Dealing with uncertainty in ecosystem models along three axes; resolution, forcing and projections

Ina Nilsen

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Preface

This synthesis and collection of scientific papers are submitted for the degree of philosophiae doctor (PhD) in oceanography at the Institute of Marine Research and the Geophysical institute at the University of Bergen. This PhD was funded by the Nansen Legacy project, a 6-year research project (2018–2023) which gathers the Norwegian research community in a joint effort to study the changes in the Arctic. The thesis was also partly funded by Fishcom by a three-month extension period.

The thesis consists of an introductory part and three scientific papers. Chapter 1 gives the motivation and scientific background of the work, where the first part sets this thesis into scientific context, discussing ecosystem modelling and future climate changes. The raised objectives and motivation behind the study are listed at the end of chapter 1. Chapter 2 gives a brief introduction to the models used, as well as the area that was studied. An introduction to the papers is given in chapter 3: stating the papers objective; a short summary of each study and briefly stating how this thesis contributes to closing current research gaps. Lastly, future research priorities are discussed in chapter 4. The three papers constituting this thesis are included in chapter 5, and are listed below in progressive order:

Articles:

1. Nilsen, I., Hansen, C., Kaplan, I., Holmes, E., Langangen, Ø., 2022. *Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach.* Fish and Fisheries 1–16. https://doi.org/10.1111/faf.12671
2. Nilsen I., Fransner F., Olsen A., Tjiputra J., Hordoir R., Hansen C., 2023. *Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas*, In review at Fisheries Oceanography
3. Nilsen I., Kaplan, I., Hansen C., *A shifting chessboard: projections of prawn, capelin, mesopelagic fish, zooplankton, and their Nordic and Barents Seas food web under climate change,* Manuscript ready for submission

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- Dr. Øystein Langangen (*Department of Biosciences, University of Oslo) Oslo, Norway*
- Dr. Isaac Kaplan (*Northwest Fisheries Science Center, NOAA Fisheries) Seattle, USA*

Scientific contributions during the PhD period that are not a part of this thesis:

Nilsen, I., Kolding, J., Hansen, C., Howell, D., 2020. Exploring Balanced Harvesting by Using an Atlantis Ecosystem Model for the Nordic and Barents Seas. Frontiers in Marine Science 7. https://doi.org/10.3389/fmars.2020.00070

Olsen, E., Hansen, C., Nilsen, I., Perryman, H., Vikebø, F., 2019. *Ecological Effects and Ecosystem Shifts Caused by Mass Mortality Events on Early Life Stages of Fish.* Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00669

Institute of Marine Research	The University of Bergen	The Nansen Legacy

Abstract

With the imminent threat of climate change, there is an urgent need to understand how warmer temperatures will affect marine ecosystems. Models provide the best tools to study the future, but although great efforts have been made to understand the impacts of warming temperatures, there is still large uncertainties related to the model projections. The uncertainties can arise from structural uncertainty of the ecosystem model, uncertainties regarding climate projections, or uncertainties related to how species will respond to future climate changes. In this thesis, we therefore apply ecosystem models of varying complexity, climate models of varying resolution and climate projections under various emission scenarios to understand and quantify uncertainty. By assessing the uncertainty, we highlight consistent results that suggest higher confidence, and areas where differences in the results suggest that more research is needed. The results from this thesis are divided into three research papers.

The first paper deals with structural uncertainty regarding model complexity, as we explore the role of Northeast Atlantic cod (*Gadus Morhua*) in the Barents Sea food web by using a multi-model approach. We apply two ecosystem models of different complexity; the minimalistic Gompertz model and the highly complex Atlantis model, to study how capelin and polar cod respond to changing levels of cod. We highlight consistent results across the models and identify diverging results due to differences in spatial structure and number of foodweb components, and conclude that for fishery management purposes, the two models can complement each other.

The second paper deals with uncertainty regarding the resolution of climate projections used to force ecosystem models, where we apply physics (temperature, salinity, volume transport and sea ice) from a regional model (Nemo-NAA10km) and its driving global climate model (NorESM2) to the Nordic and Barents Seas Atlantis ecosystem model (NoBa). We found that few higher trophic level (TL>3) species

were affected by using forcing from a global versus a regional model, and there was a general agreement in future biomass trends and distribution patterns. Yet, our results showed how a slight difference in temperature can have dramatic consequences for specific species and demonstrate that species projection uncertainty could arise from poor representation of the physical forcing, as well as due to uncertainty in the ecosystem model parameterization.

In the third and final paper, we deal with the uncertainty regarding ecosystem responses to future climate changes. We apply physics from three different climate projections (SPP1-2.6, SSP2-4.5 and SSP5-8.5) to study the impact of rising temperatures in the Nordic and Barents Seas using NoBa. To account for uncertainty in the response of phytoplankton and zooplankton to future climate change, we included variation in phyto- and zooplankton growth levels. We identify potential winners and losers in a warming climate and focus on the underlying mechanisms that drives the changes in the model, including spatial differences, thermal tolerance, and species interactions.

Through our work we have demonstrated the value of using ecosystem models of varying complexity, climate models of varying resolution and climate projections under various emission scenarios to quantify uncertainty regarding model projections. By investigating uncertainty along these three axes, we learn more about the models and the mechanisms that drives the changes and provide valuable insight for management and future ecosystem studies.

Sammendrag (Norwegian)

Med klimaendringer som en overhengende trussel, er det et stort og økende behov for å forstå hvordan varmere temperaturer vil påvirke marine økosystemer. Modeller er et av de viktigste verktøyene for å studere hvordan utviklingen vil bli, men selv om stor innsats har blitt lagt ned for å forstå konsekvenser av varmere temperaturer, er det fortsatt stor usikkerhet knyttet til modell-projeksjonene. Usikkerheten kan skyldes strukturell usikkerhet i økosystemmodellene, usikkerhet knyttet til klimaprognoser eller usikkerhet knyttet til hvordan ulike arter vil reagere på fremtidige klimaendringer. I denne oppgaven bruker vi derfor økosystemmodeller med varierende kompleksitet, klimamodeller med varierende oppløsning og ulike klimascenarier for å belyse denne usikkerheten. På den måten kan vi rapportere resultater som samsvarer med høyere pålitelighet, og påpeke forskjeller i resultatene som tilsier at det vil være behov for mer forskning. Resultatene fra denne avhandlingen er delt inn i tre forskningsartikler.

Den første artikkelen omhandler strukturell usikkerhet knyttet til modellkompleksitet. Ved å benytte to modeller av ulik kompleksitet (den minimalistiske Gompertz-modellen og den svært komplekse Atlantis-modellen) gransker vi rollen til nordøstatlantisk torsk (*Gadus Morhua*) i Barentshavet ved å studere hvordan lodde og polartorsk reagerer på endrede nivåer av torsk. Vi synliggjør samsvarende resultater på tvers av modellene og identifiserer divergerende resultater som oppstår på grunn av forskjeller i romlig struktur og antall økosystem-komponenter. Konklusjonene våre er at fiskeriforvaltningen kan dra nytte av å bruke flere modeller, og at de to modellene utfyller hverandre.

Den andre artikkelen omhandler usikkerhet rundt oppløsningen av klimamodellene, og i hvilken grad høy oppløsning av fysikken er nødvendig for å studere effekter i økosystemmodeller. Her bruker vi fysikk (temperatur, saltholdighet, volumtransport og havis) fra en regional modell (Nemo-NAA10km) og dens drivende globale

klimamodell (NorESM2) i en Atlantis modell (NoBa) for de Nordiske hav og Barentshavet. Resultatene viste at få arter på høyere trofisk nivå (TL>3) ble påvirket av å bruke fysikk fra en global versus en regional modell, og at det var en generell enighet om fremtidige biomassetrender og distribusjonsmønstre. Likevel så vi hvordan selv små temperaturforskjeller kan ha dramatiske konsekvenser for enkelte arter, og hvordan slike forskjeller kan oppstå både med utgangspunkt i usikkerhet rundt fysikken, samt usikkerheter i hvordan modellen representerer artenes temperaturtoleranse.

I det tredje og siste artikkelen studerer vi usikkerheten knyttet til påvirkning av fremtidige klimaendringer på økosystemet i de Nordiske hav og i Barentshavet. Ved å anvende av tre ulike klimascenarier (SPP1-2.6, SSP2-4.5 og SSP5-8.5) studerer vi hvordan økende temperaturer vil påvirke artene i NoBa-modellen. For å ta høyde for usikkerhet i fremtidige nivåer av plante- og dyreplankton, inkluderte vi variasjon i disse gruppene. Fokus i studien ligger på de underliggende mekanismene som driver endringene i modellen, og vi identifiserer potensielle vinnere og tapere i et varmere klima.

I denne avhandlingen fremhever vi verdien av å bruke økosystemmodeller av varierende kompleksitet, klimamodeller med varierende oppløsning og ulike utslippsscenarier for å håndtere usikkerhet i modellene våre. Ved å undersøke usikkerhet langs disse tre aksene lærer vi mer om modellene og mekanismene som driver endringene, samt gir verdifull innsikt for forvaltning og fremtidige økosystemstudier.

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I've learnt so much working with the four of you this year, and I´m truly grateful for having such professional and caring supervisors to be a part of this project. The completion of this Ph.D. would not have been possible without the guidance and support from you all.

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Stavanger, March 9th, 2023
Ina Nilsen

Content

1. Background and motivation

1.1 Background

The United Nations Sustainable Development Goals (SDGs) addresses in SDG2 zero hunger, in SDG13 climate changes and in SDG14 conserving and sustainable use of life below water, as three of the 17 most important issues in the world (United Nations, 2015). The oceans provide essential ecosystem services that allow our planet to function in a healthy way, as well as jobs for over 3 billion people, and 20 % of the animal protein consumed worldwide (FAO, 2022). The oceans play a key role in climate regulation, especially by mitigating the effects of increasing levels of carbon dioxide in the atmosphere and rising global temperatures (Reid et al., 2009). With a rapidly growing human population, likely approaching 10 billion by 2060 (United Nations, 2022), and global fisheries and aquaculture production at an all-time high, there is no doubt that the ocean will play an increasingly important role in providing food and jobs in the future (FAO, 2022).

