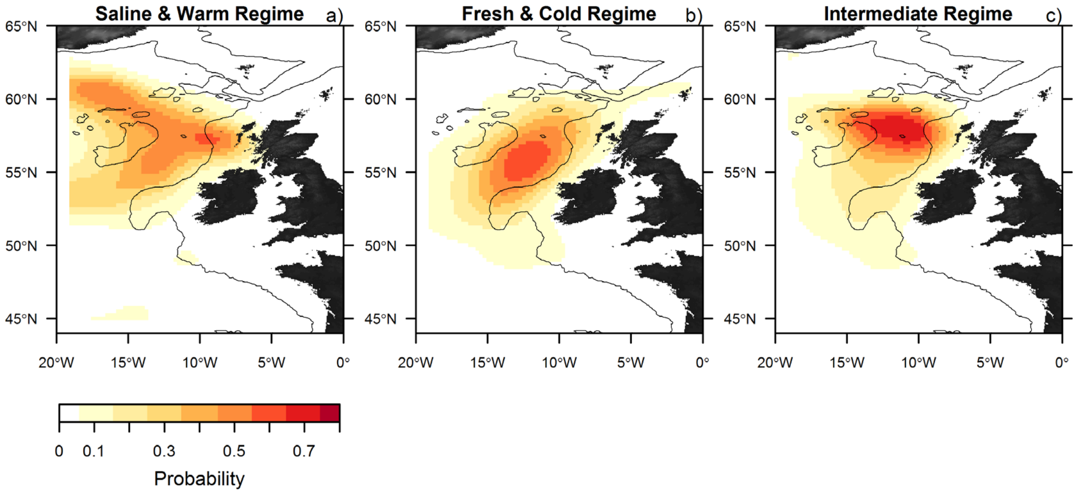


Figure A S2. Map of predicted larval-presence probabilities as a proxy for blue whiting spawning distributions produced by the SDM during a) the more saline and warmer and b) and fresher and colder and the intermediate c) regime in April (1951-2016). The black lines indicate the 700 m isobaths.

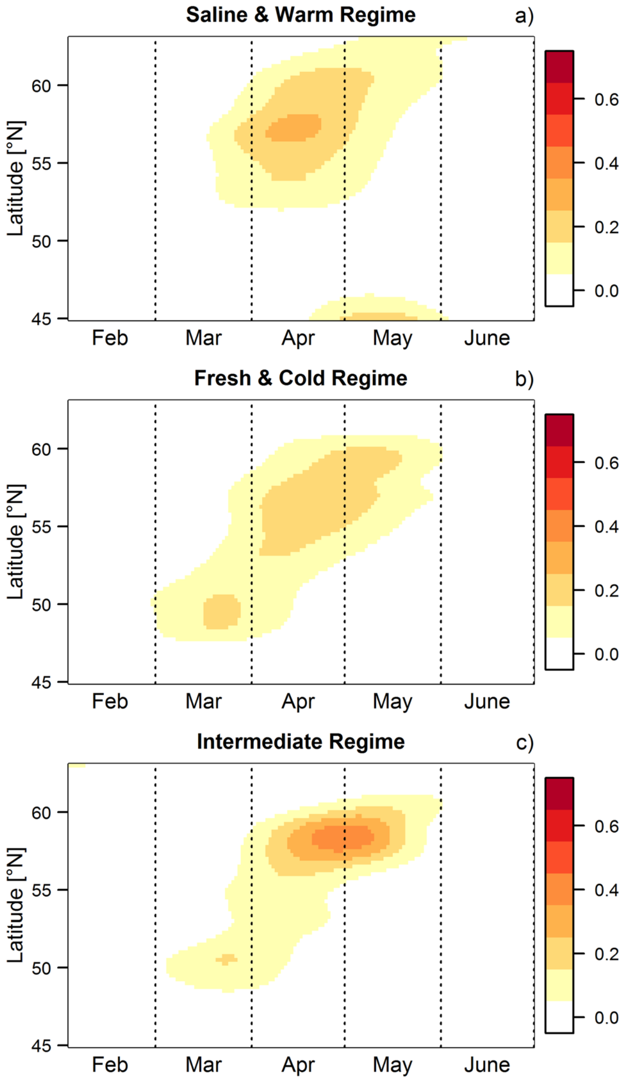
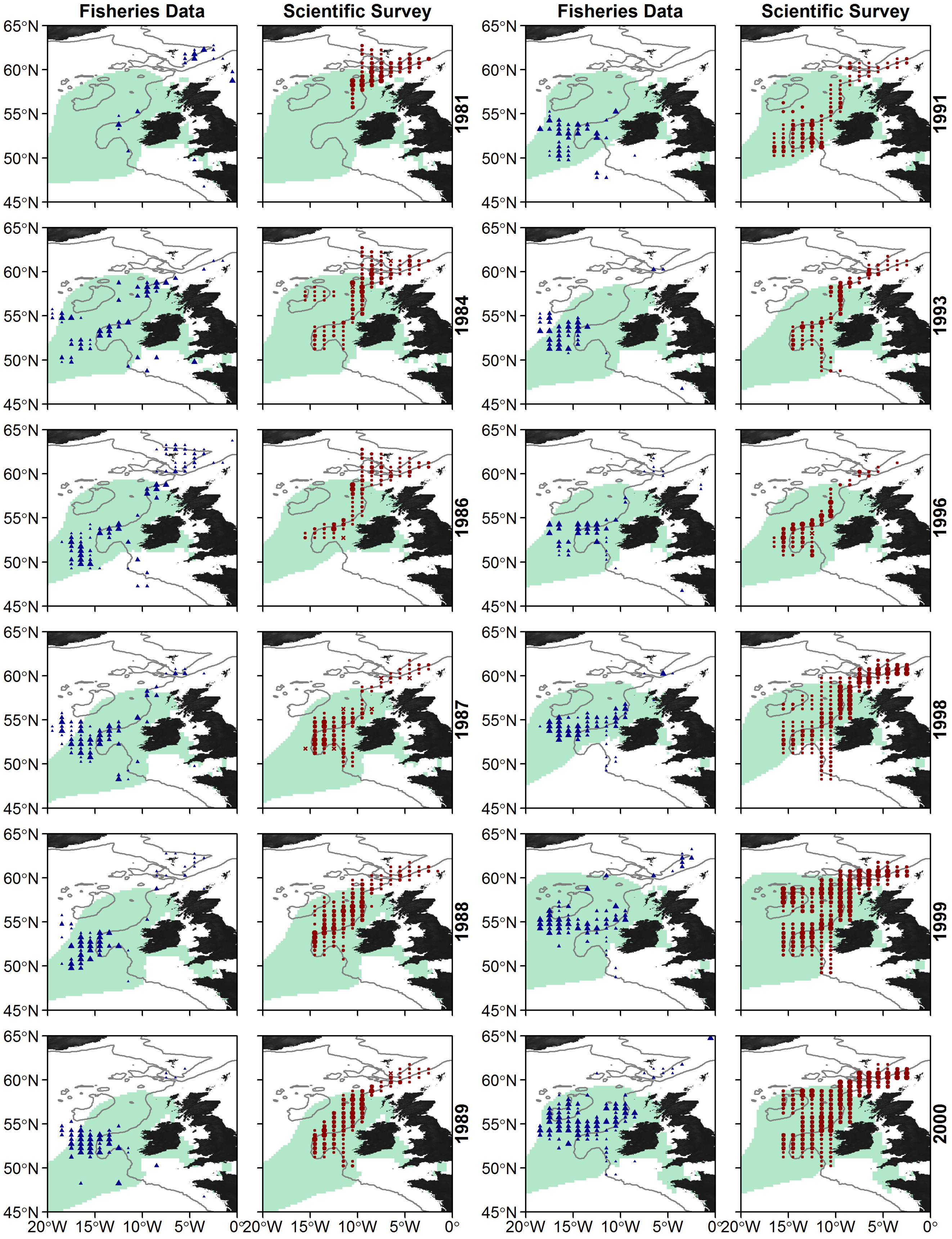


Figure A S3. Latitude-Time plot of larval-observation probability during the saline and warm a), fresh and cold b) and intermediate regime c) of the space-time interpolation (STI2, Table A 2).

On the following pages:

Figure A S4. Annual distribution of blue whiting observed by the North East Atlantic Fisheries Commission (blue triangles) and the International Blue Whiting Spawning Stock Survey (red circles). The size of the symbol increases with the amount of blue whiting caught/observed. The black lines indicate the 700 m isobaths. The green area indicates the window of optimum salinity for spawning of blue whiting ($35.3 < S < 35.0$), averaged over blue whiting's spawning depth (250 to 600 m) for March.

Catch [t]	Biomass [1000 t]
× 0	× 0
▲ 0 < x ≤ 100	● 0 < x ≤ 2000
▲ >100	● >2000
▲ >600	● >6000
▲ >1700	● >17000


Fisheries Data
Scientific Survey
Fisheries Data
Scientific Survey
65°N
60°N
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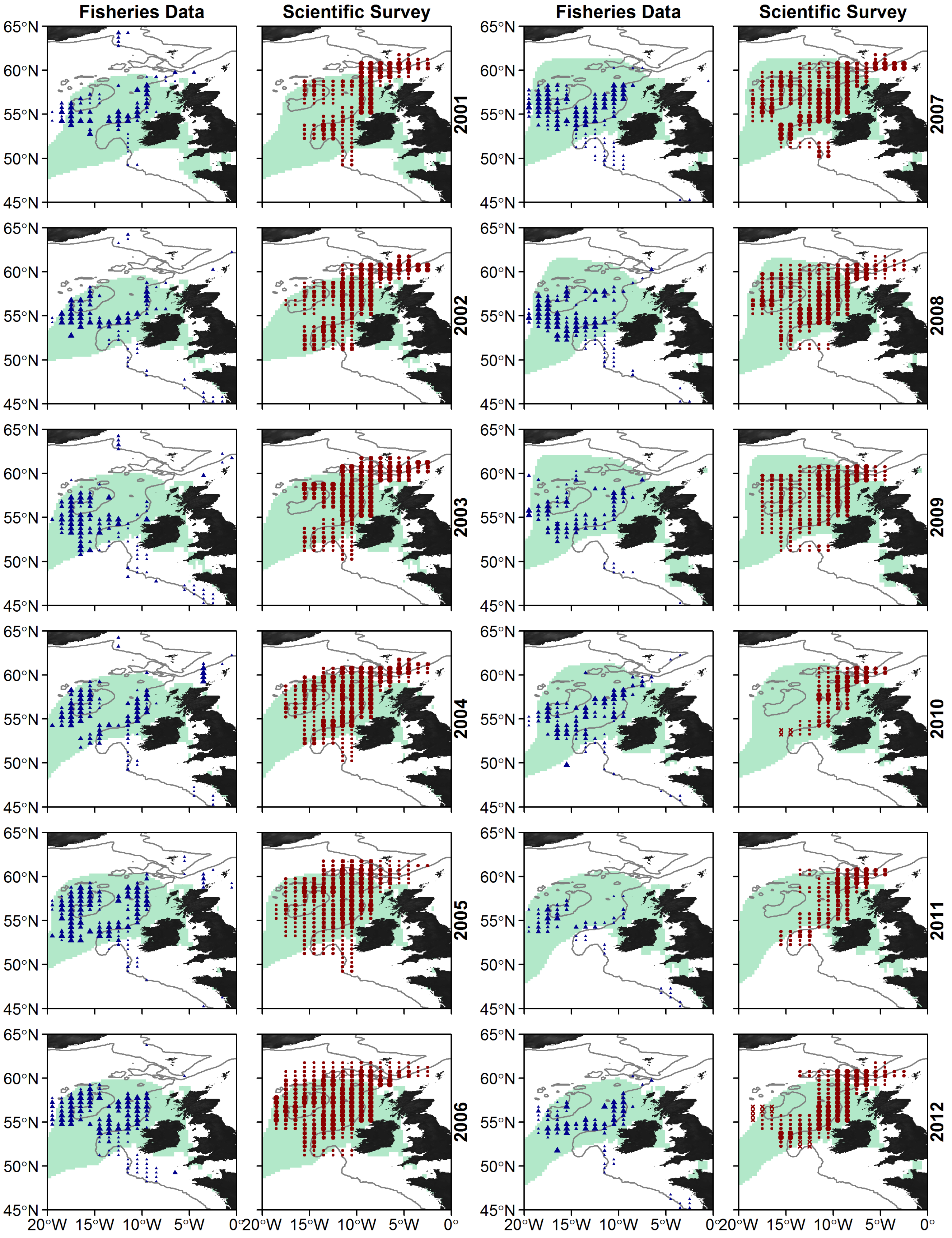
Fisheries Data
Scientific Survey
Fisheries Data
Scientific Survey
2001
2002
2003
2004
2005
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2007
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2009
2010
2011
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65°N
60°N
55°N
50°N
45°N
20°W
15°W
10°W
5°W
0°

Appendix B

EXPLORING THE POTENTIAL OF FORECASTING FISH DISTRIBUTIONS IN THE NORTH EAST ATLANTIC WITH A DYNAMIC EARTH SYSTEM MODEL, EXEMPLIFIED BY THE SUITABLE SPAWNING HABITAT OF BLUE WHITING

This appendix contains a manuscript, which is under review for publication in *Frontiers in Marine Science*:

Miesner, A.K., Brune, S., Pieper, P., Koul, V., Baehr, J., and Schrum, C. (*under review*) Exploring the potential of forecasting fish distributions in the North East Atlantic with a dynamic Earth System Model, exemplified by the suitable spawning habitat of blue whiting. Frontiers in Marine Science

The contribution of Anna Miesner (A.M.) and others to this paper is as follows: A.M. conceived the work, performed the analysis and wrote the manuscript. S.B. created the MPI-ESM hindcast and assimilation experiments. A.M., S.B., V.K. and P.P. discussed the results. C.S. and J.B. provided guidance on the overall direction of the work. All authors reviewed the manuscript.

Exploring the potential of forecasting fish distributions in the North East Atlantic with a dynamic Earth System Model, exemplified by the suitable spawning habitat of blue whiting

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(Submitted on 15 September 2021)

ABSTRACT

The spawning distribution of blue whiting (*Micromesistius poutassou*) is greatly influenced by local oceanographic variability. Here, we explore the potential of using a dynamic Earth System Model (ESM) to forecast the suitable spawning habitat of blue whiting to assist management.
First, we use a decadal prediction system based on the Max Planck Institute ESM (MPI-ESM) to produce retrospective forecasts (i.e. hindcasts) of the marine climate in blue whiting's spawning region for lead times up to five years. We assess the quality of the MPI-ESM-hindcast ensemble by comparing it against two reference products: the EN4 objective analysis and the corresponding MPI-ESM assimilation experiment. We find that temperature and particularly salinity can be predicted with significant skill within blue whiting's spawning region and spawning depth (250 - 600 m) during the peak months of spawning. While persistence forecasts perform well at shorter lead times (≤2 years), MPI-ESM-hindcast is clearly more skilful than persistence in forecasting salinity at longer lead times.

Subsequently, we create retrospective forecasts of the suitable spawning habitat of blue whiting. We compare two ways to define the suitable spawning habitat, one where species distribution models are directly applied, and another one based on the previously defined suitable salinity for spawning, with the latter showing better agreement with observations from scientific surveys and fisheries. A promising result is the high predictive skill for both the marine climate and the suitable spawning habitat around one year ahead in the area of Rockall-Hatton Plateau.
A clear advantage of MPI-ESM is its better ability to differentiate between the presence and absence of suitable habitat over Rockall Plateau, compared to EN4. The success of MPI-ESM over Rockall Plateau relates to the dynamic consistency of the ESM and its ability to account for hydrodynamic steering,~~,~~ which highlights the value of applying an ESM for creating coupled

physical-biological forecasts. Moreover, MPI-ESM's skill in predicting temperature and particularly salinity beholds the auspicious prospect of anticipating shifts in the distribution of marine organisms in the North East Atlantic. Our results highlight, that ESMs are crucial for developing distributional forecasts of marine organisms in the North East Atlantic.

B1 INTRODUCTION

Current advances of dynamic Earth System Models (ESMs) have permitted skilful predictions of the marine climate (i.e. temperature and salinity) on seasonal to decadal timescales and thereby sparked the development of marine ecological forecast products (Payne et al. 2017; Tommasi, Stock, Hobday, et al. 2017). When a link between the marine climate and marine organisms is identified, forecasts of the marine climate can be converted into biological forecasts of productivity, phenology or distribution and thereby enhance climate resilience of marine resource management (Payne et al. 2017; Tommasi, Stock, Hobday, et al. 2017) and enable “dynamic ocean management” (Hobday et al. 2016a). Until now, the majority of operational examples are distributional forecasts of marine organisms, mostly fish, which are provided at near-real-time to seasonal timescales (Malick et al. 2020; Kaplan et al. 2016; Siedlecki et al. 2016; Hobday et al. 2011; Eveson et al. 2015; Lehodey et al. 2018). This is far below the predictive potential of the ocean where skilful predictions are possible several years and even a decade in advance, as shown in particular for the North Atlantic (Shaffrey et al. 2017; Matei et al. 2012; Tommasi, Stock, Pegion, et al. 2017; Yeager and Robson 2017). Accordingly, the North Atlantic is promising for exploring the predictive potential of coupled physical-biological forecasts beyond seasonal time scales. An economically important North East Atlantic fish species with an established link between the marine climate and its spawning distribution is blue whiting (*Micromesistius poutassou*; Hátún, Payne and Jacobsen, 2009; Miesner and Payne, 2018). Therefore, this species serves as an ideal case study to explore the potential of forecasting distributional changes at inter-annual to multi-annual time scales with a dynamic ESM.