Growing human pressures, including climate change, have profound and diverse consequences for marine ecosystems (United Nations, 2015). Effects of climate change on marine ecosystems involve rising temperatures, changes in primary production, ocean acidification, sea ice retreat and changes in species distributions and abundance (Bryndum-Buchholz et al., 2019). Furthermore, climate change can interact with other stressors such as overfishing (Fu et al., 2018; Griffith et al., 2012), which can threaten the ecosystems (Tittensor et al., 2019) and influence the societal benefits derived from the ocean (Boyce et al., 2020). An overall reduction in global yields has occurred over the past 80 years (Free et al., 2019), and understanding the risks of climate change for marine ecosystems and the benefits of mitigating these changes is therefore highly important.

Global warming is causing large-scale impacts in sub-Arctic and Arctic Ocean regions, with temperatures rising quickly and sea ice receding (Comiso, 2011; Smedsrud et al., 2013). The Nordic and Barents Seas are recognized as one of the fastest warming places on Earth (Isaksen et al., 2022), where warmer temperatures are already altering the ecosystem by displacing southern, boreal species further north, while arctic species are retreating and declining (Fossheim et al., 2015; Frainer et al., 2017; Kjesbu et al., 2021, 2014). This area also stands out as particularly interesting (Paasche et al., 2015) for contrasting responses in the living resources, representing annual landings of several million tonnes (FAO, 2020), which extend over considerable areas with different manifestations of warming impacts (Drinkwater, 2005; Gullestad et al., 2020; Payne et al., 2021; Peck and Pinnegar, 2018; Simpson et al., 2011). With the increasing number of marine environmental stressors (Henson et al., 2017), there is therefore an urgent need to understand how these ecosystems will respond to these changes (Fagundes et al., 2020)

Climate change affects ecosystems directly through changes in ocean physics, as well as indirectly by altering regional productivity (Moloney et al., 2011). Although great efforts have been made to estimate climate effects on productivity, there is still high uncertainty regarding how lower trophic levels might respond in high latitude ecosystems. The reduction of sea ice will increase light availability which is expected to have a positive effect on primary production. Yet, primary production also depends on nutrient availability, and increasing temperatures and decreasing salinity due to melting ice might lead to increased vertical stability, which limits nutrients supply to the photic sone (Farmer et al., 2021). However, increasing winds due to more extreme weather or regions becoming ice-free might lead to more mixing and increase the nutrient levels at the surface (Hordoir et al., 2022; Qu and Liu, 2020). Yet, too much turbulence and storms could affect primary production negatively by transporting phytoplankton below their critical depth at which there is enough light to grow (Wolfe et al., 2016) or by reducing light availability through sediment resuspension (Stockwell et al., 2020). Ice algae species that are sensitive to light and depend on ice are also expected to decrease in diversity as the sea ice is reduced (Hop et al., 2020), and the effect on total primary production is thereby highly uncertain. Regional studies in Arctic regions and high-latitude systems have demonstrated how difficult it is to capture future responses in primary production. Some models project increased production due to more light (Steinacher et al., 2010), while others project a decreasing trend due to higher stratification (Steinacher et al., 2010) and some show no changes at all (Skogen et al., 2018). Model ensemble studies have also found less consistent trends at lower trophic levels compared to higher trophic levels at a global scale, which highlights the uncertainty regarding lower trophic level responses to climate changes (Lotze et al., 2019; Tittensor et al., 2021).

Both global and regional studies of climate change have indicated amplified effects on higher trophic level species (Kirby and Beaugrand, 2009; Lotze et al., 2019). Great efforts have been made to understand the effects of future climate changes on higher trophic level species, ranging from qualitative, expert assessments (Hare et al., 2016; Kjesbu et al., 2021) to more quantitative model-based studies (Fulton, 2011; Hansen et al., 2019b; Skogen et al., 2018; Tittensor et al., 2018), as well studies which combines expert assessment and model efforts (Sandø et al., 2022). Still, the uncertainty regarding responses to climate changes remain high (Heneghan et al., 2021; Lotze et al., 2019). One of the most prominent effects are the displacement of species further north (Fossheim et al., 2015; Frainer et al., 2017; Kjesbu et al., 2021, 2014). Changes in distribution are constrained by species-specific habitat availability, ocean circulation patterns and bathymetry (Gullestad et al., 2020) as well as physiological features like metabolic processes restricted to tolerable thermal windows (Cheung et al., 2013; Payne et al., 2021; Pörtner and Peck, 2010). Although there is some agreement on how temperature impacts physiological processes in general (Kooijman, 2009), there is less agreement on how these impacts vary across functional groups, body sizes, and different processes such as growth and metabolism (van Denderen et al., 2020). The temperature range for a given species typically extends over a temperature interval with optimal conditions in the middle of the temperature range and decreasing tolerance towards upper and lower limits for survival. However, realized growth also depends on ecological factors and evolutionary adaptation that might be equally or more important (van Denderen et al., 2020).

To deal with the threat of substantial changes in marine ecosystems from climate change, a number of quantitative approaches to describe marine ecosystems for management purposes have emerged (Collie et al., 2016). Most quantitative approaches involve ecosystem models to organize and quantify our understanding of ecological processes and project likely consequences of regulations on populations and communities in the context of a changing ecosystem (Dickey-Collas et al., 2014). Ecosystem models are used to systematically arrange and utilize information from observations. Thereby, we can draw conclusions and gain mechanistic understanding that would be difficult to achieve without the model (Skogen et al., 2020). In addition to understanding the current state of an ecosystem, models are commonly used to study the sensitivity and variability of species in so-called what-if scenarios. Ecosystem model can therefore both be used to understand the current state, project the future, and inform about the past (Hyder et al., 2015).

Selecting the appropriate level of detail for a model (Levins, 1966) is often considered as one of the most difficult aspects of the modelling process (Brooks and Tobias, 1996; Law, 1991). To maintain a manageable model, one approach is to simplify the description of each component. Yet, overly simple models may not be able to represent important aspects of ecosystem dynamics and can thus have large model bias. On the other hand, more complex models require increased understanding of species and environmental interactions to specify the dynamics in greater detail. The uncertainty in these models shifts from model bias to parameter uncertainty, due to the higher number of parameters and amount of data needed to estimate them (Collie et al., 2016). While the need for realism pushes model choice towards complexity, the need for empirically based parameters of the system limits complexity, and balancing the desire to represent many components of an ecosystem with the limitations of available data and the modelling objective is therefore challenging (Geary et al., 2020). The uncertainty that is introduced by assuming a certain model structure over any other is often referred to as model uncertainty or structural uncertainty (Geary et al., 2020; Hill et al., 2007).

Various strategies for dealing with this model uncertainty have previously been proposed (Collie et al., 2016; Fulton, 2010; Geary et al., 2020; Ianelli et al., 2016; Knutti, 2010; Spence et al., 2018). One way is to use a set of distinct, plausible models that permit multimodel inference and can be treated as an ensemble. Using multiple models for projections through model intercomparison projects (so called MIPs) can quantify variability between models, drive model development, assess within- and among-model uncertainty, and provide ensemble projections of future change under specified scenarios (Tittensor et al., 2018). Model ensembles are commonly used for analysis in fields such as weather forecasting (Tracton and Kalnay, 1993; Zhou and Du, 2010) and long-term climate prediction (Semenov and Stratonovitch, 2010; Tebaldi and Knutti, 2007), and have been applied to study ecological impacts due to fishing (Spence et al., 2018), species eradications and invasions (Baker et al., 2017) and climate change (Lotze et al., 2019; Reum et al., 2021; Tittensor et al., 2021). The most prominent MIP is the Coupled Model Intercomparison Project (CMIP) (IPCC, 2022), which is currently in its sixth phase of Earth system model simulation experiments, forming an crucial contribution to the sixth IPCC Assessment Report (IPCC AR6).

The Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP) is another example, which was established to explore uncertainty and provide more robust assessments of climate impacts on marine ecosystems through the analysis of multi-model ensembles (Tittensor et al., 2018). Fish-MIP has explored effects of climate changes at global (Lotze et al., 2019; Tittensor et al., 2021) and regional (Bryndum-Buchholz et al., 2020b, 2020a, 2019) scales over the coming century and their potential socioeconomic consequences (Boyce et al., 2020). However, Lotze et al. (2019) found that the spread of changes in biomass under the high emission scenario was larger than change between the median biomass of the low emission and high emission scenarios. This means that structural uncertainty across global marine models is greater than climate scenario uncertainty, which is problematic for the goal of using these models to provide assessments of climate impacts on marine ecosystems and the societal services they provide.

To study potential responses in ecosystem function and structure to climate change, output from climate models is often used as forcing for ecosystem models (Lotze et al., 2019; Tittensor et al., 2021). In the same way as weather forecasts, climate models simulate average weather conditions over a given period, and the models can make predictions about the atmosphere, the oceans, ice, evaporation and the carbon cycle. The models are based on the laws of physics and an understanding of solar radiation, the motions of the Earth, and the properties of the atmosphere, oceans and land. Over the past few years, the IPCC has through the CMIP project used an ensemble of global climate models to develop five narratives to describe alternative pathways for future society (IPCC, 2022). The Shared Socioeconomic Pathways (SSPs) contain a range of baseline scenarios spanning between 1.9 and 8.5 W/m^2 of radiative forcing by 2100 (Riahi et al., 2017) and play an important role in facilitating integrated research across multiple climate modeling communities (O'Neill et al., 2016).