Blue whiting is a migratory fish species that is distributed meso-pelagically from the Strait of Gibraltar to off-shore Greenland (Post, Fock, and Jansen 2019) and the Barents Sea (ICES 2019; Heino, Engelhard, and Godø 2008). Most fishing takes place during spring in an area west of the British Isles where blue whiting aggregate to spawn (NEAFC 2013). While spawning commonly takes place in the deep waters along the European Continental Shelf, in some years changes in the marine climate trigger a westward expansion of the spawning distribution onto Rockall Plateau and Hatton Bank (Figure B 1c; Hátún, Payne and Jacobsen, 2009; Miesner and Payne, 2018). This area of Rockall-Hatton Plateau (RHP) straddles both international and national waters (with disputed economic boundaries; Yiallourides, 2018; Johnson et al., 2019) and forecasting changes in the spawning distribution at inter-annual to multi-annual time scales could therefore be beneficial for a range of stakeholders and nations.

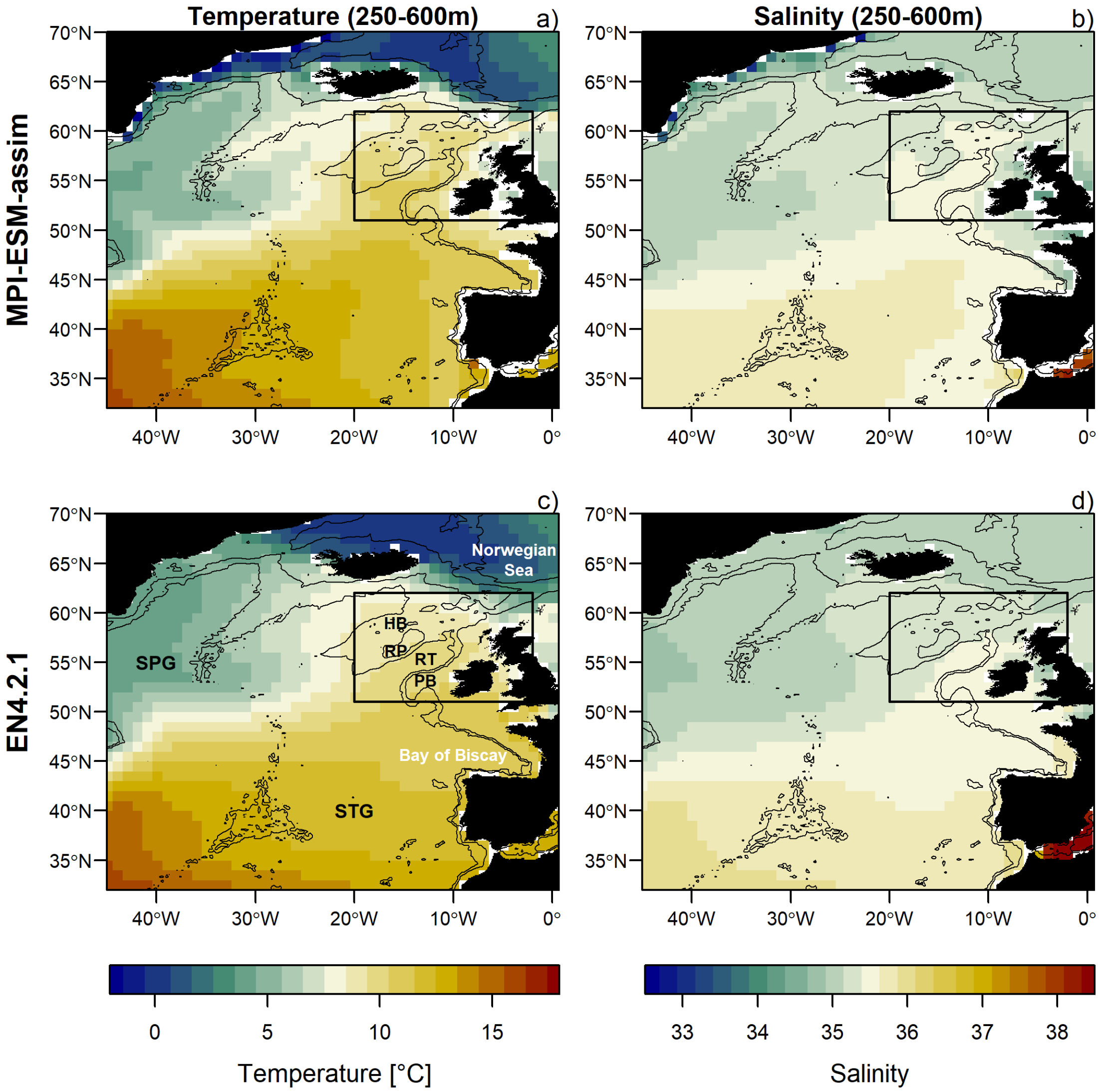

Figure B 1. Mean oceanographic conditions in FMA (climatology of 1965-2016) within the spawning depth of blue whiting (250-600m) in terms of temperature (left; a,c) and salinity (right, b,d) for *MPI-ESM-assim* (top; a,b) and *EN4* (bottom; c,d). The black rectangle delineates the study area: the spawning region of blue whiting. Labels in c) show the geographic features Hatton Blank (HB), Rockall Plateau (RP), Rockall Trough (RT), Porcupine Bank (PB) and the two dominant gyre systems North Atlantic subpolar gyre (SPG) and the subtropical gyre (STG). Bathymetry is indicated by 600 and 2000 m isobaths.

The oceanographic conditions in the spawning region of blue whiting are characterized by a mixture of subtropical (saline) Eastern North Atlantic Water coming from the south and subpolar (fresh) Western North Atlantic Waters from the north (Hátún et al. 2009; Holliday et al. 2000). The relative mixture of these water masses is related to changes in the North Atlantic Subpolar

Gyre (SPG) and creates a distinct marine climatic regime to which blue whiting respond through changes in their spatial distribution (Miesner and Payne 2018; Hátún, Payne, and Jacobsen 2009). Generally, a strong SPG leads to fresher and cooler conditions in the spawning region, causing blue whiting to cluster along the continental shelf (Hátún, Payne, and Jacobsen 2009). A weak SPG promotes more saline and warm subtropical water masses which leads to a westward expansion of the spawning distribution onto Rockall Plateau and Hatton Bank (Figure B 1; Hátún, Payne and Jacobsen, 2009; Miesner and Payne, 2018). A modelling study based on blue whiting larvae found that spawning is confined to a certain range of salinity and proposed that this link could form the basis of forecasting changes in the spawning distribution of blue whiting (Miesner and Payne 2018).

Forecasting spatial changes of the spawning distribution could also be useful for the monitoring and management of blue whiting. Every spring the International Blue Whiting Spawning Stock (IBWSS) survey samples the core spawning region of blue whiting (ICES 2015a). In particular, sampling on RHP is challenging, both because of the great distance to the ports and because of frequent bad weather conditions which have resulted in insufficient survey coverage on RHP in some years (e.g. 2010) which can lead to an underestimation of the stock's biomass (ICES 2010a). Forecasting blue whiting in its spawning region with a special focus on RHP (e.g. whether spawning is going to take place on RHP) could be valuable for the IBWSS planning group (pers. communication with Jan Arge Jacobsen, member of the ICES Working Group of International Pelagic Surveys, Faroe Marine Research Institute). Accordingly, a forecast at interannual to multiannual timescales could be used as an objective decision-making tool to adjust the IBWSS survey coverage on RHP.

Forecasting the spatial distribution of marine organisms is related to the theory of the ecological niche or suitable habitat of a species (Payne et al. 2017). Previous work established the mechanistic link between the marine climate (i.e. salinity) and the spawning distribution of blue whiting based on species distribution modelling (Miesner and Payne 2018). Species distribution models (SDMs) are also termed ecological niche models or habitat models, and represent a common method to define the suitable (i.e. potential) habitat of a species by means of correlative models that link species distribution data with environmental observations (Wiens et al. 2009; Elith and Leathwick 2009). However, the definition of the suitable habitat is not straightforward, since the distribution of a species not only depends on abiotic factors, like temperature or salinity but also on a variety of biotic interactions (e.g. predation and feeding conditions), which are not accounted for in correlative SDMs (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Colwell and Rangel 2009). Despite such limitations, the suitable habitat of a species is commonly used as a proxy for its spatial distribution and applied in marine ecological forecasts such as for the spatial management of southern bluefin tuna in Australian waters (Hobday and Hartmann

2006; Eveson et al. 2015) or Pacific sardine in Californian waters (Kaplan et al. 2016; Siedlecki et al. 2016).

Based the previously developed SDM (Miesner and Payne 2018) and persistence of salinity, first attempts to operationalize a forecast of the suitable spawning habitat of blue have been undertaken (Payne and Lehodey 2019; ICES 2018) and are currently provided two months prior to the IBWSS survey (Payne 2021). In persistence forecasts, future conditions are expected to be the same as past conditions, which might be an appropriate assumption when variability is low and for short-term forecasts based on near-real-time observations (e.g. Hobday et al. 2018). However, due to the highly variable nature of the marine environment, the management of living marine resources, such as fish, challenges the stationary assumption (Tommasi, Stock, Hobday, et al. 2017). Accordingly, we explore the potential for developing a forecast of the suitable spawning habitat of blue whiting based on a dynamic, coupled ocean-atmosphere model on annual to multi-annual time scales, namely the Max Planck Institute ESM (MPI-ESM; Giorgetta et al. 2013), which could be valuable for both augmenting monitoring surveys and enhancing long-term management of the species.

In the first part of the study, we assess whether the marine climate, i.e. temperature and salinity, is predictable within the region and depth at which blue whiting spawn during the months of spawning. We judge the quality of the MPI-ESM hindcast by comparing it to two reference data sets: the EN4 objective analysis (Good, Martin, and Rayner 2013) and the MPI-ESM ensemble Kalman filter assimilation (Brune and Baehr 2020; Polkova et al. 2019). In the second part of the study, we analyse two ways to extract information on the suitable spawning habitat from SDMs and explore the potential of forecasting the suitable spawning habitat of blue whiting up to five years ahead.

B2 MATERIALS AND METHODS

B2.1 MODELLING AND ANALYSIS STRATEGY

Specifically, we analyse the skill of 5-year predictions of the marine climate and subsequently of the suitable spawning habitat of blue whiting. These are based on decadal retrospective forecasts, in the following called hindcasts, of the dynamical state of the ocean with MPI-ESM (Polkova et al. 2019; Brune and Baehr 2020). While a hindcast predicts the possibly observed state at a certain time in the past, only including information available prior to the respective time (e.g. Jolliffe and Stephenson 2012), a true forecast predicts the yet unobserved future state. Consequently, we assess forecast quality by quantifying hindcast skill.

In the first part of the study, we analyse whether we can make skilful predictions of the marine climate with the MPI-ESM hindcast at spatial and temporal scales relevant for spawning blue whiting. We assess the quality of the hindcast by comparison to two reference data sets: the EN4 objective analysis (Good, Martin, and Rayner 2013) and the MPI-ESM ensemble Kalman filter assimilation (Brune and Baehr 2020; Polkova et al. 2019), hereafter referred to as *EN4* and *MPI-ESM-assim*, respectively. The EN4 data set provides an invaluable collection of quality controlled ocean temperature and salinity profiles (Good, Martin, and Rayner 2013). However, observations of temperature and salinity in the ocean are sparse, especially at depth, and before Argo sampling was initiated in 2000 (Good, Martin, and Rayner 2013; Tesdal et al. 2018). The spatially complete *EN4* objective analysis provides *one* way of filling the gaps between observed oceanic profiles using iterative optimal interpolation (Good, Martin, and Rayner 2013). Another approach is used by *MPI-ESM-assim,* where EN4 profiles are incorporated into the ocean model component of a dynamic ESM. The predictive skill of the hindcast is assessed retrospectively by comparison to reference forecasts based on *EN4* and *MPI-ESM-assim* persistence.

In the second part of the study, we explore two ways to extract information on the suitable spawning habitat from SDMs. While we create novel SDMs based on either *MPI-ESM-assim* or *EN4* in the first approach, the second method employs the salinity defined as suitable for spawning by Miesner and Payne (2018) to delineate the suitable spawning habitat. The approach that is superior in representing the observed spawning distribution of blue whiting is subsequently employed for the creation of coupled physical-biological forecasts. Here, the suitable spawning habitat of blue whiting is forecasted retrospectively based on the MPI-ESM hindcast and two persistence forecast and their predictive skill is judged against fishery and survey observation.

B2.2 STUDY REGION AND TIME PERIOD OF INTEREST

The study region covers the core spawning area of blue whiting west of the British Isles which is sampled annually by the ICES IBWSS survey (ICES 2015a): 20°W to 2°W and 51°N to 62°N (black rectangle in Figure B 1) and will henceforth be referred to as spawning region. We RHP by the local bathymetry, following the 1000 m depth isobath around Rockall Plateau, George Bligh Bank and Hatton Bank finishing west at the border of the IBWSS sampling region.

The majority of spawning blue whiting are observed between 300 and 600 m depth (ICES 2019). The eggs are spawned at depth and upon hatching, larvae gradually ascend to the surface with the greatest concentration of eggs and non-feeding larvae observed between 250 and 600 m (Coombs, Pipe, and Mitchell 1981), 300 - 400 m (Hillgruber and Kloppmann 1999) and 300 to 600 m (Ådlandsvik et al. 2001). To encompass the depth range where eggs, non-feeding larvae and spawning adults have been observed, we define the spawning depth of blue whiting between 250 and 600 m.

The main spawning activity of blue whiting takes place during late March and early April which corresponds to the timing of the IBWSS survey (ICES 2015a; Bailey 1982). Since blue whiting larvae are observed in the surface waters mainly between March and May with a peak in April (Miesner and Payne 2018; Pointin and Payne 2014) and need around 3 weeks for the ascent to the surface (Ådlandsvik et al. 2001), it is likely that spawning ranges from February to April. Accordingly, the average temperate and salinity between February and April (FMA) at 250 to 600 m depth within the spawning region of blue whiting resembles the oceanographic conditions, i.e. the marine climate, experienced by the spawning adults and the larvae.

B2.3 OBSERVATIONS AND RETROSPECTIVE FORECASTS OF TEMPERATURE AND SALINITY

B.2.3.1 Observations of Temperature and Salinity

Monthly observations of ocean temperature and salinity are available from the Met Office Hadley Centre's EN4 data set (Good, Martin, and Rayner 2013). Besides quality controlled in situ profiles, hereafter termed EN4 profiles, a spatially comprehensive objective analysis is available which uses an iterative optimal interpolation to fill all observational gaps. We use the EN4 objective analysis version 4.2.1 with corrections based on Gouretski and Reseghetti (2010), which is available from 1900 to the present and contains 42 vertical levels and a regular 1° horizontal resolution (Good, Martin, and Rayner 2013) and will be referred to as *EN4*. Since *EN4* relaxes to climatology in the absence of observations, Good et al. (2013) suggest that reanalysis products based on numerical models might be superior during periods of low observational coverage. We select the time period 1958 to 2016 and average yearly FMA-mean values of temperature and salinity vertically over 252 - 596 m to characterize the marine climate in the spawning region and depth of blue whiting.

B.2.3.2 Assimilation and Dynamical Hindcasts of Temperature and Salinity

Another way of creating a spatially complete data set that serves as a good estimate of the true state of the ocean, is to incorporate (i.e. assimilate) oceanic observations into a coupled ocean-atmosphere model. We use an experiment from the Max Planck Institute ESM at low resolution (MPI-ESM; Giorgetta et al. 2013). Its ocean component (Jungclaus et al. 2013) contains 40 levels and has a horizontal resolution of 1.5° near the equator which gradually increases towards the grid poles over Antarctica and Greenland, with an effective resolution of around 0.6° - 0.9° within the spawning region. Monthly observations of oceanic temperature and salinity from EN4 profiles (Good, Martin, and Rayner 2013) are assimilated into MPI-ESM using a full-value 16-member ensemble Kalman filter (EnKF) approach (Brune and Baehr 2020; Polkova et al. 2019). Additionally, the dynamical state of the atmospheric component is nudged toward ERA40/ERAInterim reanalyses from ECMWF (Dee et al. 2011; Uppala et al. 2005), and the model is forced by external boundary conditions, which influence the Earth's radiative budget, such as solar irradiance, greenhouse gas concentration or volcanic aerosols. Here, external forcings of the Phase 5 Coupled Model Intercomparison Project (CMIP5) were applied (Taylor, Stouffer, and Meehl 2012).We run MPI-ESM with these settings from 1958 to 2016 and simulate an assimilation which will henceforth be referred to as *MPI-ESM-assim*. Thereby, *MPI-ESM-assim* dynamically interpolates the incomplete observed state of the ocean to a structured grid with well-defined resolution (Brune and Baehr 2020). Even though the primary goal of *MPI-ESM-assim* is to initialize predictions of the future oceanic climate in a model-consistent way (Brune and Baehr 2020), it represents another qualified way to represent observational fields of temperature and salinity.

Based on *MPI-ESM-assim*, a 16-member hindcast ensemble is created (Brune and Baehr 2020), which will be referred to as *MPI-ESM-hindcast*. *MPI-ESM-hindcast* is initialized every year from the 1st of November 1960 to 2016. In this study, each initialization is running for 5 years. The time counting from the initialisation date of the hindcast is termed lead time. Accordingly, if the initialisation date is November 1960 and the hindcast is for March (or FMA) 1961, the (mean) lead time is 4 months and within lead year 1, while a hindcast for March (or FMA) 1962 has a lead time of (around) 1 year and 4 months, or within lead year 2.

We regrid both *MPI-ESM-assim* and *MPI-ESM-hindcast* to a 1° × 1° regular grid and create the average of the 16 ensemble members (i.e. the ensemble mean) which we analyse throughout the study. For *MPI-ESM-assim* and *MPI-ESM-hindcast* we average annual FMA-mean values of temperature and salinity vertically between 240 - 600 m to derive the environmental conditions within the spawning depth of blue whiting.

B2.3.3 Persistence Forecast

Persistence forecasts are a common reference in seasonal to decadal forecasting used to judge the skill of a hindcast: hindcasts which outperform persistence exemplify the benefit of using a dynamic ESM (Jolliffe and Stephenson 2012; Wilks 2011). Persistence forecasts presume that future conditions are equal to past conditions, e.g. a persistence forecast of FMA in 1965 with a lead time of two years, uses observations of FMA in 1963 as a forecast by assuming stationarity for the duration of the forecast (i.e. 2 years). We create persistence forecasts for *EN4* and *MPI-ESM-assim* for five lead years, termed *EN4-persist* and *MPI-ESM-persist*, respectively.

B2.3.4 Predictability of Temperature and Salinity within the Spawning Region of Blue Whiting

The performance of any prediction system is judged retrospectively based on the given observational data set. Here, we compare retrospective forecasts (i.e. *MPI-ESM-hindcast*, *MPI-ESM-persist* and *EN4-persist*) to *MPI-ESM-assim* and *EN4*, by means of the anomaly correlation coefficient (ACC) and the root-mean squared error (RMSE) which are common measures of forecast accuracy (Jolliffe and Stephenson 2012; Wilks 2011). While the ACC measures the correspondence between forecast and observation and is positively oriented, with higher values indicating a more accurate forecast the RMSE measures their difference and is negatively oriented (Jolliffe and Stephenson 2012; Wilks 2011). We calculate anomalies based on the mean temperature and salinity of the common time period (1965 – 2016; e.g. FMA 1965 minus mean FMA from 1965 to 2016). In order to remove the influence of long-term trends, such as global warming, on the predictive skill, we detrend anomalies before assessing their predictive skill.

To account for the uncertainty in predictive skill, we perform a bootstrap with 500 iterations of ACC and RMSE for the common time period (the years 1965 to 2016 are shuffled 500 times with replacement and the ACC/RMSE calculated for each lead year). Significance of the ACC is defined from the 95% confidence interval of the bootstrap. Throughout the study, we show the median ACC and RMSE.

To analyse predictive skill over lead time the detrended anomalies are averaged over the study region and ACC and RMSE calculated. For this, the mean bias between forecast and observation is calculated and subtracted from the forecast for each year before RMSE and ACC are calculated from the respective time series. The confidence interval calculated from the bootstrap is defined as the interquartile range between the lower quartile (25th percentile) and the upper quartile (75th percentile) of the bootstrapped data. For the spatial representation of predictive skill, ACC and RMSE are calculated for each grid point where water depth exceeds 600 m. Water depth is based on NOAAs ETOPO1 product (Amante and Eakins 2009).

Since the ACC is dependent on the gridded estimate of climatology (Jolliffe and Stephenson 2012) also shorter time periods (1965-1990 & 1991-2016) were initially considered. However, the main conclusions from the analysis are insensitive to changes in the climatological time period.

B2.4 FORECASTING THE SUITABLE SPAWNING HABITAT OF BLUE WHITING RETROSPECTIVELY

B2.4.1 Retrospective Forecasts of the Suitable Spawning Habitat based on SDMs

We create novel SDMs with observations of blue whiting larvae from the Continuous Plankton Recorder (CPR) survey (Reid et al. 2003) obtained from the Marine Biological Association in Plymouth. The probability of observing blue whiting larvae is modelled as a function of a fixed geographical model component, including latitude and the day-of-the-year, bathymetry, the solar elevation angle and varying environmental variables (Table B S1) using Generalized Additive Models (Wood 2006) analogous to Miesner and Payne (2018). Thus, the SDM accounts for the meridional migration of adults (Bailey 1982) and the diel vertical migration of larvae (Hillgruber and Kloppmann 2000) which can affect the capture efficiency of the CPR (Pointin and Payne 2014). CPR observations on land are considered erroneous and hence removed prior to analysis.

We create two sets of SDMs: one calibrated with environmental data from *EN4* and another one calibrated with *MPI-ESM-assim*, in order to account for the difference in these products in handling the spatially incomplete EN4 profiles. We calculate the salinity and temperature at the spawning depth of blue whiting during the time of spawning (S_{SPAWN} and T_{SPAWN}), i.e. one month prior to a CPR observation (Miesner and Payne 2018), by averaging vertically over 252 - 596 m for EN4 and 240 - 600 m for MPI-ESM, since the depth layers slightly vary between the two. At locations where water depth is shallower than 252 m for *EN4* or shallower than 240 m for MPI-ESM, we select variables closest to the seafloor. In order for the SDMs to be comparable, we couple the same CPR observations to *EN4* and *MPI-ESM-assim*, containing 48 years from 1958 to 2005 including 68 229 observations with 938 presences of blue whiting larvae. The resulting spatial distribution of larval-presence probability can be understood as a proxy for the suitable spawning habitat of blue whiting (Miesner and Payne 2018).

Validation of the SDM and model selection is in line with Miesner and Payne (2018). As a primary metric for model selection, we choose the Akaike Information Criteria (AIC). It measures the trade-off between model complexity and model fit, with the smallest AIC indicating the "best" (i.e. most parsimonious) model within the set (Burnham, Anderson, and Huyvaert 2011; Anderson 2008). The explained deviance is equivalent to the coefficient of determination (R^2) and considered an overall indicator of model quality.

We derive the capability of the models to distinguish between the presence and absence of larvae from a contingency table (Table B 1). We convert the predicted probability of blue whiting larval-occurrence from the SDM into presences and absences by selecting the threshold so that the total number of presences in the prediction data set is equal to the number of presences in the observed dataset, in accordance with Freeman and Moisen (2008). Moreover, we calculate mean values of the true skill statistic (TSS), positive predictive value (PPV) and negative predictive value (NPV) based on 4-fold cross validation with 75% of the data used for training and the remaining for validation, with every 4th year included in one fold. The TSS, also called Peirce Skill Score (Peirce 1884), measures the average net prediction success for presences and absences (Liu, White, and Newell 2011; Jolliffe and Stephenson 2012). The probability that a site where the presence is predicted is indeed a site of presence is summarized by the PPV, while the probability that a site where no presences are predicted is actually an absence by the NPV (Table B2). Additionally, we consider the area under the receiver operating characteristic curve (AUC), which relates the relative proportions of correctly and incorrectly classified predictions (HR and FAR, respectively) over a range of threshold levels (Liu, White, and Newell 2011; Brown and Davis 2006).

We base the choice of the best performing SDM on two steps. First we create a subset for each of the two SDM sets (one calibrated with *EN4* and the other with *MPI-ESM-assim*) with all models having AIC differences smaller than 15 (Table B S1), since models with an AIC difference larger than 15 are considered to be very dissimilar (Anderson 2008). From these subsets, we select the SDM with the highest predictive performance in terms of TSS, PPV, NPV and AUC as the "best" performing model and analyse it further.

Table B 1. Contingency table used to evaluate the predictive accuracy of binary events. The numbers of observations and predictions in each category are represented by TP, FP, FA and TA.
TP (true positives): correctly predicted presences, hits; FP (false positives): erroneously predicted presences, false alarms; FA (false absences): erroneously predicted absences, misses; TA (true absences): correctly predicted absences.

		Observation	
		Presence	**Absence**
Prediction	**Presence**	TP (hits)	FP (false alarms)
	Absence	FA (misses)	TA (correct negatives)

Table B 2. Verification Scores. The perfect result of the score is underlined. TP, FP, FN and TN are entries in the contingency table (Table B 1)

Name Quality Measure (Abbreviation)	**Definition**	**Range**
Positive Predictive Value (PPV)	TP/(TP+FP)	[0, 1]
Negative Predictive Value (NPV)	TA/(TA+FA)	[0, 1]
Hit Rate (HR)	TP/(TP+FA)	[0, 1]
False Alarm Rate (FAR)	FP/(FP+TA)	[0, 1]
True Skill Statistic (TSS)	HR - FAR	[-1, 1]

We create retrospective forecasts of the suitable spawning habitat by coupling the best performing SDMs (Table B 3) to retrospective forecast of the marine climate for up to five lead years. Specifically, we employ the best performing SDM calibrated with *MPI-ESM-assim* for retrospective forecasts based on *MPI-ESM-hindcast* and *MPI-ESM-persist*. While we use the best performing SDM fitted to *EN4* for retrospective forecasts based on *EN4-persist*. Within the SDM, we select the 15th of each month as the day-of-year owing to the monthly resolution of environmental data and fix the solar elevation angle to 0°, representative of sunrise or sunset, in line with Miesner & Payne (2018). SDMs are calibrated with full-value temperature and salinity data from *MPI-ESM-assim* and *EN4*, respectively, and transform this information into blue whiting larval presence probability. Therefore forecasts based on SDMs can be directly compared and there is no need for bias correction.

B2.4.2 Retrospective Forecasts of the Suitable Spawning Habitat based on Salinity

As an alternative approach to creating new SDMs, solely the suitable salinity for spawning is used as a proxy for the suitable spawning habitat. A previous study based on SDMs, observations from the CPR and an earlier version of the EN4 objective analysis (EN4.1.1) showed a dome-shaped relationship between salinity (S_{SPAWN}) and the probability of observing blue whiting larvae with a non-zero likelihood of observing larvae at salinities between 35.28 - 35.53 (Miesner and Payne, 2018: SDM 3, Table 4, Figure A 9). This suitable salinity for spawning corresponded well to independent observations from both fishery and scientific surveys (Miesner and Payne 2018) and is in line with the re-calibrated SDM based on *EN4* that is applied in this study (SDM_S_{EN4}).

The suitable salinity for spawning in MPI-ESM is bias-corrected to offset the mean deviations between *MPI-ESM-assim* and *EN4* within the spawning region and during the time period for which validation data is available (0.06 for 1977-2012). Retrospective forecasts of the suitable salinity for spawning are based on full-value retrospective forecasts of salinity with *MPI-ESM-hindcast*, *MPI-ESM-persist* and *EN4-persist*. The respective isohaline where the salinity is defined suitable is used as a proxy for the suitable spawning habitat.

B2.4.3 Observations of Adult Blue Whiting

Observations of adult blue whiting during the peak months of spawning (March and April (ICES 2015a; Bailey 1982)) within the spawning region are used to analyse the agreement with the suitable spawning habitat definitions and to quantify the predictive skill of the retrospectively forecasted suitable spawning habitat. The first data set comprises of acoustic surveys of blue whiting spawning aggregations from 1981 to 2013, spanning 25 years due to incomplete time series. Before 2004 the observations were solely based on Norwegian surveys of the spawning stock, while data from 2004 onwards originate from the from the IBWSS survey that is carried out annually for two weeks from late March to early April (ICES 2016b). The survey records acoustic data continuously along its cruise tracks and provides estimates of blue whiting biomass. While most years had a resolution of 0.5° latitude x 1° longitude, the data resolution is coarser for the period 2002 - 2006 with 1° latitude x 2° longitude.

The second set of independent observations consists of monthly fishery catch statistics of blue whiting from 1977 to 2012 from the NEAFC (NEAFC, 2013) targeting spawning adults with a resolution of 0.5° latitude x 1° longitude. The fishery data is averaged over March and April, in congruence with the IBWSS survey data.

For both, the survey and the fishery data, the grid cells within the spawning region where blue whiting were observed or caught are treated as presence. All remaining cells are treated as absences, since absences of fish are hardly reported in catch statistics (e.g. for the months March and April only 0.1 % of the available fisheries data within the spawning region were absences) and are also low in the survey (0.9 % within the spawning region). Therefore, including the absence data would render the observations unfit for model- and forecast evaluation.

B2.4.4 Predictive Skill of the Suitable Spawning Habitat Forecast

Observations of adult blue whiting in March and April are compared to retrospective forecasts of blue whiting's suitable spawning habitat averaged over March and April and for each lead year (0-5) using binary verification metrics based on the contingency table (Table B 1). Accordingly, the output of the biological forecasts are brought to the same spatial grid as the observations (0.5° latitude x 1° longitude). Predicted presence-probabilities from the SDM are converted into presence and absence by selecting the threshold where predicted prevalence from the SDM is equal to observed prevalence (Freeman and Moisen 2008). For the forecast based on the suitable salinity for spawning, each grid cell within the range of the suitable salinity for spawning is defined as presence (of suitable habitat) and the remaining as absence.

We quantify predictability via TSS, the difference between Hit Rate and False Alarm Rate (Table B 2). While a TSS of 1 indicates that the forecast's accuracy is perfect, a TSS of zero is associated with a purely random forecast (Table B 2). In each grid point, all entries of the contingency table must be sufficiently filled for our analysis to be robust and viable. To ensure statistical reliability, we prescribe this condition for each 500-fold bootstrap iteration. In practice, the counts of true presences (TP) and false absences (FA) are the critical indicators. Thus, we neglect grid-cells when the sum of both critical indicators is equal to zero in at least one bootstrap iteration.

First, we evaluate both definitions of the suitable spawning habitat against fishery and survey data. Afterwards, we select retrospective forecasts of the suitable spawning habitat at lead year 0 with best observational agreement in terms of TSS for more detailed analysis.
We analyse the predictive skill at RHP by pooling the bootstrapped forecast verification metrics (i.e. TSS) for each lead year over this region (averaging 40 and 46 grid cells for the survey and the fishery data, respectively). Uncertainty is expressed in terms of the interquartile range between the lower quartile (25th percentile) and the upper quartile (75th percentile) of the bootstrapped data. We define significance of the TSS by the 95% confidence interval of the bootstrap.
In order to analyse inter-annual variations in skill, we calculate the annually TSS averaged over RHP for retrospective forecasts made approximately one year ahead. Due to the different initialization dates we compare *MPI-ESM-hindcast* with a lead time of around 16 months (lead year 2) to persistence forecasts at 12 months lead (lead year 1 for *EN4-persist* and *MPI-ESM-persist*).

B2.4.5 The Suitable Spawning Habitat as an Indicator for Spawning on Rockall-Hatton Plateau (RHP)

Finally, we evaluate whether retrospective forecast of the suitable spawning habitat can be applied to anticipate whether spawning takes place on RHP. For each year, the spatial coverage of blue whiting observations on RHP is calculated as the percentage of grid cells within RHP containing presences of blue whiting from fishery/survey observations in March and April. Likewise, the percentage of grid cells within RHP containing suitable habitat in RHP is calculated for each year in March and April, based on retrospective forecasts with *MPI-ESM-hindcast* for lead year 2 (16 months ahead) and persistence forecasts for lead year one (12 months ahead) with *EN4-persist* and *MPI-ESM-persist*.

B3 RESULTS AND DISCUSSION

B3.1 MODELLING AND ANALYSIS STRATEGY

At a first glance, the climatology of temperature and salinity from February to April (FMA) is similar in *MPI-ESM-assim* and *EN4* within the spawning depth of blue whiting (250-600 m; Figure B 1). From the centre of the study region (around Rockall Trough) towards the north-west temperatures and salinities gradually decrease, forming a distinct cold and fresh region west of the study area northwards of around 50°N in the western subpolar North Atlantic, while warm and saline waters reside towards the south west. This gradual freshening and cooling from Rockall Trough towards the north-west, corresponds to observations that have been made along the Extended Ellet Line (Holliday et al. 2015). Moreover, the major oceanographic features in the North Atlantic, such as the SPG carrying cold and fresh water masses and subtropical gyre (STG) with its warmer and more saline waters (Hátún et al. 2005) are resolved in both *MPI-ESM-assim* and *EN4*.

However when focussing on distinct bathymetric features, such as the seamount Rockall Plateau, the channel Rockall Trough or the European Continental Shelf, differences in *MPI-ESM-assim* and *EN4* become obvious. In *MPI-ESM-assim* temperature and salinity follow the bathymetry around Rockall Plateau and Porcupine Bank and along the continental shelf into Rockall Trough (Figure B 1a,b), while contours of temperature and salinity appear rather smooth and disconnected from bathymetry in *EN4* (Figure B 1c,d).

These differences in the spatial representation of the marine climate arise from the different methods that are used in *EN4* and *MPI-ESM-assim* to distribute information of observed oceanic temperature and salinity profiles over the study region in time and space. As a dynamic ocean model, *MPI-ESM-assim* inherently accounts for dynamics and bathymetric features by distributing oceanic properties such as temperature and salinity dynamically consistent around ridges and seamounts such as Rockall Plateau and through channels like Rockall Trough (Figure B 1a,b). In contrast, in *EN4* observational gaps are filled by means of statistics and not physics. The objective interpolation used in *EN4* statistically interpolates between observed profiles and is therefore less capable of representing hydrodynamics, resulting in rather smooth contours of temperature and salinity, disconnected from bathymetry.