Further, regional downscaling of the global models may be applied. Here, a high-resolution regional ocean circulation model is initiated from, and/or nested into, a global climate model (Skogen et al., 2018). This is done to translate coarse global information into finer scale resolution in order to simulate regional processes more accurately and obtain climate information on scales that are relevant to society (Ekström et al., 2015). Regional models also have the advantage of better-calibrated parameterizations targeted for the study regions (Hordoir et al., 2022). Previous studies have explored the impact of downscaling and found that higher-resolution physical forcing produces results closer to observations and provides a better representation of ocean dynamics and variability (Busecke et al., 2019; Kirtman et al., 2012; Langehaug et al., 2019; Melsom et al., 2009; Sandø et al., 2014; Skogen et al., 2018). However, the process of downscaling physical forcing is both time consuming and labor demanding (Chassignet et al., 2020), which can delay or limit the physical forcing available for ecosystem modelers (Sandø et al., 2014). Some ecosystem models also have resolution grids coarser than those of high-resolution downscaled products (Hansen et al., 2016; Lindstrøm et al., 2009; Pedersen et al., 2021; Planque et al., 2022, 2014; Stige et al., 2019), which suggests that a rigorous test of the value of downscaled physics for these ecosystem models is warranted.

The need to evaluate the effects of climate changes on ocean ecosystems is crucial and using ecosystem models in combination with physics from climate models can help us organize and quantify our understanding of how climate changes affect ecological processes. However, as previous efforts have shown, there is still a great amount of uncertainty regarding future modelling projections. This uncertainty can arise from model uncertainty related to the level of complexity of the ecosystem model, uncertainty regarding future climate projection or uncertainties regarding species responses to temperature change. Explicitly considering different forms of uncertainty is therefore a primary concern.

1.2 Motivation and objectives

The motivation behind this study is to address the uncertainty regarding future ecosystem responses by applying multiple ecosystem models, physical models, and climate scenarios to study ecosystem responses. By quantifying this uncertainty, we can highlight consistent results that suggest higher confidence, and areas where differences in the results suggest that more research is needed.

The objective behind this thesis was threefold:

1. Study the structural uncertainty in model predictions by applying ecosystem models of different complexity.
2. Study the uncertainty regarding the resolution of climate projections by applying physical forcing of various resolution.
3. Study the effects of future climate change in the Nordic and Barents seas and explore temperature dependence in ecosystem components.

By addressing these objectives, we build upon an extensive amount of previously conducted research. Although incorporation of multi-model approaches for ecosystem studies is increasingly utilized (Spence et al., 2018; Tittensor et al., 2018), there have been few studies specifically investigating the effect of model structure on the behavior of marine ecosystem models (Fulton et al., 2003). Kaplan et al. (2019) represent an example of such a study, where the role of Pacific sardine in the California Current food web was investigated by using three ecosystem models of varying complexity. Studies of the impact of increased model resolution on the physics (Busecke et al., 2019; Kirtman et al., 2012; Langehaug et al., 2019; Melsom et al., 2009; Sandø et al., 2014; Skogen et al., 2018) and how this affects timing of spring bloom and net primary production (Hansen and Samuelsen, 2009; Skogen et al., 2018) have also previously been conducted. Yet, few studies have focused on the effects on higher trophic levels, and how the benefit of downscaling translates to a coarse resolution ecosystem model. This is highly important to understand to what degree climate from global models can be used to project effects of climate changes for these types of studies.

Assessing climate risk is now shifting from qualitative, expert judgment (Hare et al., 2016), to quantitative predictions of climate impacts on particular species (Kjesbu et al., 2021; Sandø et al., 2022). Using ecosystem models to study the effects of future climate change in the Nordic and Barents seas have been done (Hansen et al., 2019b), but mainly by using single climate scenarios. In our study we address the uncertainty regarding the species responses to temperature change by considering various climate scenarios and alternate responses in lower trophic levels. By comparing the responses under the various climate scenarios, we identify potential winners and losers in in a warmer future and explore the species' vulnerability to changes in lower trophic levels.

Although climate change has many different manifestations (e.g. ocean acidification, thermohaline circulation alteration, stratification, oxygen (Doney et al., 2012)) we mainly focus on the effects of temperature changes in our study, but we also account for effects of decreasing sea ice cover, light availability and various responses in lower trophic levels. An important advantage of simulated data is their potential to disentangle which driving mechanisms lead to the simulated response, and thereby advance our understanding of the natural system (Skogen et al., 2020). Understanding the underlying mechanisms of ecosystem changes is key to improve scientific advice and develop to forecasts to inform fishery management (Karp et al., 2019). In this thesis we therefore focus on the mechanisms that drives the changes when analyzing the results.

2. Ecosystem models and study area

In this chapter we give a brief introduction to the ecosystem models that were applied in thesis, as well as a description of the Nordic and Barents Seas

2.1 NoBa Atlantis

The Atlantis modelling framework (Audzijonyte et al., 2019; Fulton et al., 2011) is one of the most complex marine end-to-end ecosystems models in the world (Plagányi, 2007), and is designed to cover the entire ecosystem and integrate all relevant economic and social aspects (Fulton et al., 2011). The model was originally developed at the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia by Dr. Elizabeth A. Fulton and her team and have been applied to several places around the world, mostly in Australian, U.S, and European waters (Weijerman et al., 2016), and models for other areas are under development (CSIRO, 2022). The Atlantis model used for this thesis is the Nordic and Barents Seas Atlantis model (hereafter NoBa) developed by Hansen et al. (2016).

The NoBa model includes all trophic levels from phytoplankton to marine mammals, represented by 53 species and functional groups (Figure 1). Most species are modelled as individual species or aggregated into functional groups with species of similar life history and ecological characteristics. The species are connected through a diet matrix where the proportion of prey in the predator´s diet is defined. The availability of prey also depends on spatial and temporal overlap, as well as the gape size limit which relates to the size of the prey compared to the mouth of the predator. Most vertebrate species are age-structured while invertebrates are gathered into biomass pools. The biomass of vertebrates is also divided into numbers-at-age and weights-per-individual. This separation enables detection of changes driven by population dynamics (numbers) or growth and consumption (weights).

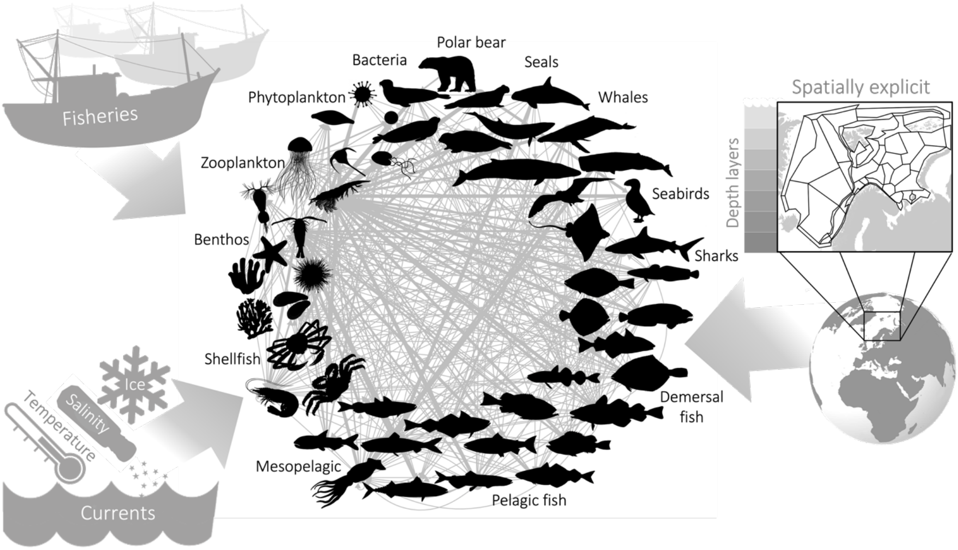

Figure 1. Conceptual figure of the NoBa Atlantis model showing species and functional groups connected through the diet matrix, an overview of the polygons in the model domain as well as impacts from fisheries and physical forcing including temperature, salinity, currents, and ice. Modified from Nilsen et al. (2022)

The model combines oceanography, population dynamics, spatial distributions, nutrient cycling, fisheries, and species interactions in a spatially explicit domain. The total area of 4 million km^2 is divided into 60 polygons with up to 7 depth layers depending on total water column depth (Hansen et al., 2016). The species can move between polygons and layers either actively through swimming (e.g., fish, whales) or passively transported by currents (e.g., plankton, egg, larvae, nutrients). While planktonic species drift along with currents, the majority of the vertebrate species swim actively and have forced migration to ensure seasonal movement patterns throughout the year (Audzijonyte et al., 2017).

NoBa is forced bottom-up by daily inputs of mean temperature, salinity and sea-ice in each polygon and depth level, as well as currents through net transport of water ($m^3 s^{-1}$) between the polygons. The physical forcing from Regional Ocean Circulation models (Hordoir et al., 2019; Shchepetkin and McWilliams, 2005) covering the Northeast Atlantic are normally used.

The temperature affects the species growth and consumption equations (Audzijonyte et al., 2017), but an additional temperature sensitivity option, here referred to as "thermal niche", can also be applied. The thermal niche restricts the species to spawn or reside in polygons within their tolerated temperature range, and the temperature ranges set in NoBa were based on literature (Hansen et al., 2016). The presence of sea ice affects the primary production by limiting the availability of light, and a species-specific sensitivity to ice can also be included where species are either positively or negatively affected by ice.

NoBa Atlantis includes a harvest sub-model that allows for multiple fishing fleets with their own set of features like gear selectivity, target species and management structures. In this thesis, historical fishing levels were applied for the hindcast period (year 1980-2020) using catch assessments and total stock biomass data (ICES, 2021, 2020). After this, the fishing mortality for the last year (year 2020) was applied each year for the rest of the simulation. The fishing mortality was applied to the adult stock and was evenly distributed across the model domain.