Within the spawning region and spawning depth of blue whiting, anomalies of temperature agree well in *EN4* and *MPI-ESM-assim* (overall correlation in FMA of 0.85, bias 0.66 °C; Figure B 2a), while differences are more pronounced in terms of salinity (correlation 0.51; bias 0.08; Figure B 2b). *EN4* and *MPI-ESM-assim* disagree in particular around 1999 and 2010 in terms of salinity. In this period, *EN4* shows more saline conditions than on average (Figure B 2b) also in agreement with observations from the Ellet Line (Holliday et al. 2020; 2015). In contrast, *MPI-ESM-assim* shows negative anomalies of salinity during these years.
However, *EN4* and *MPI-ESM-assim* show similar temporal deviations from climatology and multi-decadal variability in both temperature and salinity. Both observational products show more saline and warmer water up to the 1970's and rather low anomalies around 1975 and from 1986 to around 1995, followed by an increase up to around 2010 and a stark decrease in subsequent years, again in line with observations from the eastern Ellet Line around Rockall Plateau (Holliday et al. 2015; 2020). During some periods, e.g. around 1965 and 1995 there is a tendency of *MPI-ESM-assim* to show a higher amplitude of deviations in terms of salinity than *EN4* (Figure B 2b). A possible reason for this might be the inherent behaviour of the *EN4* analysis to approach mean oceanographic conditions (i.e. climatology) of 1971-2000 in the absence of observations (Good, Martin, and Rayner 2013). Since the time series chosen as background climatology of *EN4* neither includes the periods of high salinity around 1965 and 2005, nor observations from the Argo project which started in 2000 (Tesdal et al. 2018; MacIntosh, Merchant, and von Schuckmann 2017)), it potentially underestimates the oceanographic variability when and where observations are sparse. Deviations from climatology are less pronounced for *MPI-ESM-hindcast*, as shown for lead year 2, in particular for salinity during the past 20 years of the study period (Figure B 2b).

The co-varying changes of temperature and salinity in the spawning region of blue whiting are related to changes in the strength of the SPG, which affects the relative contribution of different water masses in the eastern North Atlantic. *MPI-ESM-assim* and *EN4* both capture the fresh and cold periods during the mid 1970's, mid 1990's and around 2015 (Figure B 2) which have also been observed along the eastern part of the Extended Ellet Line (Holliday et al. 2015) and are associated with a strong SPG (Koul et al. 2020). During these years, changes in the atmospheric circulation (i.e. a positive North Atlantic Oscillation and higher wind stress curl) extend the (southern branch of the) North Atlantic Current further to the east, which in turn results in an enhanced inflow of colder and fresher subpolar water masses from the SPG region (Western North Atlantic Water, (van Aken and Becker 1996)) into the Eastern North Atlantic (Holliday et al. 2015; 2020; Koul et al. 2020; Hátún et al. 2005). Additionally the inflow of warmer and more saline subtropical water masses from the south is impeded (Koul et al. 2020) leading to fresher and colder conditions into the spawning region. While a weak SPG shifts the North Atlantic Current westwards of Rockall Plateau permitting warm and saline water masses of subtropical origin that usually trace the continental shelf (Eastern North Atlantic Water) to spread throughout the eastern North Atlantic (Holliday et al. 2015). Thereby a weak SPG leads to more warm and more saline conditions in the spawning region as was observed around 2003 to 2013 (Figure B 2). Accordingly, the marine climate in the spawning region of blue whiting is influenced by the low-frequency dynamics of the SPG that contributes to recurrent periods of relatively high or relatively low salinity spanning over 5 to 10 years (Holliday et al. 2000; Koul et al. 2019) which could lend to a high predictability of the marine climate, in particular salinity.

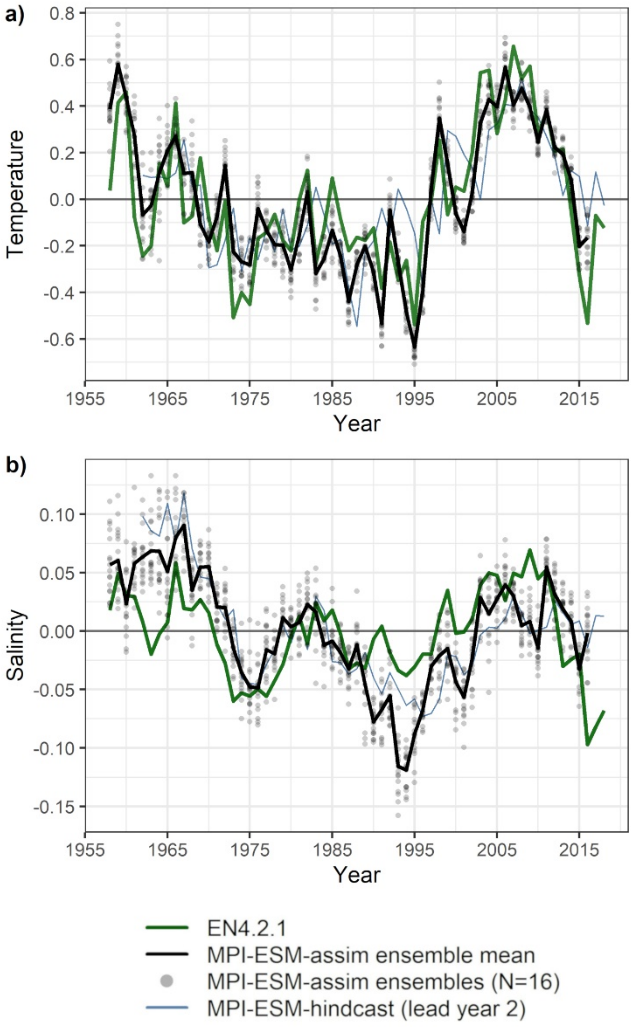

Figure B 2. Mean FMA temperature (a) and salinity (b) anomalies averaged over the spawning depth of blue whiting (250 - 600 m) within the spawning region (black rectangle in Figure B 1). Data from *EN4* is indicated by the green line. The ensemble mean of the assimilation run of MPI-ESM (*MPI-ESM-assim*) is indicated by the black line and its individual ensembles are shown as grey dots, where overlapping ensembles create darker shades. *MPI-ESM-hindcast* of lead year 2 is added as blue line.

B3.2 PREDICTIVE SKILL OF THE MARINE CLIMATE

Within the spawning region of blue whiting, *MPI-ESM-hindcast* shows greater predictive skill for salinity compared to temperature and is more skilful than *MPI-ESM-persist*, when compared to *MPI-ESM-assim* (Figure 3). The salinity within the spawning region and spawning depth can skilfully be predicted for more than 4 years ahead (Figure B 3b,d). In terms of the ACC, the hindcast of salinity outperforms persistence for all analysed lead years (Figure B 3b), while the predictive skill of temperature is similar to persistence and degrades further after lead year 3 (Figure B 3a). Moreover, salinity is more predictable than temperature, with a median ACC above 0.6 for all lead years analysed (Figure B 3a,b).

Since the ACC is dependent on the time period chosen for calculating the climatology (Jolliffe and Stephenson 2012), different time periods were initially considered. However, the main conclusions from the analysis remain unchanged. Likewise, Brune et al. (2018) analysed the predictive skill of SPG temperatures in *MPI-ESM-hindcast* for different time periods and found similar ACC values up to lead year five.

In terms of the RMSE *MPI-ESM-hindcast* is more skilful than *MPI-ESM-persist* in predicting both temperature and salinity, with most pronounced differences for temperature (Figure B 3c,d), indicating that the hindcast is superior in representing the amplitude of observed variations in salinity, and in particular temperature. The RMSE of the persistence forecasts increases with increasing lead times, while the RMSE is rather constant for the hindcast from lead year 2 onwards, indicating a greater accuracy of the hindcast with increasing lead times compared to persistence.

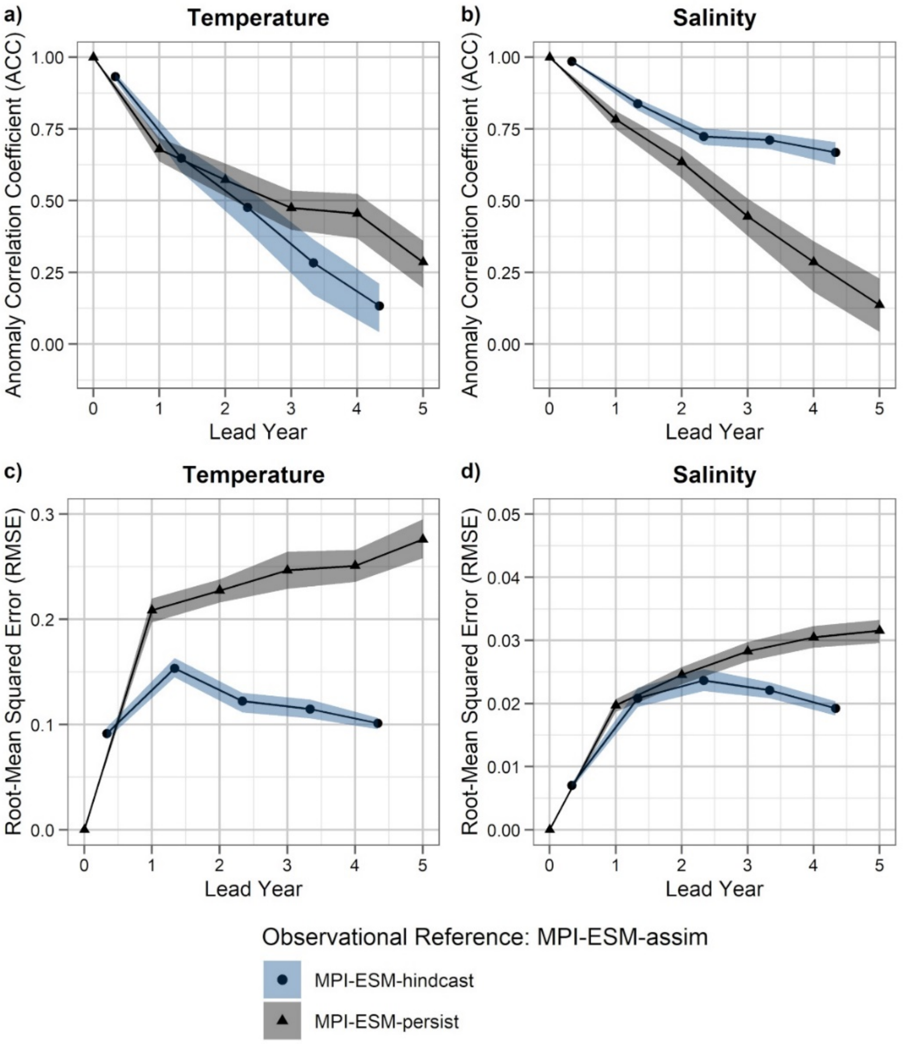

Figure B 3. Predictability of temperature (left; a,c) and salinity anomalies (right; b,d) averaged over 250-600 m in FMA within the spawning region (black rectangle in Figure), measured in terms of the anomaly correlation coefficient (ACC; top row) and root-mean squared error (RMSE; bottom row) of *MPI-ESM-hindcast* (bullet; blue area) and *MPI-ESM-persist* (triangle; grey), judged against *MPI-ESM-assim*. The connected bullets/triangles indicate the median and the blue/grey shaded areas indicate spread based on the lower and the upper quartile of a 500-fold bootstrap. Two correlations (or RMSEs) are markedly different when their respective shaded areas show no overlap.

Comparing *MPI-ESM-hindcast* to *EN4* shows a similar pattern for temperature; however, *MPI-ESM-hindcast* shows for salinity has a higher uncertainty and outperforms *EN4-persist* only after lead year 3 (Figure B 4). Overall, the predictive skill of *MPI-ESM-persist* (Figure B 3) and *EN4-persist* (Figure B 4) is nearly identical and both show slightly higher ACC for salinity than for temperature. Accordingly, considering both oceanographic reference products, a clear advantage of using *MPI-ESM-hindcast* in contrast to persistence is found after lead year three for salinity (Figure B 3b,d, Figure B 4b,d). This indicates that salinity can skilfully be predicted with *MPI-ESM-hindcast* at multi-annual lead times within blue whiting's spawning region and spawning depth during the peak months of spawning. For temperature, the hindcast is only superior in predicting the amplitude, but not the phase of observed variations, as indicated by significantly different values of RMSE but similar values of ACC when comparing persistence to *MPI-EM-hindcast* (Figure B 3a,c; Figure B 4a,c).

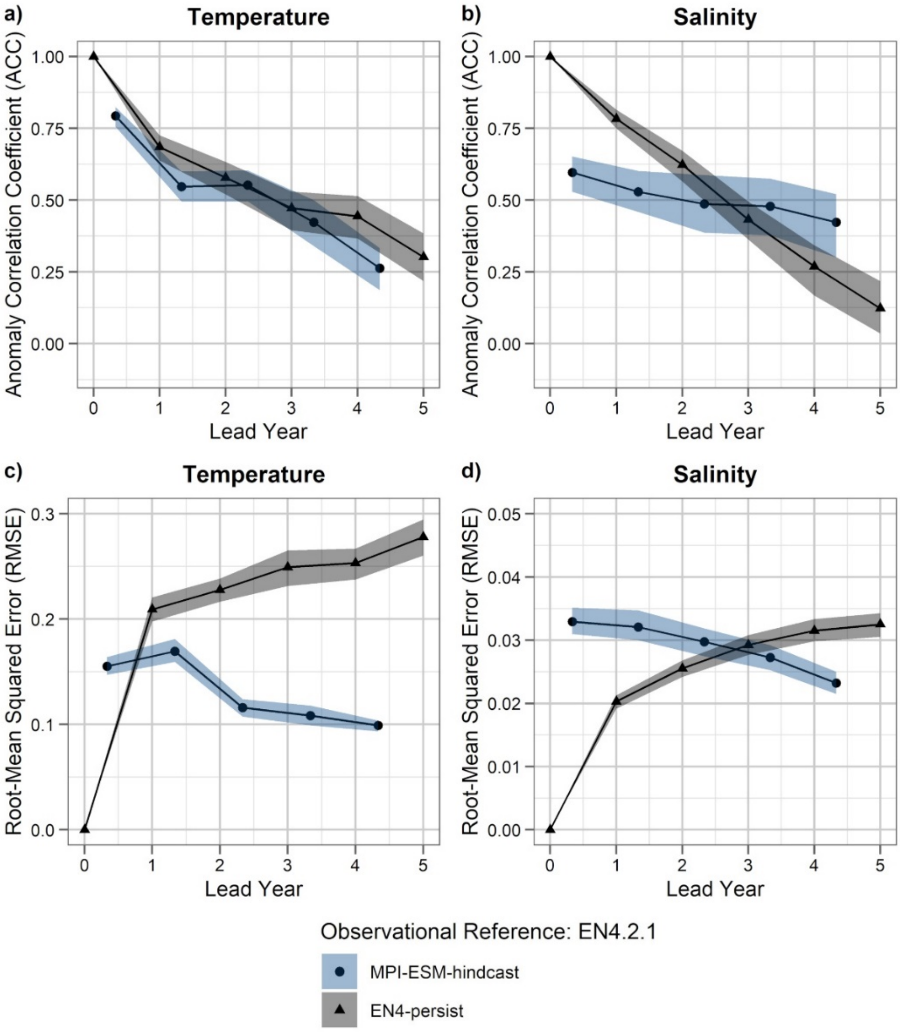

Figure B 4. Same as Figure B 3 but here *MPI-ESM-hindcast* (bullet; blue area) and *EN4-persist* (triangle; grey) are judged against *EN4*.

The lower frequency variation of salinity compared to temperature (Figure B 2) and the higher predictive skill of salinity, in particular over longer lead times (Figure B 3; Figure B 4), might be attributed to the property of salinity to act as a passive tracer (Mauritzen, Hjøllo, and Sandø 2006). Since temperature is the main determinant of ocean density in subpolar North Atlantic, temperature anomalies within the SPG are removed via buoyancy adjustment, while the salinity signal is passively advected with the general ocean circulation towards the North East Atlantic (Mauritzen, Hjøllo, and Sandø 2006) and thereby into the spawning region of blue whiting.

Therefore changes in the SPG are more pronounced in terms of salinity than in temperature (Koul et al. 2019; Hátún et al. 2005; Mauritzen, Hjøllo, and Sandø 2006). As such, salinity acts as an indicator for circulation changes in the subpolar North Atlantic (Mauritzen, Hjøllo, and Sandø 2006) and the low-frequency dynamics of the SPG that acts on (multi-) decadal timescales (Koul et al. 2019) likely contributes to the high predictability of salinity in the spawning region of blue whiting.

Few studies explicitly compare the predictability of salinity and temperature. One exception is a perfect model experiment that indicated that sea surface salinity is potentially more predictable at inter-annual timescales than sea surface temperature for most oceanic regions of the mid to high latitudes, including the Northeast Atlantic (Koenigk and Mikolajewicz 2009). In another study, sea surface salinity within the SPG region showed a higher potential predictability compared to both sea surface temperature and upper 300 m heat content with ACC of salinity as high as 0.8 for lead year 2-5 (Mignot et al. 2016), similar to the skill of *MPI-ESM-hindcast* versus *MPI-ESM-assim* in our study (Figure B 3b). While the mean RMSE for lead year 2-5 of around 0.5 for temperature and 0.05 for salinity (Mignot et al. 2016) is slightly higher than our results indicate (Figure B 3c,d; Figure B 4c,d).

Interestingly, the two oceanographic reference products, *EN4* and *MPI-ESM-assim*, show a larger difference for salinity than temperature (Figure B 2). Also a comparison of *MPI-ESM-hindcast* to two reference products, yields larger differences in the predictive quality and forecast horizon of salinity compared to temperature (Figure B 3, Figure B 4). While both observational reference data sets yield similar levels of predictive skill for temperature, correlations (ACC) for salinity range between 0.45 and 0.85 with differences being particularly pronounced in the first two lead years. Additionally, the projected forecast horizon differs considerably for salinity when judged against *EN4* and *MPI-ESM-assim*, with the former indicating a higher skill of *MPI-ESM-hindcast* only after lead year two, and the latter a higher skill of the hindcast for all analysed lead years. Similarly, sea surface temperature and sea surface salinity in the North Atlantic showed different forecast horizons for salinity when judged against different observational and reanalysis products, while the forecast horizon was the same for temperature, which Mignot et al. (2016) attribute to the larger observational uncertainty of salinity.

Since gaps in observations are filled differently in *EN4* and *MPI-ESM-assim*, their difference is likely to be more pronounced when and where observations are sparse. Therefore, a possible reason for the bigger discrepancy in salinity than in temperature between *EN4* and *MPI-ESM-assim* might lie in the different number of temperature and salinity observations contained in the EN4 profiles which both enter *MPI-ESM-assim* and the *EN4* analysis product, considered here. Generally, the observational coverage of salinity is considerably lower compared to temperature (MacIntosh, Merchant, and von Schuckmann 2017) in particular at depth and prior to the onset of Argo sampling (Tesdal et al. 2018), which is also visible in the study region during FMA

(Supplementary Figure 1). Due to this observational bias reconstructions and reanalysis of salinity are subject to larger levels of uncertainty than temperature.

Another difference between the two oceanographic reference data sets is, that *MPI-ESM-assim* represents observed atmospheric variability, by nudging the atmospheric component toward ERA40/ERAInterim reanalyses (Brune and Baehr 2020). Since changes in the SPG are connected to large scale atmospheric variability, atmospheric forcing is important for regulating both temperature and salinity of the subpolar North Atlantic (Holliday et al. 2020). Moreover, it has been suggested that the integration of atmospheric observations into the atmospheric compartment of an ESM could be beneficial in constraining its oceanic compartment, in particular in cases of scarce observational coverage (Brune and Baehr 2020). As such, *MPI-ESM-assim* might provide a more realistic representation of the marine climate, in particular salinity, in the North East Atlantic compared to *EN4*. Accordingly, the large range of predictive skill of salinity in *MPI-ESM-hindcast* when judged against *MPI-ESM-assim* and *EN4*, respectively (Figure B 3b,d, Figure B 4b,d), is partly attributable to the sparsity of salinity observations and amplified by inherent differences in model structure and assimilation technique (i.e. dynamic ocean-atmosphere ESM vs. statistic ocean-only optimal interpolation). This confirms the assumption of Good et al. (2013) that numerical models might perform better than *EN4* during periods of low observational coverage and underlines the aptitude of *MPI-ESM-assim*.

There are two large regions of high predictive skill of *MPI-ESM-hindcast* during FMA: one in the SPG region south west of Iceland and within the STG west off the European mainland, which are separated by a region of low predictive skill entering the spawning region from the south-west (Figure B 5, Figure B 6). A similar, “horseshoe” pattern has been observed for predictive skill of sea surface temperature and upper 700 m temperatures in an earlier version of MPI-ESM (Matei et al. 2012), for differently initialized MPI-ESM hindcasts (Brune et al. 2018) and in perfect model set ups analysing the potential predictability of sea surface salinity and temperature (Koenigk and Mikolajewicz 2009) and sea surface temperature, pH and oxygen (Frölicher et al. 2020).

Zooming into the spawning region of blue whiting, the predictive skill is highest around Rockall Plateau and within Rockall Trough from Porcupine Bank towards the northeast, while predictive skill within the spawning region is lowest in the south-west around 45°N - 50°N (Figure B 5 and Figure B 6). In terms of the ACC, *MPI-ESM-hindcast* of salinity is superior to temperature. However, for lead year 3 a strong decay in predictive skill is seen with regions towards the south-west of the spawning region, where correlations between *MPI-ESM-hindcast* and *MPI-ESM-assim* become insignificant for our analysis (Figure B 5). Similarly, predictive skill in terms of RMSE is lowest towards the south-west (Figure B 6).

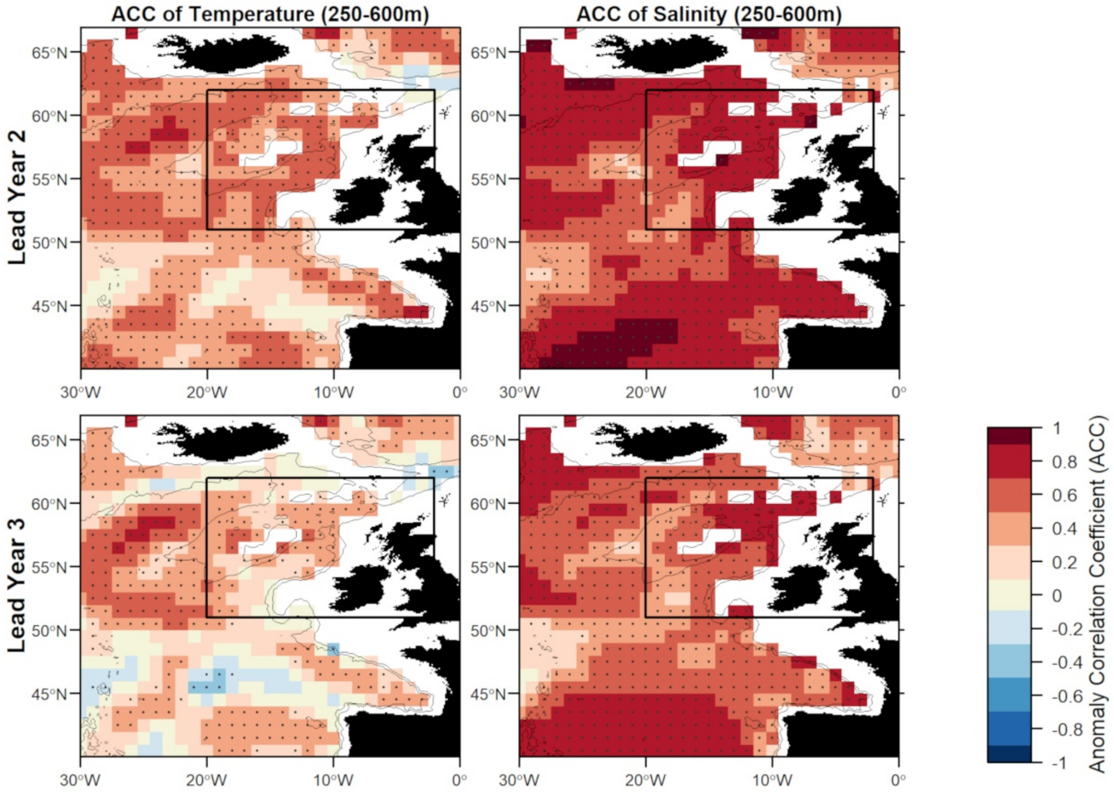

Figure B 5. Anomaly correlation coefficient (ACC) of temperature (left) and salinity (right) in FMA at lead year 2 (≈16 months, top) and lead year 3 (≈ 28 months, bottom) comparing *MPI-ESM-hindcast* to *MPI-ESM-assim*. Dots show significant correlations at the 95% confidence level, calculated from 500 bootstrap samples. The black rectangle delineates the study area: the spawning region of blue whiting; and black lines indicate the 600 m and 2000 m isobath.

The region of low predictability that enters the spawning region from the south-west at the entrance of Rockall Trough reflects a region of high oceanographic variability. Rockall Trough is one of the main pathways of the North Atlantic Current, in particular, when the SPG is strong, while the current branches off west of Rockall Plateau, when the SPG is weak (Holliday et al. 2020; Hátún et al. 2005). Since variations in the strength of the SPG affect the position and flow trajectory of the North Atlantic Current they introduce oceanographic variability in the area of Rockall Trough (Hátún et al. 2009; Koul et al. 2019; Holliday et al. 2000). This oceanographic variability affects the predictability of the marine climate in the Eastern North Atlantic resulting in particularly low predictive skill at the entrance of Rockall Trough in the south-western area of the spawning region.

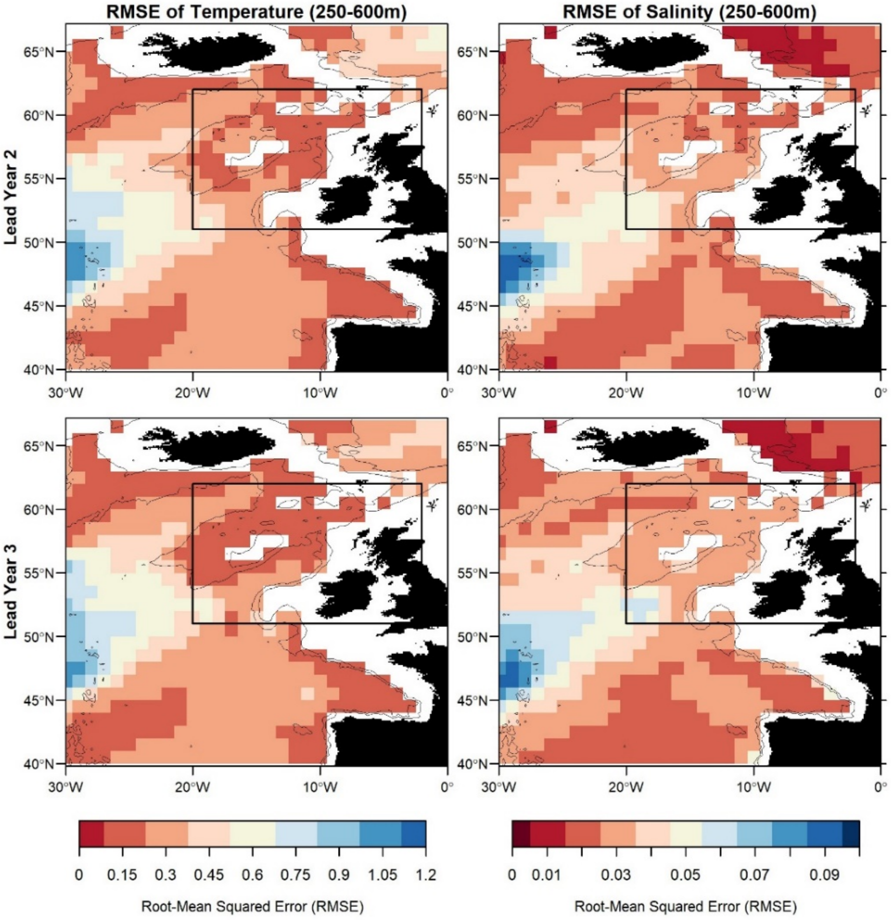

Figure B 6. Root-mean squared error (RMSE) of temperature (left) and salinity (right) in FMA at lead year 2 (≈16 months, top) and lead year 3 (≈ 28 months, bottom) comparing *MPI-ESM-hindcast* to *MPI-ESM-assim*. The black rectangle delineates the study area: the spawning region of blue whiting.

Overall, the better hydrodynamic representation of *MPI-ESM-assim* compared to *EN4* together with the high predictive skill of salinity, specifically over longer lead times and in the area around RHP, with *MPI-ESM-hindcast*, encourage the design of coupled-physical biological forecasts based on MPI-ESM.

B3.3 The Suitable Spawning Habitat of Blue Whiting defined via SDMs and Salinity

We explore two ways of defining the suitable spawning habitat of blue whiting. In the first approach, species distribution models (SDMs) are calibrated using various combinations of temperature and salinity from either *MPI-ESM-assim* or *EN4* (Table B S1). For each oceanographic reference product the SDM with the highest predictive performance are SDM_ST$_{\mathrm{MPI}}$ and SDM_S$_{\mathrm{EN4}}$ (Table B 3). These two SDMs are analysed further.

Table 5. Model fitting results for species distribution models (SDM) calibrated with different environmental reference data (Env. Data). The salinity and temperature at the spawning depth of blue whiting during the time of spawning is denoted by S_{SPAWN} and T_{SPAWN}, respectively. The geographical baseline model (GEO) includes latitude x day-of-the-year + solar elevation angle + log-transformed depth; in accordance with Miesner and Payne (2018). With DevExpl, explained deviance; AIC, Akaike Information Criteria; ΔAIC, difference in AIC relative to the smallest AIC value within the model set. For predictive skill measures the mean value based on 4-fold cross validation is given: TSS, true skill statistic; PPV, positive predictive value; NPV, negative predictive value, area under the relative operating characteristic curve (AUC). For full model sets, see Table B S1.

Env. Data	Model	Model Formulation	DevExpl	AIC	ΔAIC	TSS	PPV	NPV	AUC
EN4	SDM_S_{EN4}	GEO + S_{SPAWN}	0.476	5268	32	0.367	0.376	0.992	0.966
	SDM_ST_{EN4}	GEO + S_{SPAWN} x T_{SPAWN}	0.476	5271	35	0.342	0.350	0.991	0.964
MPI-ESM-assim	SDM_S_{MPI}	GEO + S_{SPAWN}	0.471	5319	83	0.360	0.368	0.991	0.965
	SDM_ST_{MPI}	GEO + S_{SPAWN} x T_{SPAWN}	0.482	5236	0	0.368	0.377	0.991	0.966

Specifically, for SDMs calibrated with environmental data from *MPI-ESM-assim*, including salinity and temperature at the spawning depth of blue whiting clearly yields the best performing model in terms of model parsimony with larval CPR data, showing the lowest AIC values and highest explained deviance (SDM_ST_{MPI}, Table B 3). However, the cross-validated predictive skill of SDM_ST_{MPI} is similar to SDM_S_{EN4}, which is the best performing SDM calibrated with *EN4* which solely includes salinity as environmental variable (Table B 3). Therefore, considering the predictive skill it seems irrelevant whether we use *MPI-ESM-assim* or *EN4* to calibrate the SDMs. For all SDMs the NPV is much larger than the PPV (Table B 3), indicating that the SDMs are better in describing the absence of suitable habitat than its presence.

In order to compare output from the SDMs to the suitable salinity for spawning, we convert the likelihood of observing larvae into a binary variable, namely the presence and absence of suitable habitat. The threshold for this conversion is a probability of approximately 0.3 (i.e. for *EN4* (*MPI-ESM-assim*): 0.28 (0.31) in the survey data, and 0.29 (0.34) in the fishery data). Probabilities that exceed (subceed) this threshold translate to presences (absences) of suitable habitat.

For both SDMs, the region defined as suitable for spawning (probability $\gtrapprox$ 0.3) is centred within the spawning region spanning from the European Continental Shelf onto Rockall Plateau. For SDM_ST_{MPI}, however, the suitable spawning habitat extends further west beyond RHP which is not supported by observations (Figure B 7a,b). Generally, both SDMs show a more contracted distribution towards the continental shelf in 1991 and a slightly more expanded westward distribution in 2005, however, both fail to reveal the full extent of the observed distributional changes.

The second approach uses the suitable salinity for spawning as a proxy for the suitable spawning habitat and there are large differences between the two approaches in the way the suitable habitat is spatially expressed (Figure B 7). While SDMs delineate the core spawning region west of the

British Isles, which is recognized to be the main spawning region of blue whiting (Bailey 1982; ICES 2019), they underestimate the spatial (i.e. latitudinal) extent of the spawning distribution. Possible reasons are that the SDMs are constrained by geographic and spatio-temporal parameters and the choice of the threshold for converting probabilities into presences of suitable habitat.
The suitable salinity for spawning has a considerably larger spatial extent than the suitable habitat based on SDMs and thereby is a better general definition of the potentially suitable habitat that rather overestimates suitable habitat in areas beyond the spawning region of blue whiting. An example of this behaviour is visible in both *EN4* and *MPI-ESM-assim*. The westward branch of the suitable salinity for spawning seems to trace the North Atlantic Current. This is a clear case of potential habitat where salinity is suitable for spawning but no observations of blue whiting are present, indicating that this region is not used for spawning by the species. Accordingly, both approaches have in common that predictions of suitable habitat outside of the original geographical modelling domain (i.e. the spawning region), also termed model extrapolations, have a higher uncertainty than model interpolations, since no observations support the predictions (Elith and Leathwick 2009).