The Atlantis modelling framework has been rated as one of the best "what if" scenario models in the world (Plagányi, 2007), and the NoBa model has been thoroughly tested to ensure that the model behaves reasonably (Hansen et al., 2019a). Previous studies have also used Atlantis models to evaluate impacts of fishing strategies (Hansen et al., 2019b; Nilsen et al., 2020), ocean acidification (Fay et al., 2017; Kaplan et al., 2010; Olsen et al., 2018), potential oil spills (Olsen et al., 2019), spatial management (Kaplan et al., 2012) as well as climate changes (Bossier et al., 2018; Fulton, 2011; Ortega-Cisneros et al., 2018). More detail about the model set-up can be found in Hansen et al. (2016), and information about how the model was used in our studies can be found in each paper.

2.2 Gompertz

In the first paper we compared the NoBa Atlantis model to a Gompertz model. Gompertz models are widely applied in biology, and have been used to describe animal growth and multispecies dynamics as well as bacteria growth and cancer (Hampton et al., 2013; Ives et al., 2003; Laird, 1964; Langangen et al., 2014; Stige et al., 2018; Vaghi et al., 2020; Winsor, 1932; Zwietering et al., 1990). For this study, a state-space version of the Gompertz model was used and analyzed. This model was originally developed by Stige et al. (2019) to study the direct and indirect effects of sea ice cover on the major zooplankton groups and planktivorous fish in the Barents Sea, and will hereafter be referred to just as "Gompertz".

Gompertz is a relatively minimalistic ecosystem model that focus on five species or species groups: capelin, polar cod, krill, amphipods, and copepods (Figure 2). These five species are modelled dynamically. The effects of the two key predators; cod and herring, as well as impacts from fishery and ice cover are included as covariates.

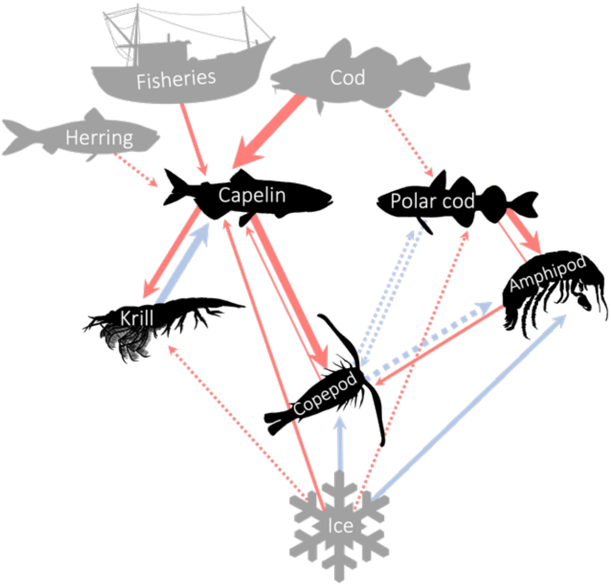

__Figure 2.__ Conceptual figure of the Gompertz model including the dynamically modelled species (black), and other key abiotic or biotic variables (grey). Thickness and color of arrows represent estimated effect of positive (blue) or negative (red) interaction, while line type indicates significance. Modified from Nilsen et al. (2022) and Stige et al. (2019)

Climate is represented through a time series of annual winter sea ice concentration, while fishing is given as a fraction of biomass removed. Fishing is applied to capelin as it is the only dynamic species that was significantly harvested historically during the period with available data (1980-2015).

The model is fitted in a Bayesian state-space framework, where the species and processes are described by a set of state variables and equations referred to as the "process model". The process model consists of five equations, one for each of the dynamically modelled species. The compact form representing log-scaled biomass is given in equation 1. The process model describes how the biomass (X) at time (t) of a species depends on productivity (a), density dependence (b) and biotic and abiotic effects from the other species (c). In addition, process error (δ) was included, which account for environmental factors not included in the model. With the Bayesian state-space approach, the process model is linked to data by an observation model, which estimates the strength of the interactions between the species while accounting for uncertainties about biological processes and observation noise.

The general compact form:

$$x_t = \quad a \quad + \quad bx_{T-1} \quad + \quad c\, z_{T-1} \quad + \quad \delta T \tag{1}$$

More information regarding how the model was set up can be found in Stige et al. (2019), and details of how it was used in our study can be found in Paper I, chapter 5.1, Nilsen et al. (2022).

2.3 The Nordic and Barents seas

Throughout history the seas surrounding Norway have provided an abundant supply of fish as a nutritious and high-quality source of food. Even though it is a small country in terms of people, Norway has one of the longest coastlines in the world and is managing ocean areas of 2,3 mill km^2.

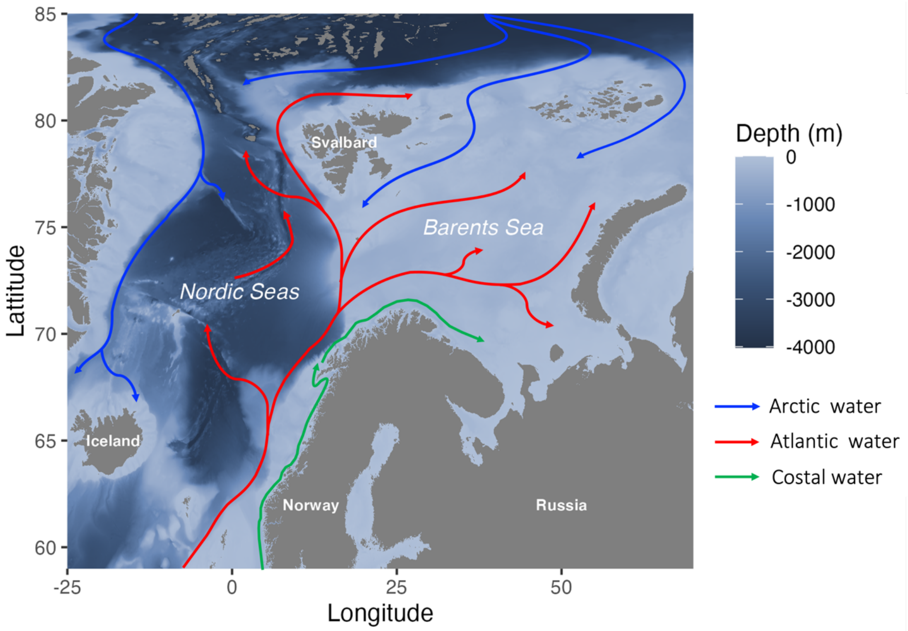

Figure 3. *Map of the bathymetry and surface circulation of the Nordic and Barents Seas. The Atlantic currents are included in red, the Arctic or Polar Waters are in blue and the Coastal Waters are in green. The map of the currents is based on previous published figures (Lien et al., 2016; Oziel et al., 2020)*

The Nordic Seas consists of the Norwegian, Greenland and Iceland seas, which covers an area of 2.5 million km^2 in the most northern part of the Atlantic Ocean. The eastern part is characterized by a relatively warm surface water of Atlantic origin, whereas the deep water masses below 750m are of Arctic origin, with temperatures below 0°C (Blindheim and Østerhus, 2005). In the western part, the waters are of Arctic origin and generally cold. The Nordic Sea is divided into several separate basins of 2000-4000 meters depth, with maximum depth of 4020 m.

The Barents Sea is a subarctic shelf sea of approximately 1.4 million km^2 located north of Norway and Russia. It is separated from the Nordic Seas by the continental slope between Norway and Svalbard. Despite being the deepest of the Arctic Shelf Seas, it has a relatively shallow average depth of 230 m, although deeper channels and basins of 500 m exist (Sakshaug et al., 2009). The Barents Sea is seasonally covered by sea-ice (ranging from maximal ice cover in March and the lowest sea ice cover in September (Onarheim et al., 2018), although annual sea ice cover has decreased since the 1980s (Onarheim and Årthun, 2017).

Oceanography

The circulation in the Nordic and Barents Seas is strongly affected by the topography (Mork & Skagseth, 2010). From the south flows warm, high salinity Atlantic water which gradually becomes cooler and less salty on its way north due to mixing with the coastal current and arctic water, as well as precipitation and heat loss to the atmosphere (Østerhus et al., 2005; Skagseth et al., 2011). This heat transport along the Norwegian coast and the vertical heat flux in the Barents Sea are part of the so-called Atlantic Meridional Overturning Circulation (AMOC), where warm and salty water is transported northwards near the surface were it gradually cools and sink and is then transported southwards at depth. Cold, low salinity Polar Water, which originates in the Arctic Ocean, is transported by the East Greenland Current into the Nordic Seas along the east coast of Greenland, while the low salinity Norwegian Coastal Current which originates primarily from the Baltic and the freshwater runoff from Norway flows northwards along the Norwegian coast (Sætre, 2007).