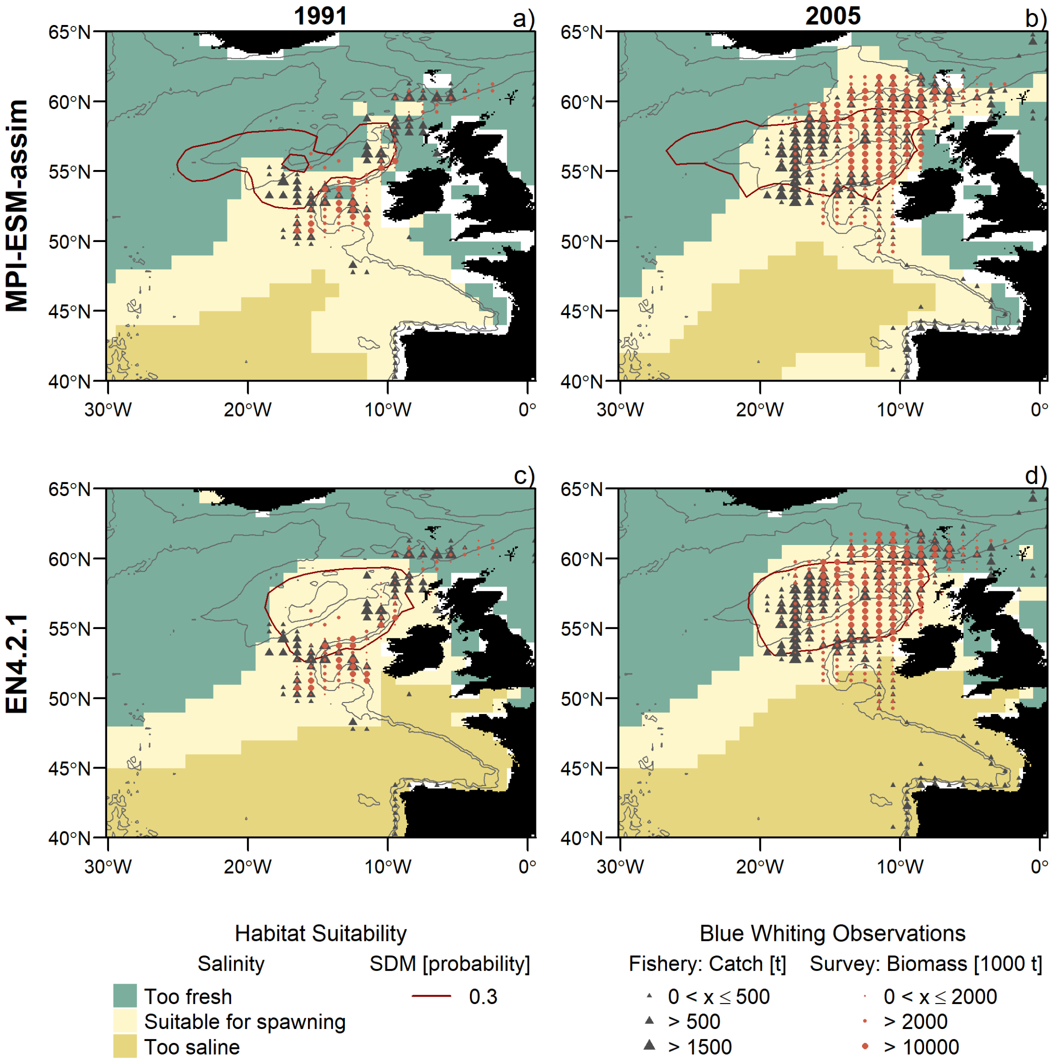

Figure B 7. Blue whiting habitat suitability in 1991 (left; a,c) and 2005 (right; b,d) for *MPI-ESM-assim* (top; a,b) and *EN4* (bottom; c,d) compared to observations of adult blue whiting from scientific surveys (IBWSS; red bullet) and fishery catch data (NEAFC; grey triangle) during March and April. Habitat suitability is shown for both the suitable salinity for spawning (background fill) and the probability of observing blue whiting larvae from SDMs (red contour lines; a,b: SDM_ST$_{MPI}$; c,d: SDM_S$_{EN4}$), where 0.3 resembles the threshold for converting the larval-presence probability into presence and absence of suitable habitat. Bathymetry is indicated by 600 and 2000 m isobaths.

Furthermore, different spatial representations of the marine climate from the two oceanographic reference products affect the spatial distribution of the suitable spawning habitat (Figure B 7). The suitable spawning habitat of blue whiting is more affected by the vicinity of bathymetric features, in particular Rockall Plateau, when based on *MPI-ESM-assim* in comparison to *EN4*, with differences being most pronounced for the suitable salinity for spawning. This increased bathymetry-sensitivity of *MPI-ESM-assim* indicates a closer relation to dynamic, oceanographic properties compared to *EN4*.

The difference between *MPI-ESM-assim* and *EN4* becomes most apparent, however, when comparing the suitable salinity for spawning for two years with contrasting marine climatic regimes. In 1991 the marine climate in the spawning region of blue whiting is characterised by rather cold and fresh conditions (Figure B 2) and most blue whiting are observed along the continental shelf from northern Scotland towards Porcupine Bank and south of Rockall Plateau within Rockall Trough (Figure B 7a,c). To the contrary in 2005, conditions become more warm and saline in the spawning region (Figure B 2) and in response, blue whiting show an expanded spawning distribution that stretches from the continental shelf over RHP with a larger north-westward extent (Figure B 7b,d). This longitudinally contracted, more southward distribution of blue whiting during colder and fresher years, and the more expanded and northward distribution with more spawning on Rockall Plateau under more saline and warmer conditions have been reported previously (Hátún, Payne, and Jacobsen 2009; Miesner and Payne 2018).
While these spatial changes imprint on in the suitable salinity for spawning in *MPI-ESM-assim*, *EN4* fails to resolve changes between the two years. In particular in the area around RHP, *EN4* shows hardly any difference between the two years (Figure B 7d,e), while *MPI-ESM-assim* reproduces the absence of suitable habitat on Rockall Plateau in 1991 (Figure B 7a) and the presence of suitable habitat over most of RHP in 2005 (Figure B 7b). Accordingly, the dynamic properties of *MPI-ESM-assim* and its ability to account for bathymetric constraints might be better suited to reflect the suitable spawning habitat of blue whiting, in particular in the area of RHP.

Another difference between the two reference products, that is visible for both years is that in *MPI-ESM-assim* the suitable salinity for spawning extends southward along the continental shelf passing the Spanish and Portuguese coast (Figure B 7a,b). This extension is supported by fishery observations (Figure B 7a,b). Spawning of blue whittling starts in the southern distribution range, where some larvae have been observed in deep waters in the Bay of Biscay, and progresses northward (Bainbridge and Cooper 1973; Pointin and Payne 2014). Accordingly, the southward extension of the suitable salinity for spawning along the European Continental Slope in *MPI-ESM-assim* might reflect the southern path of the spawning migration where the habitat is suitable and spawning occurs occasionally. Accordingly, the suitable salinity for spawning leads to the best agreement with independent observations when focussing on the spawning region.

Table B 4. Agreement of the suitable spawning habitat with independent observations of adult blue whiting observed in the IBWSS survey and caught in fishery (NEAFC) during March and April within the spawning region. The suitable spawning habitat comprises of the best performing species distribution models (SDM, SDM_S$_{EN4}$ and SDM_ST$_{MPI}$) and based on the suitable salinity for spawning calibrated with different environmental reference data (Env. Data, *MPI-ESM-assim* and *EN4*); i.e. resembling a retrospective forecast for lead year 0. Mean values within the spawning region were calculated from the 500-fold bootstrap, with variables noted in Table B 3.

Observation	**Habitat**	**Env. Data**	**PPV**	**NPV**	**HR**	**FAR**	**TSS**
Survey (IBWSS)	SDM	*EN4*	0.49	0.63	0.54	0.45	0.08
		MPI-ESM-assim	0.49	0.52	0.38	0.39	0.00
	Suitable Salinity	*EN4*	0.31	0.83	0.75	0.63	0.12
		MPI-ESM-assim	0.49	0.70	0.77	0.59	0.18
Fishery (NEAFC)	SDM	*EN4*	0.38	0.74	0.49	0.41	0.08
		MPI-ESM-assim	0.33	0.68	0.33	0.34	-0.01
	Suitable Salinity	*EN4*	0.24	0.87	0.77	0.62	0.10
		MPI-ESM-assim	0.33	0.77	0.72	0.59	0.10

Within the spawning region, habitat definitions based on the suitable salinity for spawning generally have a higher agreement with independent fishery and survey observations as judged by higher mean values of NPV, HR and TSS compared to habitat definitions based on SDMs (Table B 4). The SDM-based definition is only better in terms of PPV for SDM_S$_{EN4}$ and the FAR. Both habitat definitions are more useful in describing an absence of suitable habitat within the spawning region (higher NPV) than presence of suitable habitat (lower PPV).

Overall, spatially averaged values of TSS within the spawning region are low (< 0.2), however all habitat definitions show greatest agreement with observations from the IBWSS survey in the region around Rockall Plateau and north-east of it (Figure B 8). SDM_ST$_{MPI}$ shows least agreement with observations (overall TSS=0) and even displays significantly negative values of TSS in particular around Porcupine Bank (Figure B 8a), followed by SDM_S$_{EN4}$ with an overall TSS of 0.08 (Figure B 8b). The suitable spawning habitat in terms of salinity in *MPI-ESM-assim* shows best agreement with observations from the scientific survey in terms of TSS, with positive values mainly in the north-eastern part of the study region and on RHP (Figure B 8c). In contrast to *MPI-ESM-assim,* differences between the two habitat definitions are smaller for *EN4* (Figure B 8; Table B 4).

Accordingly, the definition of the suitable spawning habitat based on salinity shows better agreement with independent observations than applying the full SDMs. Therefore, we create retrospective forecast of the suitable salinity for spawning and analyse its predictive skill in further detail.

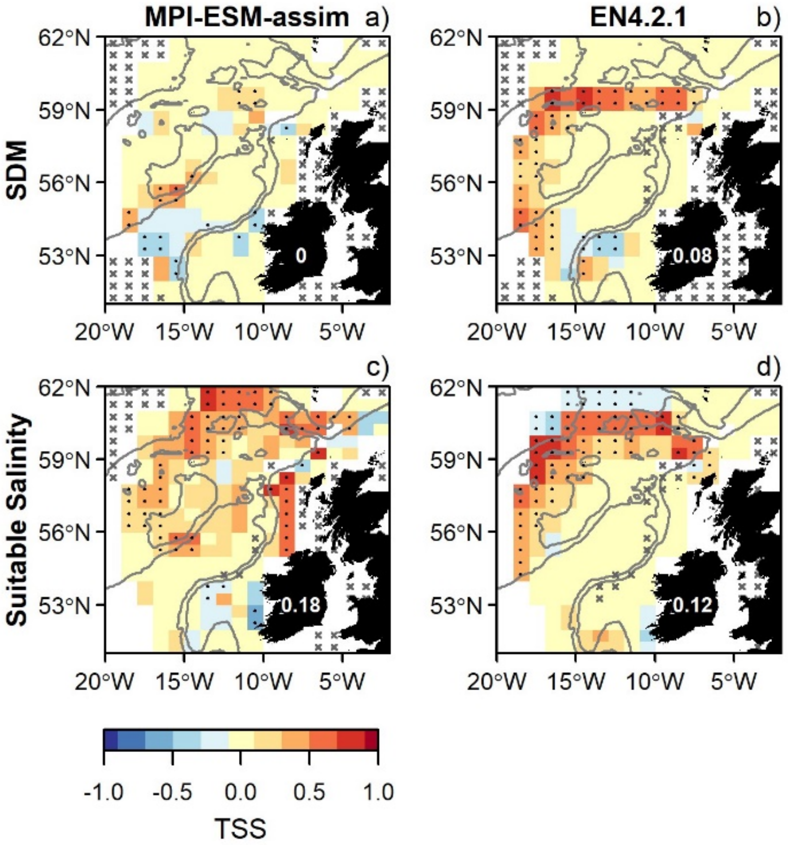

Figure B 8. Agreement between the suitable spawning habitat and observations of adult blue whiting from the IBWSS survey in terms of the True Skill Statistics (TSS) during March and April. The suitable spawning habitat is defined through Species Distribution Models (SDM; top row; a,b) or the suitable salinity for spawning (bottom row; c,d) and based on *MPI-ESM-assim* (left; a,c) and *EN4* (right; b,d). In a and b the best performing SDMs (Table 5) were chosen: SDM_ST$_{\text{MPI}}$ (a) and SDM_S_{EN4} (b). Dots show significant correlations at the 95% confidence level and crosses indicate regions where the predictive skill cannot be evaluated confidently due to sparse observational data, both based on a 500-fold bootstrap. Good predictive quality (TSS > 0) is indicated by red colours (where HR > FAR) and the mean TSS within the plotted region (excluding regions with crosses) is noted on Ireland. The grey lines indicate the 600 m and 2000 m isobath.

B3.4 PREDICTIVE SKILL OF THE RETROSPECTIVELY FORECASTED SUITABLE SPAWNING HABITAT BASED ON SALINITY

Generally, retrospective forecasts of the suitable salinity for spawning based on *MPI-ESM-hindcast* approximately one year ahead have a higher predictive skill than persistence based forecasts (Figure B 9). However, overall values of TSS are low with 0.13 when compared to both survey and fishery data and differences to persistence-based forecast are small and in the range of 0.02-0.03 (Figure B 9a-c).

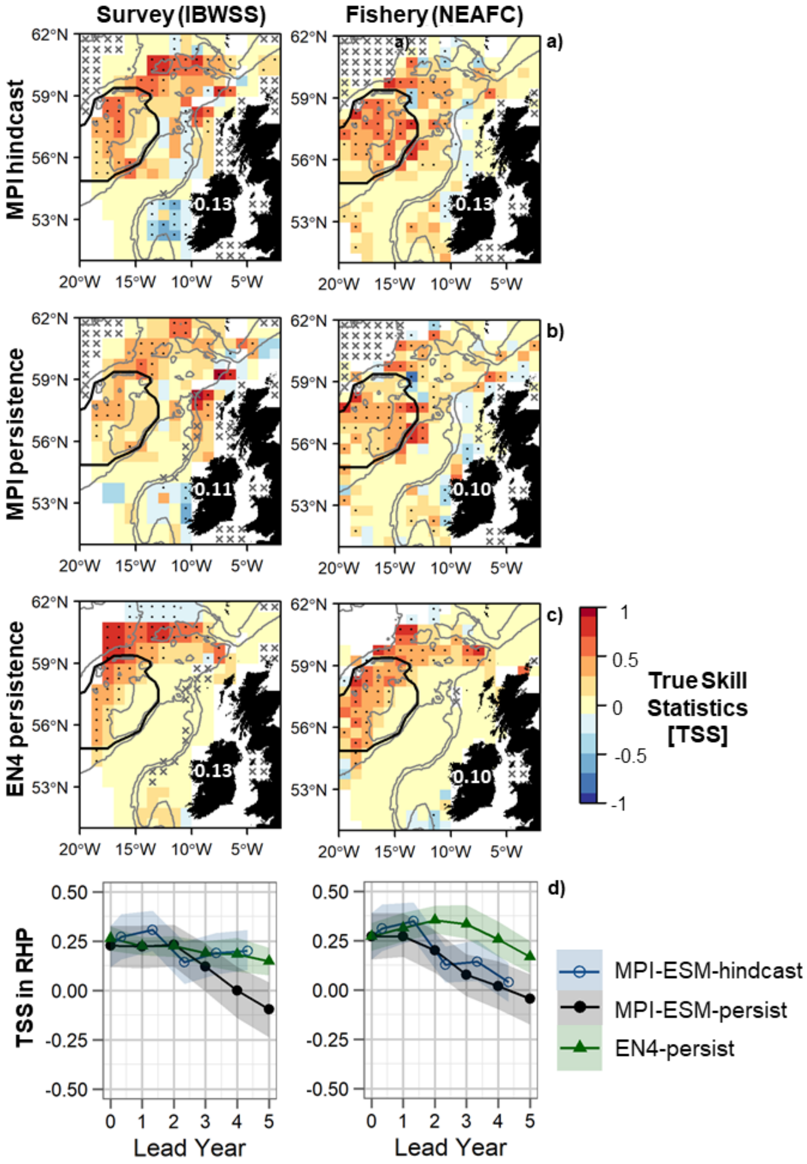

Figure B 9. Predictive quality of retrospectively forecasted suitable spawning habitat based on the suitable salinity for spawning with *MPI-ESM-hindcast* (a), *MPI-ESM-persist* (b) and *EN4-persist* (c) in terms of the True Skill Statistics (TSS) for March and April judged against observations of adult blue whiting from surveys (IBWSS; left) and fishery (NEAFC; right) approximately one year ahead (a-c); and spatially averaged over Rockall-Hatton Plateau (RHP; region delineated in black in the maps above) for each lead year (d).
The last row (d) shows *MPI-ESM-hindcast* (blue circle), *MPI-ESM-persist* (black bullet) and *EN4-persist* (green triangle) with the shaded areas indicating the spread based on the lower and the upper quartile of a 500-fold bootstrap. Retrospective forecasts are distinctly different when their respective shaded areas do not overlap. Due to the different initialization dates, Figure a-c show the hindcast with a lead time of around 16 months and the persistent forecasts with a 12 months lead.
In a) to c) dots show significant correlations at the 95% confidence level and crosses indicate regions where the predictive skill cannot be evaluated confidently, both based on a 500-fold bootstrap. Good predictive quality (TSS > 0) is indicated by red colours (where HR >FAR) and the mean TSS within the plotted region (excluding regions with crosses) is noted over Ireland. The grey lines indicate the 600 m and 2000 m isobaths.