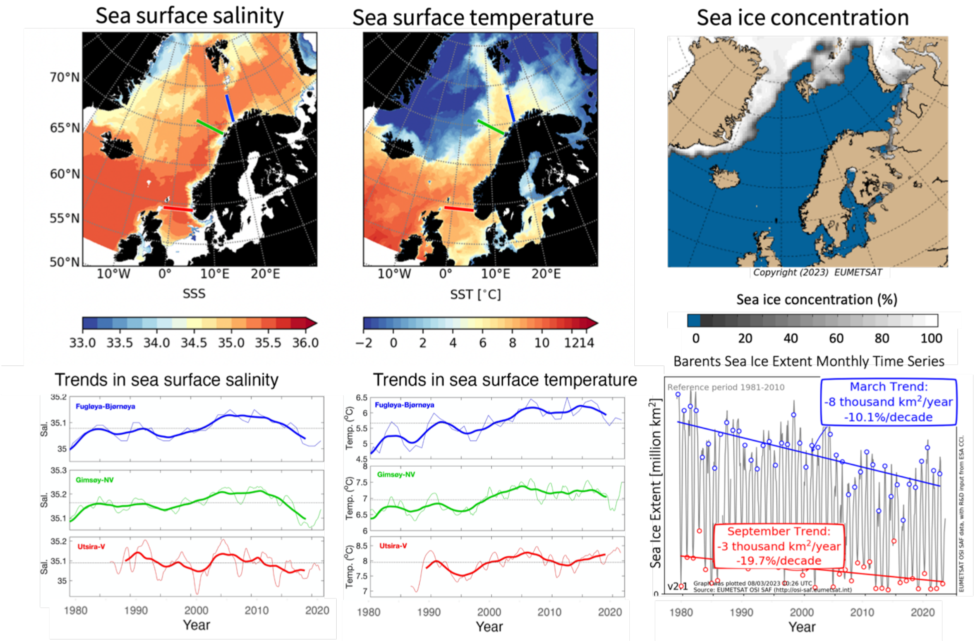

Figure 4. *Map of simulated sea surface salinity (SSS), simulated sea surface temperature (SST), and observed sea ice cover (top) where SSS and SST are based on model outputs from Nemo-NAA10km and show simulated winter values for year 2000 as an illustration, while the ice cover is based on observations from EUMETSAT OSI SAF. Trends over the last 40 years are also included (bottom) where SSS and SST observations from three various transect along the Norwegian coast (marked in map) are included (Havforskningsinstituttet, 2022), as well observed trends in ice cover for winter (March, blue) and summer (September, red) (EUMETSAT OSI SAF).*

Over the past decades, the Nordic and Barents Seas have experienced changes due to climate change (Skagseth et al., 2020). The change in sea ice cover in the Barents Sea is one of the most visible signs, where observations document a 50% decline in the winter sea-ice extent (Årthun et al., 2012). In the Barents Sea, sea surface temperature has increased by 1°C during the last 40 years (Timmermans & Ladd, 2019), and temperatures have also increased in the Nordic Seas (Tsubouchi et al., 2021). Salinity have also been increasing leading to a shift in the Nordic and Barents Seas from cold and fresh conditions during the 1980s and 1990s to relative warm and saline conditions towards 2010. However, the last couple of years this trend has declines, especially for salinity which is now at lower levels similarly to the 1970s (Havforskningsinstituttet, 2022).

Ecosystem

The ecosystem in the Nordic Seas has a relatively low biodiversity, but the food chain is productive and certain species occur in very large numbers. The phytoplankton establishes the bottom of the food chain and is found in enormous quantities during the short, but intense spring blooms. Zooplankton species, like *Calanus finmarchicus*, is consumed by abundant pelagic fish and a variety of marine mammals including minke whales and larger whales such as humpback and fin whales (Gjøsæter et al., 2009).

The fish community in the Nordic Seas is characterized by large stocks of medium sized pelagic species such as Norwegian spring spawning herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*). These stocks are highly migratory and none of them spend their entire life cycle within the Norwegian Sea. Both blue whiting and mackerel spawn west of the British Isles and the North Sea, before migrating back into the Nordic Seas. Norwegian spring spawning herring, on the other hand, has its main spawning and feeding areas in the Nordic Seas, but the main nursery area is in the Barents Sea. Mackerel vertical distribution is typically closer to the surface, herring is often distributed somewhat deeper, while the blue whiting has the deepest distribution (ICES, 2008). Other abundant species include whales, seabirds, as well as mesopelagic fish like pearlside (*Maurolicus muelleri*) and lanternfish (*Benthosema glaciale*), which have a dial vertical migration and are important as food for several commercial species.

The ecosystem of the Barents Sea is surprisingly diverse considering its northern distribution. Krill and amphipods are key components in the diet of many ecologically and economically important fish species in the Barents Sea. Juvenile herring drifts along the Norwegian coast after hatching and also ends up in the Barents Sea (Olsen et al., 2010), and is along with capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) considered as key species in the Barents Sea food-web, transferring energy from lower trophic levels to higher trophic levels (Hop & Gjøsæter, 2013). Northern shrimp (*Pandalus borealis*) is an important prey for several fish species, and is also commercially harvested (ICES, 2008).

The Barents Sea holds the largest cod stock (*Gadus morhua*) in the world, and cod is considered the most important predator in the area feeding on a variety of prey. Haddock (*Melanogrammus aeglefinnus*) and saithe (*Pollachius virens*) also represent important predators that are commercially harvested. Beaked redfish (*Sebastes mentella*) and golden redfish (*Sebastes norvegicus*) are slow-growing, deep-water species that have been heavily fished, and their fishing is now strictly regulated to rebuild the stocks. Greenland halibut (*Reinhardtius hippoglossoides*) is found around the eastern shelf and is also commercially exploited. Snow crab (*Chionoecetes opilio*), is a new species in the Barents Sea where it was first observed in 1996 (Kuzmin et al., 1999), and has gradually increased its abundance in the later years. Seabirds and whales are also present, and minke whales are by far the most abundant whale species (Øien, 2009).

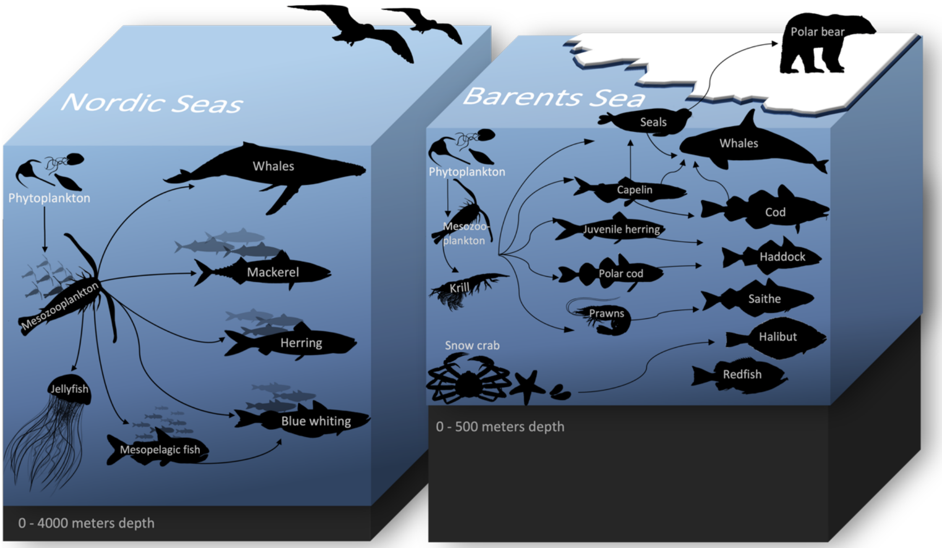

Figure 5. *Simplified representation of some of the key ecosystem components in the Nordic and Barents Seas. The lines indicate how energy flow from lower to higher trophic levels.*

The species of the Nordic and Barents Seas are exposed to extensive seasonal variability in terms of light availability, fluctuations in temperature as well as formation and melting of sea-ice. Through the course of evolution these species have adapted to these variable conditions with their own sets of unique physiological and biochemical traits that are necessary for surviving in these harsh conditions (Jakobsen and Ozhigin, 2012).

However, the recent warming due to climate change in the Nordic and Barents Seas has led to a change in spatial distribution of fish communities, with boreal communities expanding northwards as the Arctic is warming (Frainer et al., 2021). Arctic species, on the other hand, suffer from increased competition and predation from boreal species, as well as decreases in suitable habitats (Hodapp et al., 2023) and are retracting and declining (Fossheim et al., 2015). Understanding how climate changes are altering the structure and composition of Arctic ecosystems is therefore vital.

3. Introduction to papers

This chapter briefly summarize the papers produced in this thesis, as well as important findings and contribution to science.

3.1 Paper I:

Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach

Ina Nilsen, Cecilie Hansen, Isaac Kaplan, Elizabeth Holmes and Øystein Langangen*

To address the structural uncertainty related to model complexity, we compare two different ecosystem models: a minimalistic model based on relatively few species (Gompertz) and a highly complex model (Atlantis). We apply this multi-model approach to investigate the role of the Northeast Arctic (NEA) cod (*Gadus morhua*) in the Barents Sea, with a focus on the effects of the size of the NEA cod stock on capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*).

These models differ in complexity, number of species, and the amount of time required to run and build them. However, both models are comparable in terms of spatial and temporal scale and the links between NEA cod and capelin and polar cod. To compare the response to changes in the size of the NEA cod stock, we perturbed the historical fishing pressure by ±50% and used the same NEA cod biomass in both models (Figure 6). We then identified consistent results across models, and as well as divergence between the two. Rather than trying to select a 'best' model, we compared the models mechanistically by exploring the strengths of each model, while learning from the differences between them.

The results from our study indicate that indirect effects, through other food-web components present in the Atlantis model but not in the Gompertz model, might be as important as the direct predator-prey interactions. Differences in spatial structure of the models, and therefore the overlap between species, also influenced how strongly the species responded to the perturbations. We concluded that for fishery management purposes, the two models can complement each other, and that the differences highlighted important areas where more knowledge is needed. Our study also supports the idea that fisheries management strategies could benefit from using multiple models of varying complexity, rather than relying on single models to assess ecosystem impacts of management and predator abundance.

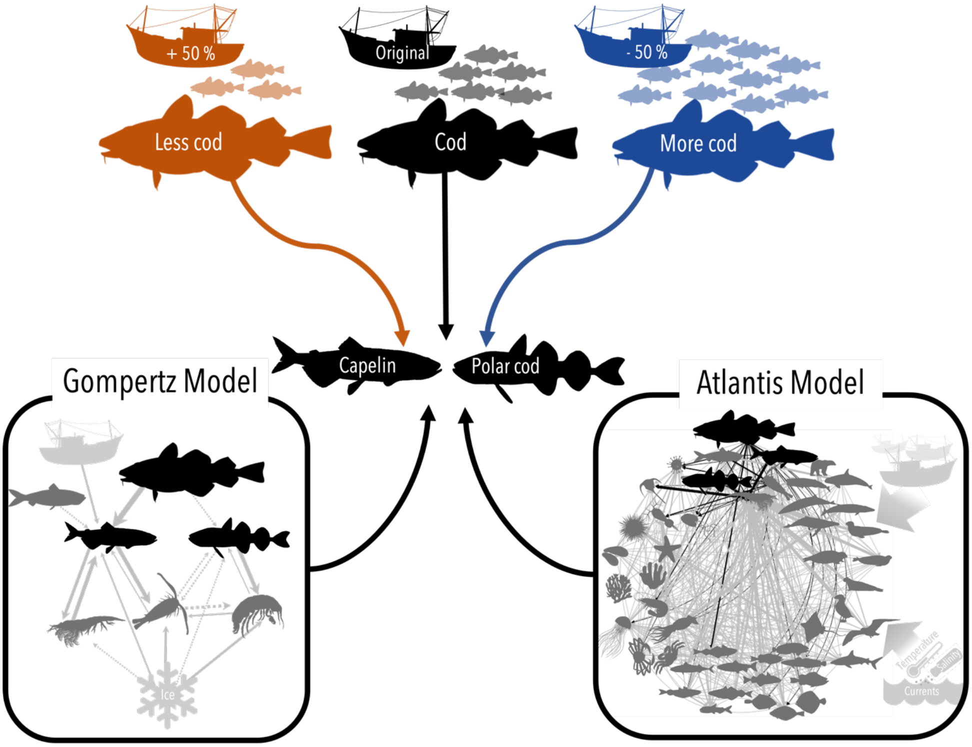

Figure 6. *Conceptual figure of the set-up of Paper I, where the biomass of cod was perturbated through fishing, resulting in three scenarios with varying levels of cod. The effect of cod on capelin and polar cod were then examined in a minimalistic Gompertz model and in a complex Atlantis model.*

3.2 Paper II:

Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas

Ina Nilsen, Filippa Fransner, Are Olsen, Jerry Tjiputra, Robinson Hordoir and Cecilie Hansen*

Downscaling physical forcing from global climate models translates coarse information to a regional scale to better capture the dynamics of primary production and lower trophic levels. However, the process is both time consuming and labor demanding, and it is not clear how important it is for representation of higher trophic levels in coarse ecosystem models.

In this study we therefore focus on higher trophic level species and apply the Nordic and Barents Seas Atlantis ecosystem model (NoBa) to study the consequences of using physical forcing from a global climate (NorESM2) model versus using that from a regional model (Nemo-NAA10km). We apply physical forcing from the SSP5-8.5 scenario and adapted the physics from the two climate models to the NoBa grid before applying it in the model.

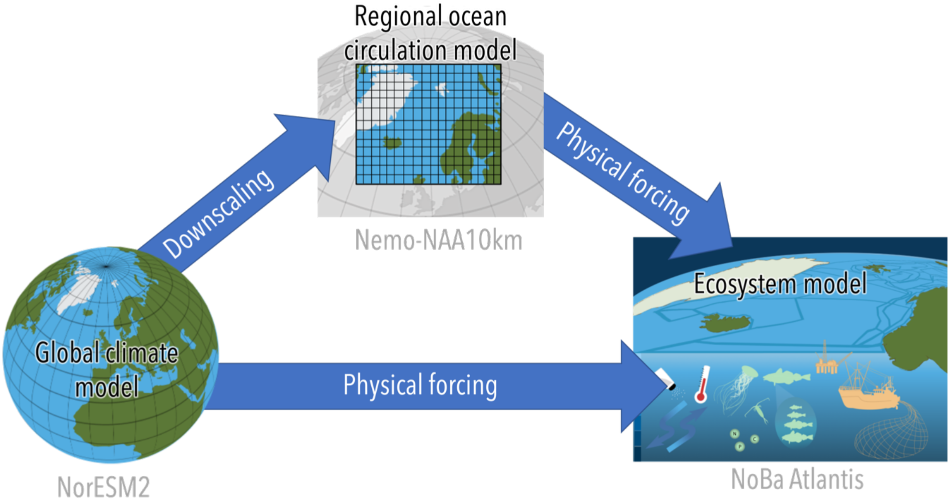

Figure 7. *Conceptual figure of the set-up for Paper II, where physical forcing from a global (NorESM2) and a regional (Nemo-NAA10km) oceanographic model was applied to an ecosystem model (NoBa).*

To investigate the extent to which a global climate model can be used for regional ecosystem predictions we addressed three research objectives:

1. How the physics from the two oceanographic models differ after being fitted to the NoBa grid.
2. How the differences in physics affect higher trophic level species.
3. How future climate changes affect the ecosystem when accounting for the uncertainty from applying two sets of physical forcing with varying resolution.

The results from our study showed slight differences in temperature, salinity and ice cover between the two sets of physical forcing after being tailored to the NoBa grid. However, we found that few higher trophic level species were affected by using forcing from a global versus a regional model, and there was a general agreement on future biomass trends and distribution patterns. However, the slight difference in temperature between the models dramatically impacted Northeast Arctic cod (*Gadus morhua*), which highlights how species projection uncertainty could arise from poor representation of the physical forcing, in addition to uncertainty in the ecosystem model parameterization.

We concluded that for modelers lacking downscaled physics, the physical forcing from a global model can be sufficient for studying higher trophic levels. Yet, the case of cod demonstrated the importance of downscaling essential ocean features for the species that are being studied, in our case the temperatures at cod spawning grounds. Our study also highlighted the value of not only using multiple ecosystem models or climate projections, but also physical forcing of varying resolution to assess uncertainty.

3.3 Paper III:

A shifting chessboard: projections of prawn, capelin, mesopelagic fish, zooplankton, and their Nordic and Barents Seas food web under climate change.

Ina Nilsen, Isaac Kaplan and Cecilie Hansen*

In this study we investigated the effect of climate change in the Nordic and Barents Seas by using the NoBa Atlantis model. We applied downscaled physics from three Shared Socioeconomic Pathways (SSPs) scenarios ranging from low (SSP1-2.6), medium (SSP2-4.5) and high CO_2-emission (SSP5-8.5) to study the differences that arise between the species for the different scenarios. To account for high uncertainty in how phyto- and zooplankton will respond to future climate change, we also included variation in the simulations by changing the growth rate of phyto- and zooplankton. This was the first study where physical forcing from three different SSP scenarios has been applied to an ecosystem model in this area, and we therefore treat the results with caution and focus on the underlying mechanisms of the model.

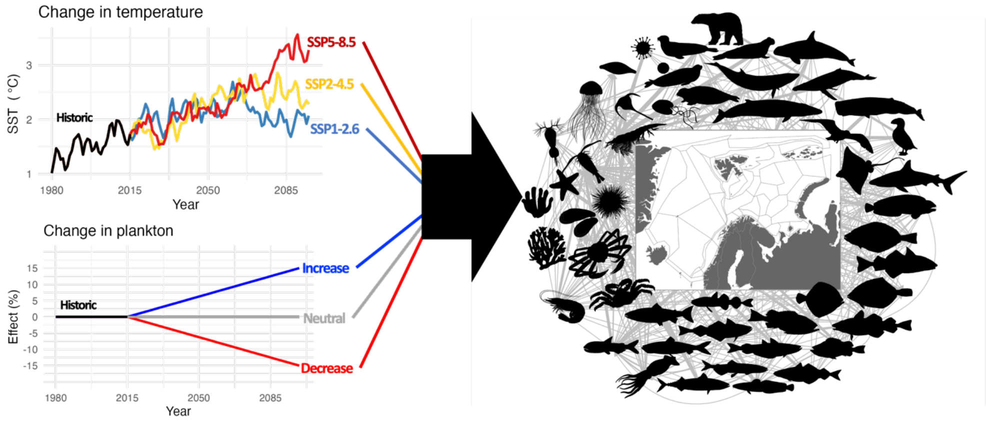

Figure 8. Conceptual figure of the set-up of Paper III, where the combined effects of changing temperatures and varying levels of plankton were examined in the NoBa Atlantis model. The black lines represent the historic period from 1980-2015, while the colored lines show how changes in physical forcing and changes in plankton was applied after year 2015

We identified several important mechanisms in the model, including thermal sensitivity, shifts in diets, predator-prey overlap and cascading effects. Key mid- and lower-trophic level groups projected to respond to climate change were mesopelagic fish, prawns, capelin, and large zooplankton, and the effects on these groups cascaded to other species, especially predators. The spatial nature of the model also allowed us to study how local changes in temperature and prey could affect entire populations.

We conclude that future ecosystem studies could benefit from both modeling and empirical studies that consider not only broad-brush impacts on primary production and trophic transfer, but also spatial considerations of local predator-prey interactions and thermal habitat and spawning-area suitability. Our results agree with previous modeling and expert-based vulnerability assessments for the Nordic and Barents Seas, but also suggest new vulnerabilities and mechanisms.

3.4 Contribution to science

Through our work we have demonstrated the value of using ecosystem models of varying complexity, climate models of varying resolution and climate projections under various emission scenarios to assess and understand the uncertainty regarding model projections. In line with other highly-profiled Intergovernmental climate assessments (IPCC, 2022; Tittensor et al., 2018) we highlighted how this can improve our understanding and build trust in ecosystem models.

We demonstrate how the use of multiple ecosystem models to study ecosystems can improve our understanding of the models and their underlying mechanisms, as well as provide useful information in terms of mechanisms we are uncertain about and point to areas that need more research. Our study supports the idea that fisheries management strategies can benefit from using models of varying complexity to capture a broad range of ecosystem responses, rather than relying on single models to assess ecosystem impacts.