The predictive skill of all retrospective forecasts is highest on RHP especially west of Rockall Plateau and in the northern part of the spawning region, while low or no predictive skill is found within deeper parts of Rockall Trough and Porcupine Bank (Figure B 9a-c). Results are similar when compared to both survey and fishery observations. However, significantly positive TSS values on Rockall Plateau and Porcupine Bank are only found for *MPI-ESM-hindcast* and *MPI-ESM-persist* when compared to fishery data (Figure B 9a,b). The high predictability of retrospective forecasts on and north-east of RHP, are in line with the high predictability of the marine climate, specifically salinity, found for this region (Figure B 5, Figure B 6).

Within RHP, retrospective forecasts of the suitable salinity for spawning perform similarly for shorter lead times (< 2 years) with *MPI-ESM-hindcast* being slightly but not significantly more skilful than persistence based forecasts (Figure B 9d). The forecast horizon at which *MPI-ESM-hindcast* is more skilful than persistence based forecast differs for the two oceanographic data sets and for the two observational data sets of blue whiting. *MPI-ESM-hindcast* has more skill than *MPI-ESM-persist* after lead year 3 when asessed by the survey data, however, when compared to the fishery data both show similar skill. *EN4-persist* shows a similar or higher predictive skill than *MPI-ESM-hindcast* after lead year 2, as judged by survey and fishery observations, respectively.

Also retrospective forecasts of the area of suitable spawning habitat of blue whiting, based on the original SDM (Miesner and Payne 2018) and an ensemble of dynamic ESMs, outperformed persistence based forecasts only after lead year four (Payne et al. 2021). This indicates that, akin to the predictability of the marine climate, persistence can also play an important role for retrospective forecasts of the suitable spawning habitat of blue whiting on multi-annual time scales.

Retrospective forecasts of the suitable spawning habitat approximately one year in advance show prominent inter-annual variations in predictive skill on RHP, which can roughly be divided into three periods (Figure B 10a): From 1985 to 1995, *MPI-ESM-hindcast* shows the highest skill with values of TSS as high as 0.89 as judged against fishery data while *EN4-persist* mainly shows no skill. Around the 2000's this reverses when *EN4-perisist* has greater values of TSS than *MPI-ESM-hindcast*. However, during this time the differences in retrospective forecast skill is high depending on the observational data set chosen and retrospective forecasts based on *MPI-ESM-persist* and *MPI-ESM-hindcast* and generally have higher TSS values and hence are more skilful when judged against fishery data in comparison to survey data, indicating a rather large uncertainty in observing blue whiting on RHP. From 2006 onwards, forecast skill converges to a range of TSS around 0 to 0.5.

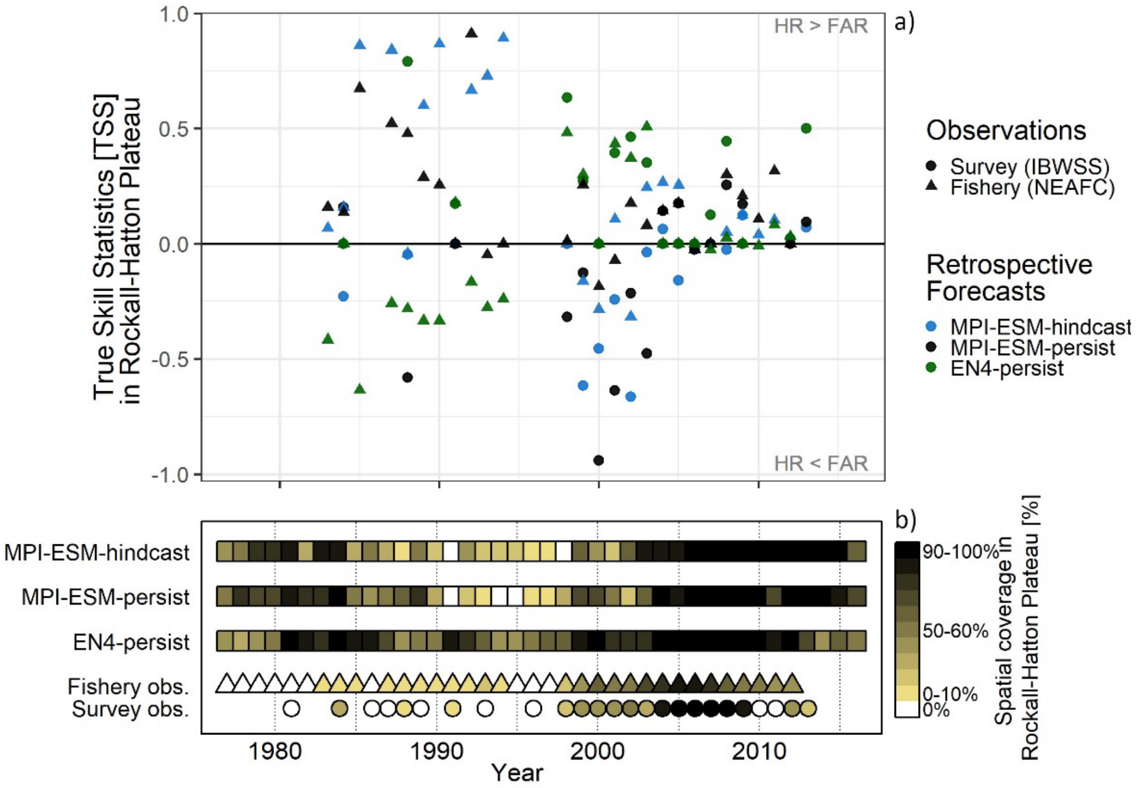

Figure B 10. Average inter-annual forecast skill on Rockall-Hatton Plateau (RHP; see Figure a-c) in terms of the True Skill Statistics (TSS; a); and the spatial coverage of suitable spawning habitat in RHP (% of grid cells; b) based on retrospective forecasts of the suitable salinity for spawning approximately one year ahead with *MPI-ESM-hindcast*, *MPI-ESM-persist* and *EN4-persist* judged against observations of adult blue whiting from surveys (IBWSS; bullet) and fishery (NEAFC; triangle) during March and April. In case observations of blue whiting were absent on RHP (b: white triangles/bullets = 0%) the TSS is not calculated. Note that observational absences can also indicate that there was no fishing in RHP and shows the absence of IBWSS survey coverage on RHP in the particular year.

These marked changes in the predictive skill over RHP (Figure B 10a) coincide with changes in the importance of RHP as a spawning ground (Figure B 10b) which in turn are affected by oceanographic variability on the spawning region (Miesner and Payne 2018; Hátún, Payne, and Jacobsen 2009). Around 1990 when the marine climate in the spawning region is characterised rather cold and fresh conditions, most spawning takes place along the continental shelf and less on RHP (Miesner and Payne 2018; Hátún, Payne, and Jacobsen 2009; Hátún et al. 2009) as shown for 1991 (Figure B 7a,c). The importance of RHP as a spawning ground stays low until 1998 with less (or equal) than 30% of blue whiting being observed or caught on RHP (Figure B 10b). Likewise, *MPI-ESM-persist* and particularly *MPI-ESM-hindcast* show only small fractions of RHP with suitable spawning habitat around 1990 (Figure B 10b), resulting in unprecedentedly high forecast skill with values of TSS of 0.85 (Figure B 10a). In contrast, *EN4-persist* constantly shows suitable habitat in more than 30% of RHP. This inability of *EN4* to show the absence of suitable spawning habitat over RHP leads to the low predictive skill of *EN4-persist* until around

1998 (Figure B 10).

After 1998 both temperature and salinity increase in the spawning region (Figure B 2) which is associated with a north- and westward expansion so the spawning distribution (Miesner and Payne 2018; Hátún, Payne, and Jacobsen 2009; Hátún et al. 2009) and blue whiting are observed over a larger area of RHP (Figure B 10b). In line with observations from the Ellet Line (Holliday et al. 2015), *EN4* shows an increase in temperature and salinity above the climatological average from around 2000-2009 (Figure B 2). *MPI-ESM-assim*, however shows negative anomalies, particularly in salinity around 2000 (Figure B 2). Accordingly, *MPI-ESM-hindcast* and *MPI-ESM-persist* both underestimate the suitability of the spawning habitat (Figure B 10b) resulting in the absence of skill over RHP around 2000 (Figure B 10a). In congruence with the period of high temperature and salinity around 2005, which is found in both *EN4* and *MPI-ESM-assim* (Figure B 2), also the spatial coverage of blue whiting over RHP peaks and blue whiting are observed over most (if not all) of RHP (Figure B 10b). Since all retrospective forecasts also show suitable spawning habitat on RHP (Figure B 10b), forecasts skill converges with mainly positive TSS values, in particular for persistence based forecasts (Figure B 10a).

These distinct inter-annual variations in predictive skill are possibly linked to the different spatial representations of the marine climate in *EN4* and MPI-ESM. Since *EN4-persist* continuously shows suitable spawning habitat on RHP (Figure B 7) it is not able to capture absence of suitable habitat on RHP, such as in the 1990s (Figure B 10b). More specifically *EN4* shows a hit rate being equal to the false alarm rate and thus no skill for both observed (Figure B 8b,d) and retrospectively forecasted habitat (Figure B 9c). Since the greatest share of blue whiting observations is from periods during which RHP was an important spawning ground, the continuous projection of suitable habitat on Rockall Plateau leads to an (artificial) inflation of forecast skill, therefore the high predictive skill of *EN4-persist* after lead year two should be viewed cautiously (Figure B 9d). The superior ability of *MPI-ESM-hindcast* to forecast the absence of suitable habitat on RHP can at least partially be attributed to the more differentiated representation of the marine climate around bathymetric features MPI-ESM, as previously discussed. Moreover it has been suggested, that predictions of the marine climate with a precursor version of *MPI-ESM-hindcast* have a higher predictive skill during strong multi-year trends, particularly during the warming in the 1990s, than under small multiyear trends (Brune et al. 2018). This could be another reason for the superior performance of *MPI-ESM-hindcast* around 1990, and possibly for its low performance around 1999-2002 when the trend was less pronounced, in particular in terms of temperature (Figure). Since observational gaps are filled differently in *MPI-ESM-assim* and *EN4*, their dissimilarity might be less pronounced for regions and time periods with higher observational coverage.

Inter-annual variations in predictive skill might also be attributed to an asymmetric forecast skill. Just like definitions of the suitable spawning habitat are more useful in describing the absence of suitable habitat than its presence (for both *EN4* and *MPI-ESM-assim* indicated by a higher NPV than PPV, Table B 4) also retrospective forecasts, in particular based on MPI-ESM, are most skilful during periods of low spawning activity on RHP, i.e. prior to 1995 (Figure B 10a). Accordingly, there are a range of factors influencing (inter-annual) variations in skill of the marine climate as well as of the habitat forecast.

In summary, a clear advantage of creating forecasts of the suitable spawning habitat of blue whiting with MPI-ESM compared to *EN4*, is the ability of MPI-ESM to differentiate between the presence and absence of suitable spawning habitat over RHP. In particular, *MPI-ESM-hindcast* skilfully forecasts distributional changes over RHP around a year in advance.

B3.5 CHALLENGES IN DEFINING AND ASSESSING THE SUITABLE SPAWNING HABITAT

A major challenge that is common to all ecological forecasts that aim at forecasting the spatial distribution of living organisms, is the way habitat is related to the distribution of a species (Payne et al. 2017). Here, the suitable spawning habitat of blue whiting delineates environmental conditions that are suitable for spawning (i.e. in terms of salinity). However, just because a region is suitable for spawning does not (necessarily) mean that the location is occupied by the fish and spawning takes place. Due to non-resolved processes such as migration dynamics, density dependent effects on distribution or other biotic interactions such competition and predation, not the entire suitable habitat is necessarily occupied by the species (Guisan and Zimmermann 2000; Elith and Leathwick 2009; Colwell and Rangel 2009). Therefore, the actual distribution might be smaller than their potentially suitable habitat, which is clearly seen for the suitable salinity for spawning (Figure B 7). Since habitat models are superior in predicting absences compared to presences, as seen for both approaches applied in this study (Table B 3, Table B 4), the skill of forecasting species distributions is asymmetric (Payne et al. 2021). Consequently, retrospective forecasts of the suitable spawning habitat (e.g. on RHP) with *MPI-ESM-hindcast*, have higher skill in predicting the absence of suitable habitat (i.e. no spawning on RHP) than their presence.

Nevertheless, instantaneous observations of freely moving animals, like fish, only provide a snapshot of their distribution. We cannot be certain whether the observed adult blue whiting were actively spawning or migrating. Additionally, observations might not cover the entire spawning distribution, e.g. fishermen focus on the most profitable regions with highest fish aggregations while smaller aggregations might be left untouched. Therefore, observations of fish carry uncertainties that affect the assessment biological forecast skill. In particular, our analysis of interannual of biological forecast skill reveals at times massive differences in skill when judged by either fishery or survey data. This highlights the need to consider alternative biological observational data sets for validating coupled physical-biological forecasts.

We define the suitable spawning habitat of blue whiting based on SDMs in a generalized additive modelling framework (Miesner and Payne 2018). There is, however, a multitude of other modelling options. We cannot rule out that another statistical SDM approach, for example, based on machine learning such as random forest (Breiman 2001) which is designed for generating predictions (Elith and Leathwick 2009) might have resulted in a better performance of SDM-based predictions. Additionally accounting for an ensemble of different modelling techniques would enable accounting for uncertainty in defining the suitable habitat (Araújo and New 2007).

Salinity seems to be a good proxy for the spawning distribution of blue whiting within its spawning region because it shows good agreement with independent observations (Miesner and Payne 2018). Therefore, we have not further evaluated alternative modelling options for defining the suitable habitat. Note, that no model tuning was performed in order to improve the agreement between modelled and observed habitat, and the predictive skill of the suitable habitat forecast could likely be improved by analysing the sensitivity of model parameters and thresholds.

Alternative to our definitions of the suitable habitat that were both grounded on SDMs with 48 years of larval (presence and absence) observations, some skilful coupled physical-biological forecasts have been built on considerably shorter time series (< 20 years) of presence-only data. For example, operational ecological forecast products have originally been created by combining oceanographic observations to tagging data of tuna (Hobday et al. 2011; Eveson et al. 2015) and sea turtles (Howell et al. 2008; 2015) to in order to delineate the (thermally) suitable habitat of the respective species. Similarly, the close correspondence between observations of adult blue whiting and salinity (i.e. Figure 9 in Miesner and Payne 2018) suggests that the suitable spawning habitat could alternatively be constructed by linking fisheries or survey observations to oceanographic reference products.

We define and skilfully forecast the suitable spawning habitat of blue whiting based on salinity. Salinity can have a direct effect on fish, in particular on early life stages, by affecting their osmoregulation (Varsamos, Nebel, and Charmantier 2005) or egg (Sundby and Kristiansen 2015) and larval buoyancy as shown for blue whiting (Ådlandsvik et al. 2001). Compared to temperature, however, salinity has a less direct effect on most marine organisms (Rijnsdorp et al. 2009). Therefore, salinity is most likely a proxy for other processes that affect the spawning distribution of blue whiting more directly. Most notably, temperature and salinity are often correlated and form central water mass characteristics. Since each water mass possesses characteristic hydrographic and biogeochemical properties, it functions as distinct habitat for marine organisms. Saline waters of subtropical origin provide a higher abundance of warm-water zooplankton species which are smaller (Hátún et al. 2009) and thus more favourable prey items of blue whiting larvae (Bailey 1982) than larger zooplankton species that occupy fresher subpolar waters (Hátún et al. 2009). Consequently, the suitable salinity for spawning might resemble subtropical water masses with good feeding conditions for blue whiting larvae. The feature of salinity to act as a passive tracer, unmodulated by atmospheric processes, might contribute to the more prominent role of salinity, as opposed to temperature, for defining the suitable spawning habitat of blue whiting.

Due to the imminent importance of salinity as water mass characteristic, it might also be promising to consider salinity for characterising the species-environment relationship of other marine organisms and for creating coupled physical-biological forecasts. The importance of salinity for anticipating distributional changes has also been shown for a range of pelagic species along the U.S. Northeast Shelf (McHenry et al. 2019). This study highlights that bottom salinity was generally more important in explaining range shifts than temperature, and that projections based solely on temperature masked the species' climate vulnerability (McHenry et al. 2019). This highlights the prominence of salinity as independent variable in statistical models that predict spatial changes of marine organisms. In agreement, we also find that salinity prediction skill bears a great potential for creating novel coupled physical-biological forecasts.

B4 CONCLUSIONS

Using blue whiting as a case study, we show that *MPI-ESM-hindcast* skilfully predicts the marine climate, specifically salinity, in the North East Atlantic several years ahead, which translates to predictability of distributional shifts in the species' suitable spawning habitat a year in advance. While the definition of the suitable habitat is species specific and requires careful consideration, many aspects from this study can be generalized and are also applicable to other species. Hence, ESMs bear great potentials for forecasting fish distributions in the North East Atlantic

One of the main advantages in delineating and forecasting the suitable habitat with MPI-ESM is the ESM's representation of hydrographic processes, which is superior to the statistical product *EN4* for the conducted analysis. The dynamic consistency and ability of an ESM to consider hydrodynamics can therefore offer advantages over a solely statistical oceanographic data product, specifically for coupled physical-biological forecasts in regions with distinct bathymetry, e.g. over seamounts, plateaus or shelfs, which typically depict preferred habitat features for many species, as seen for blue whiting. Moreover, a higher resolution could be advantageous by resolving mesoscale processes such as fronts and eddies and their recirculation around banks and seamounts. These are important features in the spawning region of blue whiting (Holliday et al. 2000) and can act strongly on the distribution of marine organism, in particular planktonic life stages (Bakun 1996). However, it is essential that the position and shape of these physical fields (i.e. temperature and salinity) are maintained. As such, also for highly resolved biological models of tuna distribution (based on 1/4° ocean models assimilated with observations), inconsistencies between predicted and observed mesoscale features remain a challenge (Lehodey et al. 2018). Accordingly, contrary to common intuition, a higher resolution of the underlying oceanographic reference products and hindcast is no guarantee for better habitat forecasts. Therefore, it is pivotal, in particular for distributional biological forecasts, to assess the spatial characteristics of the underlying oceanographic data sets and to employ a suite of different oceanographic reference products and ESMs for both, defining and forecasting the suitable habitat.