By comparing outputs from a coarse resolution ecosystem model using physics from a regional climate model and its driving global model, we found that for modelers lacking available downscaled physical forcing, using physics from a global model could be sufficient to study climate effects on higher trophic level species. In line with other studies (Drenkard et al., 2021) we support the idea that the primary objective of downscaling should be to resolve important ocean features for the species that are being studied, if those features are not captured by the global climate model. In our case this was illustrated by the importance of temperature at spawning grounds for Northeast arctic cod, which must be downscaled properly given what we know about that species and how it is represented in the ecosystem model.

Through simulating future climate change in the Nordic and Barents Seas we identified high-priority species such as mesopelagic fish, prawns, capelin, and large zooplankton, due to their responses to the changing temperature as well as their tight linkage to other species, especially predators. As in earlier projections of climate change impact in Australia (Fulton, 2011), we found both winning and losing species under climate change, but also 'surprises' that were not anticipated by earlier modeling or expert-based vulnerability assessments. Perhaps more importantly, we highlighted several important mechanisms in the model, including thermal sensitivity, shifts in diets, predator-prey overlap and cascading effects, which should be considered when studying effects of climate change.

Through working with this thesis, we have also developed three sets of downscaled physical forcing for the NoBa Atlantis model, including SSP1-2.6, SSP2-4.5 and SSP5-8.5, as well as physical forcing from a global model for SSP5-8.5. Since the NoBa Atlantis model was set up in 2016, there has only been one set of physics available representing the rcp4.5 scenario from CMIP5 (Shchepetkin and McWilliams, 2005), and the development of multiple sets of physical forcing various future climate will be highly valuable for future studies using the NoBa Atlantis model.

Our results have broad relevance not just in the Barents and Nordic Seas, but also in other regions as fishery managers must increasingly cope with the shifting distribution and productivity of species due to climate change. Karp et al., (2019) have highlighted the understanding mechanisms and evaluation of risks and priorities as two of the six steps toward climate-informed fishery management. Our results particularly address mechanisms and priorities. Our analysis specifically addresses these two issues, and points to the need for both empirical and modeling studies to understand and detect spatial considerations of local predator-prey interactions and thermal habitat and spawning-area suitability.

4. Future perspectives

By using multiple ecosystem models of varying complexity in Paper I, we identified strengths and weaknesses related to model complexity. However, according to Collie et al. (2016) there is a 'sweet spot' along the gradient from simple to complex that balances model bias and parameter uncertainty which are defined as models of intermediate complexity. Future studies could benefit from applying such intermediate models to identify how those compare to simple and complex model, whether the responses would lie somewhere in between, or be completely different from models with alternate levels of complexity. Paper I also identified uncertainties regarding polar cod, as the direction of the response of polar cod differed between the complex and simple ecosystem models. The study shows that using multiple ecosystem models are useful to improve and support a more holistic management approach.

In Paper II, where we investigated what we gained from downscaling physical forcing from a global model, we interpreted this at the resolution of the NoBa model grid. Although we demonstrated that using physics from a global model could be sufficient for studying climate effects on higher trophic levels, it is not clear how this would translate to other ecosystem models with different grid resolution or other species included. Applying physics of various resolution to ecosystem models with other grids or in other regions is therefore important to fully assess the benefits of downscaling physical forcing for ecosystem models.

For both Papers II and III, turning on the thermal niche affected the species' responses to temperature, both in terms of collapses due to temperatures being too low (Paper II) and decreases due to temperatures being too high (Paper III). The temperature ranges in NoBa are based on literature, but species temperature tolerance is uncertain, especially for the functional groups where multiple species are grouped together, and for non-commercial species where information is scarce. Increasing efforts to understand species tolerates temperature limits should therefore be prioritized, as this is an important part of projecting responses to future climate changes. In addition, the polygons in NoBa are large and the coarse resolution makes it challenging to represent temperature tolerance as there might be suitable habitats within the polygons although the mean temperature is outside the reported thermal niche. There are multiple options to determine how the thermal sensitivity affects species in Atlantis models (Audzijonyte et al., 2017), and exploring these options to include more “soft” responses to temperature (e.g. Gaussian curves instead of the currently applied cut-off shape) should therefore be investigated for future studies.

The forced migration patterns of the modelled species in NoBa also represented a limitation to this study. As the option restricts species to be in certain polygons at specific times and to follow the observed seasonal migration patterns, the option of tracking distributional changes due to climate change were reduced, as species could only redistribute within the given polygons in which they are currently observed. As recent observations and studies have shown that boreal species are increasing their distribution further north (Fossheim et al., 2015; Mueter et al., 2021), the need to study such potential shifts is essential. Currently there are no possibilities in Atlantis for combining the strong seasonal spawning and feeding migrations, with redistribution due to temperature and food availability. Recoding the Atlantis framework to allow for such potential shifts is therefore highly important and should be considered for future studies.

In high-latitude ecosystems where species are specialized to cope with extreme differences in seasonal variability, the species’ ability to adapt to climate changes should also be considered when studying the effects of climate change. Currently, climate-adaptive measures are largely missing from fisheries management policies and approaches (Barange et al., 2018; Holsman et al., 2019; Karp et al., 2019), and Intergovernmental climate assessments have highlighted the need to evaluate existing fishery management plans for maladaptation to climate change (Barange et al., 2018; IPCC, 2022). Allowing for shifts in distribution is one way to deal with this, but also considering the species capacity to adapt to changes in temperatures should be prioritized.

NoBa was the first Atlantis model to be set up for high-latitude ecosystems, with large seasonal variance in light and sea-ice (Hansen et al., 2016). The ice-module is still under development at CSIRO and has only previously been set up for an Atlantis model representing the Eastern Antarctica that is currently under development. These studies thereby represent the first attempt at applying seasonal sea ice in an Atlantis model. Our results showed that adding ice as forcing had a weak effect on the species, also Arctic species which are known to be highly dependent on ice (e.g. polar cod, polar bear) (Gjøsæter et al., 2020; Kjesbu et al., 2021). This suggests that further development of the ice parameters in the NoBa model and other Atlantis models is needed to properly address the effects of reduction on sea-ice in high-latitude ecosystems.

Although our study mainly addresses the effects of changing temperature, climate change has many different manifestations (e.g., ocean acidification, thermohaline circulation alteration, stratification, changes in oxygen levels, invasive species). In order to fully assess future climate risks, the effects of these factors also need to be thoroughly examined.

Literature

Årthun, M., Eldevik, T., Smedsrud, L.H., Skagseth, Ø., Ingvaldsen, R.B., 2012. Quantifying the Influence of Atlantic Heat on Barents Sea Ice Variability and Retreat. Journal of Climate 25, 4736–4743. https://doi.org/10.1175/JCLI-D-11-00466.1

Audzijonyte, A., Gorton, R., Kaplan, I.C., Fulton, E.A., 2017. Atlantis User's Guide Part I: General Overview, Physics & Ecology.

Baker, C.M., Gordon, A., Bode, M., 2017. Ensemble ecosystem modeling for predicting ecosystem response to predator reintroduction. Conservation Biology 31, 376–384. https://doi.org/10.1111/cobi.12798

Barange, M., Bahri, T., Beveridge, M., Cochrane, K., Funge-Smith, S., Poulain, F., 2018. Impacts of Climate Change on Fisheries and Aquaculture. Synthesis of Current Knowledge, Adaptation, and Mitigation Options, T627. FAO Fisheries and Aquaculture Technical Paper, Rome, Italy.

Blindheim, J., Østerhus, S., 2005. The Nordic Seas, Main Oceanographic Features, in: The Nordic Seas: An Integrated Perspective. American Geophysical Union (AGU), pp. 11–37. https://doi.org/10.1029/158GM03

Bossier, S., Palacz, A.P., Nielsen, J.R., Christensen, A., Hoff, A., Maar, M., Gislason, H., Bastardie, F., Gorton, R., Fulton, E.A., 2018. The Baltic Sea Atlantis: An integrated end-to-end modelling framework evaluating ecosystem-wide effects of human-induced pressures. PLOS ONE 13, e0199168. https://doi.org/10.1371/journal.pone.0199168

Boyce, D.G., Lotze, H.K., Tittensor, D.P., Carozza, D.A., Worm, B., 2020. Future ocean biomass losses may widen socioeconomic equity gaps. Nat Commun 11, 2235. https://doi.org/10.1038/s41467-020-15708-9

Brooks, R.J., Tobias, A.M., 1996. Choosing the best model: Level of detail, complexity, and model performance. Mathematical and Computer Modelling 24, 1–14. https://doi.org/10.1016/0895-7177(96)00103-3

Bryndum-Buchholz, A., Boyce, D.G., Tittensor, D.P., Christensen, V., Bianchi, D., Lotze, H.K., 2020a. Climate-change impacts and fisheries management challenges in the North Atlantic Ocean. Marine Ecology Progress Series 648, 1–17. https://doi.org/10.3354/meps13438

Bryndum-Buchholz, A., Prentice, F., Tittensor, D.P., Blanchard, J.L., Cheung, W.W.L., Christensen, V., Galbraith, E.D., Maury, O., Lotze, H.K., 2020b. Differing marine animal biomass shifts under 21st century climate change between Canada's three oceans. FACETS 5, 105–122. https://doi.org/10.1139/facets-2019-0035

Bryndum-Buchholz, A., Tittensor, D.P., Blanchard, J.L., Cheung, W.W.L., Coll, M., Galbraith, E.D., Jennings, S., Maury, O., Lotze, H.K., 2019. Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. Global Change Biology 25, 459–472. https://doi.org/10.1111/gcb.14512

Busecke, J.J.M., Resplandy, L., Dunne, J.P., 2019. The Equatorial Undercurrent and the Oxygen Minimum Zone in the Pacific. Geophysical Research Letters 46, 6716–6725. https://doi.org/10.1029/2019GL082692

Chassignet, E.P., Yeager, S.G., Fox-Kemper, B., Bozec, A., Castruccio, F., Danabasoglu, G., Horvat, C., Kim, W.M., Koldunov, N., Li, Y., Lin, P., Liu, H., Sein, D.V., Sidorenko, D., Wang, Q., Xu, X., 2020. Impact of horizontal resolution on global ocean–sea ice model simulations based on the experimental protocols of the Ocean Model Intercomparison Project phase 2 (OMIP-2). Geoscientific Model Development 13, 4595–4637. https://doi.org/10.5194/gmd-13-4595-2020

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., Watson, R., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Clim Change 3, 254–258. https://doi.org/10.1038/nclimate1691

Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K., Werner, F.E., 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish and Fisheries 17, 101–125. https://doi.org/10.1111/faf.12093

Comiso, J.C., 2011. Large Decadal Decline of the Arctic Multiyear Ice Cover. J. Climate 25, 1176–1193. https://doi.org/10.1175/JCLI-D-11-00113.1

CSIRO, 2022. Usage To Date [WWW Document]. Atlantis. URL https://research.csiro.au/atlantis/home/usage-to-date/ (accessed 2.22.23).