In regions where local predictability of the marine climate is low, a potential for creating coupled physical-biological forecasts might lie in lagged correlations from regions of high predictability, such as the SPG region. Changes in the SPG affect the relative share of water masses in the Eastern North Atlantic and result in large bio-geographical shifts of blue whiting and a variety of other marine organisms ranging from phyto- and zooplankton, to whales and seabirds (Hátún et al. 2009; Drinkwater et al. 2003). Additionally, SPG-driven changes of temperature and salinity travel downstream into the North (Koul et al. 2019; Núñez-Riboni and Akimova 2017) and Barents Sea, and thereby affect the abundance and productivity of some local fish species and introduce predictability via adjective delays (Akimova et al. 2016; Koul et al. 2021). Since retrospective forecasts of the marine climate with *MPI-ESM-hindcast* in the SPG region show significant skill (Brune and Baehr 2020; Brune et al. 2018), and Post et al. (2020) found a lagged response between the marine climate south-west of Iceland and the abundance of blue whiting and other boreal fish species in Greenlandic waters, we envision a great potential for developing coupled physical-biological forecasts of fish abundance and distribution based on MPI-ESM in the North Atlantic and its adjacent seas (Koul et al. 2021).

Another insight from this study is the higher predictive skill of deep-water salinity compared to temperature and its impending importance as water mass and habitat characteristic in the North East Atlantic. For many commercially important fish species in the North Atlantic a wealth of observational records exist and environmental drivers for distributional changes are known (Trenkel et al., 2014; and references therein). This could offer the possibility to delineate the species' suitable habitat by combining existing observations of the species in combination with skilful observational oceanographic data sets. Moreover, including salinity in coupled physical-biological forecasts could offer a valuable contribution towards predicting distributional shifts of marine living organisms and for creating novel marine ecological forecasts.

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B7 SUPPORTING INFORMATION

Table B S1. Model fitting results for the best performing species distribution models (SDM) calibrated with different environmental observations (Env. Data; *MPI-ESM-assim* and *EN4*).
The geographical baseline model (GEO) includes latitude x day-of-the-year + solar elevation angle + log-transformed depth; in accordance with Miesner and Payne (2018). Environmental variables include, sea surface salinity (SSS), sea surface temperature (SST) and salinity and temperature at the spawning depth of blue whiting during the time of spawning (S_{SPAWN} and T_{SPAWN}, respectively).
With DevExpl, explained deviance; AIC, Akaike Information Criteria; ΔAIC, difference in AIC relative to the smallest AIC value within the model set. For predictive skill measures the mean value based on 4-fold cross validation is given: TSS, true skill statistic; PPV, positive predictive value; NPV, negative predictive value, area under the relative operating characteristic curve (AUC). Models with ΔAIC < 15 are highlighted with a grey shaded background.

Env. Data	Formulation, f()	DevExpl	AIC	ΔAIC	TSS	PPV	NPV	AUC
MPI-ESM-assim	GEO + SSS	0.470	5337	101	0.358	0.367	0.991	0.964
	GEO + SST	0.470	5325	89	0.359	0.367	0.991	0.966
	GEO + S_{SPAWN}	0.471	5319	83	0.360	0.368	0.991	0.965
	GEO + T_{SPAWN}	0.466	5362	126	0.351	0.360	0.991	0.965
	GEO + SSS + SST	0.478	5259	23	0.370	0.378	0.992	0.966
	GEO + S_{SPAWN} + T_{SPAWN}	0.478	5257	21	0.366	0.375	0.992	0.966
	GEO + SSS x SST	0.479	5255	19	0.372	0.381	0.991	0.965
	GEO + S_{SPAWN} x T_{SPAWN}	0.482	5236	0	0.368	0.377	0.991	0.966
EN4	GEO + SSS	0.461	5408	148	0.349	0.358	0.991	0.964
	GEO + SST	0.468	5343	83	0.356	0.365	0.991	0.965
	GEO + S_{SPAWN}	0.476	5268	8	0.367	0.376	0.992	0.966
	GEO + T_{SPAWN}	0.469	5341	81	0.353	0.362	0.992	0.964
	GEO + SSS + SST	0.472	5309	49	0.361	0.370	0.991	0.965
	GEO + S_{SPAWN} + T_{SPAWN}	0.478	5260	0	0.351	0.360	0.991	0.964
	GEO + SSS x SST	0.474	5289	29	0.365	0.374	0.991	0.966
	GEO + S_{SPAWN} x T_{SPAWN}	0.476	5271	11	0.342	0.350	0.991	0.964

The EN4.2.1 objective analysis (*EN4*) provides estimates of the relative weighting given to the observations compared to the background in the salinity and temperature analysis, termed observation weights (Good, Martin, and Rayner 2013). In cases where observation weights approach zero, the interpolated values reflect only the background estimate (MacIntosh, Merchant, and von Schuckmann 2017). Overall, the observational density of EN4 profiles within spawning region and depth of blue whiting has slightly increased over time with inter-annual variations being particularly pronounced for salinity (Figure B S1c). While the amount of temperature observations have remained fairly constant from the mid 70's onwards, a notable increase in salinity observations has occurred from 2006 onwards in the spawning region (Figure

B S1c). The steep increase in salinity observations in the mid-2000 is attributed to the initiation of the Argo program (MacIntosh, Merchant, and von Schuckmann 2017).

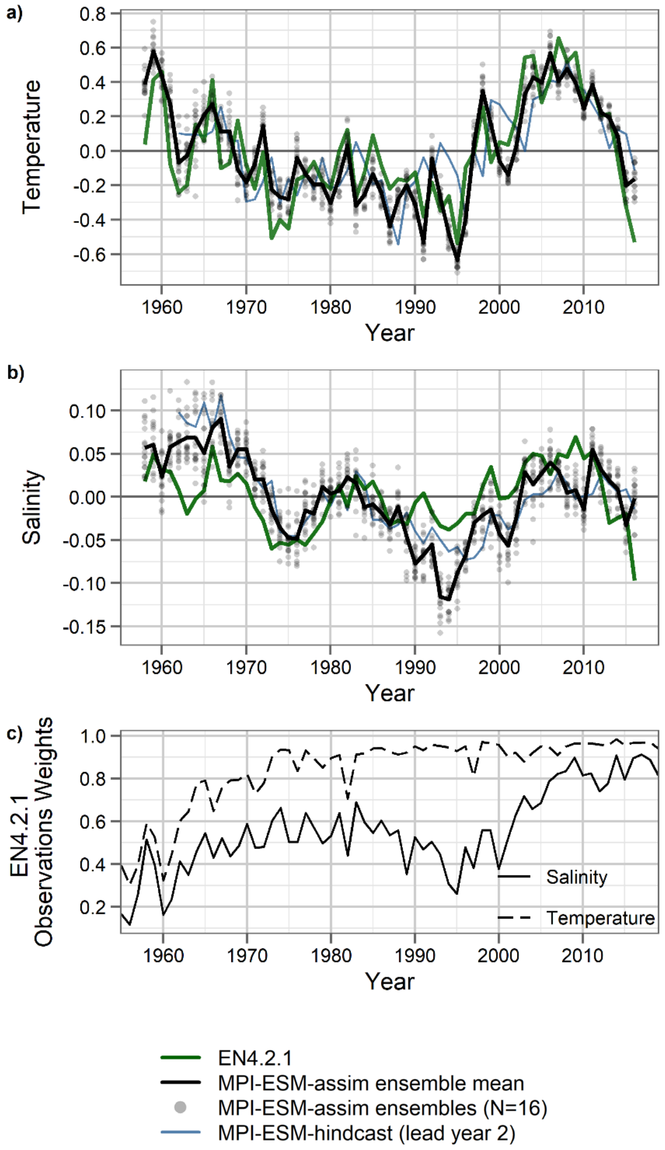

Figure B S1. Mean FMA (Feb - April) temperature (a) and salinity (b) anomalies and *EN4* observation weights (c) for salinity (solid) and temperature (dashed) averaged over the spawning depth of blue whiting (250 - 600 m) within the spawning region (black rectangle in Figure). In a and b data from *EN4* is indicated by the green line. The ensemble mean of the assimilation run of MPI-ESM (*MPI-ESM-assim*) is indicated by the black line and its individual ensembles are shown as grey dots, where overlapping ensembles create darker shades. *MPI-ESM-hindcast* of lead year 2 is added as blue line. In c) the *EN4* observation weights are an indicator for the observational

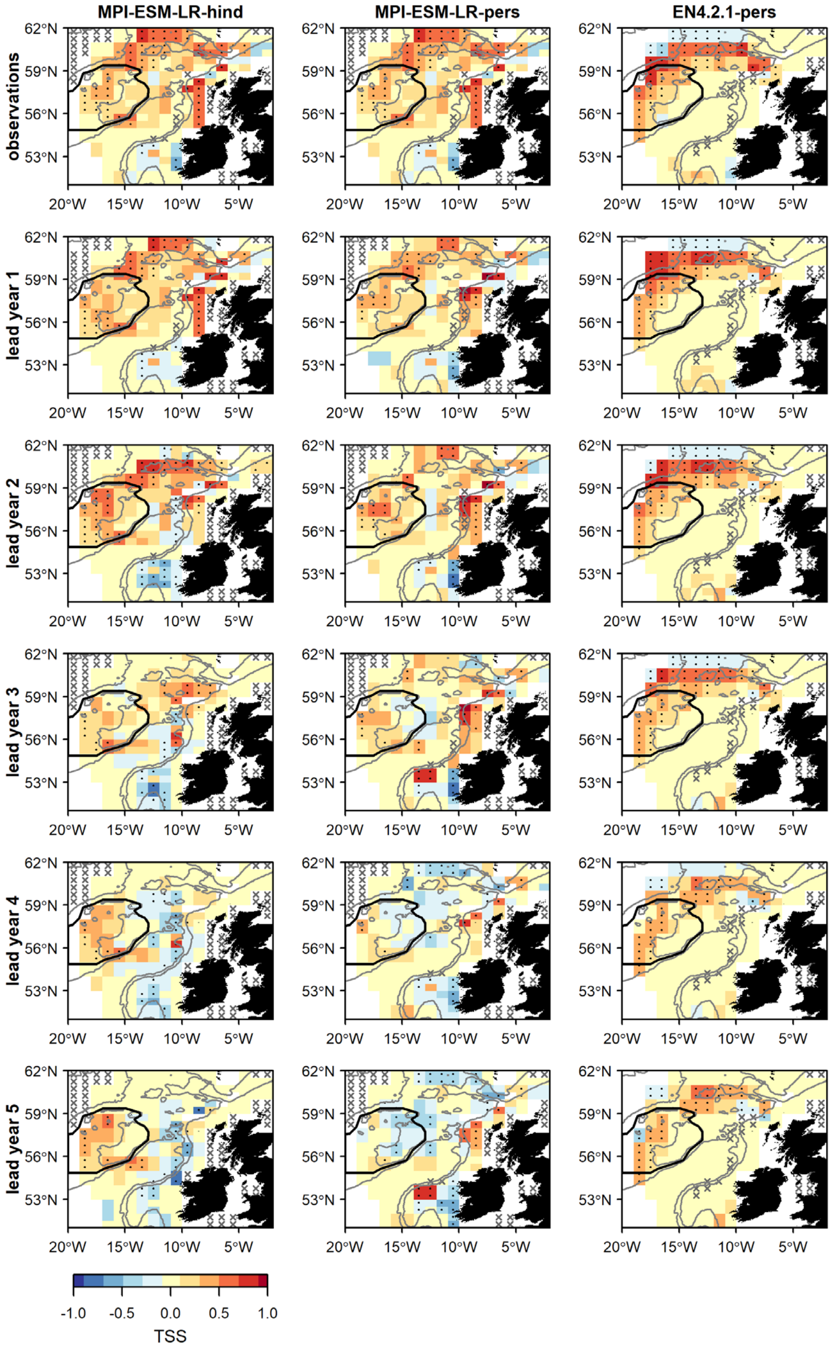

Figure B S2. Predictive quality of retrospectively forecasted suitable spawning habitat based on the suitable salinity for spawning with MPI-ESM-hindcast (left), MPI-ESM-persist (center) and EN4-persist (right) in terms of the True Skill Statistics (TSS) for March and April judged against observations of adult blue whiting from surveys (IBWSS) for lead year 0 (observations) to 5. Dots show significant correlations at the 95% confidence level and crosses indicate regions where the predictive skill cannot be evaluated confidently, both based on a 500-fold bootstrap. Good predictive quality (TSS > 0) is indicated by red colours (where HR >FAR) and the mean TSS within the plotted region (excluding regions with crosses) is noted over Ireland. Rockall-Hatton Plateau is delineated by black lines. The grey lines indicate the 600 m and 2000 m isobaths.

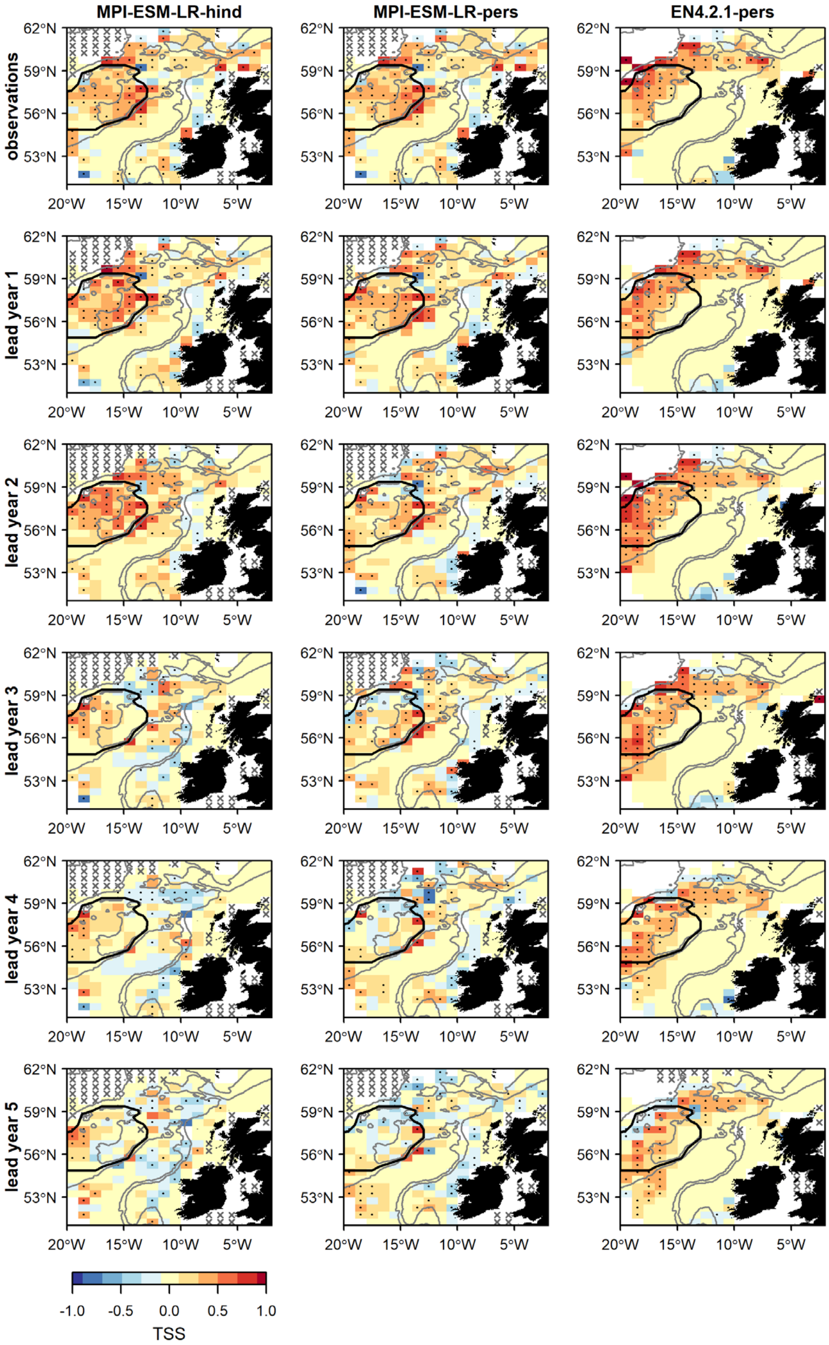

Figure B S3. Same as Figure B S2 but here retrospective forecasts are judged against fishery (NEAFC) observations.

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EIDESSTATTLICHE VERSICHERUNG

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

DECLARATION OF OATH

I hereby declare upon oath that I have written the present dissertation independently and have not used further resources and aids than those stated.

Hamburg, November 2021

Anna Katharina Miesner