Dickey-Collas, M., Payne, M.R., Trenkel, V.M., Nash, R.D.M., 2014. Hazard warning: model misuse ahead. ICES Journal of Marine Science 71, 2300–2306. https://doi.org/10.1093/icesjms/fst215

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate Change Impacts on Marine Ecosystems. Annual Review of Marine Science 4, 11–37. https://doi.org/10.1146/annurev-marine-041911-111611

Drenkard, E.J., Stock, C., Ross, A.C., Dixon, K.W., Adcroft, A., Alexander, M., Balaji, V., Bograd, S.J., Butenschön, M., Cheng, W., Curchitser, E., Lorenzo, E.D., Dussin, R., Haynie, A.C., Harrison, M., Hermann, A., Hollowed, A., Holsman, K., Holt, J., Jacox, M.G., Jang, C.J., Kearney, K.A., Muhling, B.A., Buil, M.P., Saba, V., Sandø, A.B., Tommasi, D., Wang, M., 2021. Next-generation regional ocean projections for living marine resource management in a changing climate. ICES Journal of Marine Science 78, 1969–1987. https://doi.org/10.1093/icesjms/fsab100

Drinkwater, K.F., 2005. The response of Atlantic cod (Gadus morhua) to future climate change. ICES Journal of Marine Science 62, 1327–1337. https://doi.org/10.1016/j.icesjms.2005.05.015

Ekström, M., Grose, M.R., Whetton, P.H., 2015. An appraisal of downscaling methods used in climate change research. WIREs Climate Change 6, 301–319. https://doi.org/10.1002/wcc.339

Fagundes, M., Litvin, S.Y., Micheli, F., De Leo, G., Boch, C.A., Barry, J.P., Omidvar, S., Woodson, C.B., 2020. Downscaling global ocean climate models improves estimates of exposure regimes in coastal environments. Sci Rep 10, 14227. https://doi.org/10.1038/s41598-020-71169-6

FAO, 2022. The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation. https://doi.org/10.4060/cc0461en

FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Rome, Italy. https://doi.org/10.4060/ca9229en

Farmer, J.R., Sigman, D.M., Granger, J., Underwood, O.M., Fripiat, F., Cronin, T.M., Martínez-García, A., Haug, G.H., 2021. Arctic Ocean stratification set by sea level and freshwater inputs since the last ice age. Nat. Geosci. 14, 684–689. https://doi.org/10.1038/s41561-021-00789-y

Fay, G., Link, J.S., Hare, J.A., 2017. Assessing the effects of ocean acidification in the Northeast US using an end-to-end marine ecosystem model. Ecological Modelling 347, 1–10. https://doi.org/10.1016/j.ecolmodel.2016.12.016

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R., Aschan, M., Dolgov, A., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change 5. https://doi.org/10.1038/nclimate2647

Frainer, A., Primicerio, R., Dolgov, A., Fossheim, M., Johannesen, E., Lind, S., Aschan, M., 2021. Increased functional diversity warns of ecological transition in the Arctic. Proceedings of the Royal Society B: Biological Sciences 288, 20210054. https://doi.org/10.1098/rspb.2021.0054

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A.V., Fossheim, M., Aschan, M.M., 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. PNAS 114, 12202–12207. https://doi.org/10.1073/pnas.1706080114

Free, C.M., Thorson, J.T., Pinsky, M.L., Oken, K.L., Wiedenmann, J., Jensen, O.P., 2019. Impacts of historical warming on marine fisheries production. Science 363, 979–983. https://doi.org/10.1126/science.aau1758

Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., Shannon, L.J., Fulton, E.A., Akoglu, E., Houle, J.E., Coll, M., Verley, P., Heymans, J.J., John, E., Shin, Y.-J., 2018. Risky business: The combined effects of fishing and changes in primary productivity on fish communities. Ecological Modelling 368, 265–276. https://doi.org/10.1016/j.ecolmodel.2017.12.003

Fulton, E., Smith, A., Johnson, C., 2003. Effect of Complexity of Marine Ecosystem Models. Marine Ecology Progress Series 253, 1–16. https://doi.org/10.3354/meps253001

Fulton, E.A., 2011. Interesting times: winners, losers, and system shifts under climate change around Australia. ICES Journal of Marine Science 68, 1329–1342. https://doi.org/10.1093/icesjms/fsr032

Fulton, E.A., 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems, Contributions from Advances in Marine Ecosystem Modelling Research II 23-26 June 2008, Plymouth, UK 81, 171–183. https://doi.org/10.1016/j.jmarsys.2009.12.012

Geary, W.L., Bode, M., Doherty, T.S., Fulton, E.A., Nimmo, D.G., Tulloch, A.I.T., Tulloch, V.J.D., Ritchie, E.G., 2020. A guide to ecosystem models and their environmental applications. Nature Ecology & Evolution 4, 1459–1471. https://doi.org/10.1038/s41559-020-01298-8

Gjøsæter, H., Huserbråten, M., Vikebø, F., Eriksen, E., 2020. Key processes regulating the early life history of Barents Sea polar cod. Polar Biol 43, 1015–1027. https://doi.org/10.1007/s00300-020-02656-9

Griffith, G.P., Fulton, E.A., Gorton, R., Richardson, A.J., 2012. Predicting interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. Conserv Biol 26, 1145–1152. https://doi.org/10.1111/j.1523-1739.2012.01937.x

Gullestad, P., Sundby, S., Kjesbu, O.S., 2020. Management of transboundary and straddling fish stocks in the Northeast Atlantic in view of climate-induced shifts in spatial distribution. Fish and Fisheries 21, 1008–1026. https://doi.org/10.1111/faf.12485

Hampton, S., Holmes, E., Scheef, L., Scheuerell, M., Katz, S., Pendleton, D., 2013. Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. Ecology 94, 2663–9. https://doi.org/10.1890/13-0996.1

Hansen, C., Drinkwater, K.F., Jähkel, A., Fulton, E.A., Gorton, R., Skern-Mauritzen, M., 2019a. Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. PloS one 14, e0210419. https://doi.org/10.1371/journal.pone.0210419

Hansen, C., Nash, R.D.M., Drinkwater, K.F., Hjøllo, S.S., 2019b. Management Scenarios Under Climate Change – A Study of the Nordic and Barents Seas. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00668

Hansen, C., Skern-Mauritzen, M., van der Meeren, G., Jähkel, A., Drinkwater, K., 2016. Set-up of the Nordic and Barents Seas (NoBa) Atlantis model. https://doi.org/10.13140/RG.2.1.3339.9929

Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M.A., Scott, J.D., Alade, L., Bell, R.J., Chute, A.S., Curti, K.L., Curtis, T.H., Kircheis, D., Kocik, J.F., Lucey, S.M., McCandless, C.T., Milke, L.M., Richardson, D.E., Robillard, E., Walsh, H.J., McManus, M.C., Marancik, K.E., Griswold, C.A., 2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. PLOS ONE 11, e0146756. https://doi.org/10.1371/journal.pone.0146756

Havforskningsinstituttet, 2022. Klimaet i havet [WWW Document]. Havforskningsinstituttet. URL https://www.hi.no/hi/temasider/hav-og-kyst/klimaet-i-havet/klimastatus (accessed 3.9.23).

Heneghan, R.F., Galbraith, E., Blanchard, J.L., Harrison, C., Barrier, N., Bulman, C., Cheung, W., Coll, M., Eddy, T.D., Erauskin-Extramiana, M., Everett, J.D., Fernandes-Salvador, J.A., Gascuel, D., Guiet, J., Maury, O., Palacios-Abrantes, J., Petrik, C.M., du Pontavice, H., Richardson, A.J., Steenbeek, J., Tai, T.C., Volkholz, J., Woodworth-Jefcoats, P.A., Tittensor, D.P., 2021. Disentangling diverse responses to climate change among global marine ecosystem models. Progress in Oceanography 198, 102659. https://doi.org/10.1016/j.pocean.2021.102659

Henson, S.A., Beaulieu, C., Ilyina, T., John, J.G., Long, M., Séférian, R., Tjiputra, J., Sarmiento, J.L., 2017. Rapid emergence of climate change in environmental drivers of marine ecosystems. Nat Commun 8, 14682. https://doi.org/10.1038/ncomms14682

Hill, S.L., Watters, G.M., Punt, A.E., McAllister, M.K., Quéré, C.L., Turner, J., 2007. Model uncertainty in the ecosystem approach to fisheries. Fish and Fisheries 8, 315–336. https://doi.org/10.1111/j.1467-2979.2007.00257.x

Hodapp, D., Roca, I.T., Fiorentino, D., Garilao, C., Kaschner, K., Kesner-Reyes, K., Schneider, B., Segschneider, J., Kocsis, Á.T., Kiessling, W., Brey, T., Froese, R., 2023. Climate change disrupts core habitats of marine species. Global Change Biology. https://doi.org/10.1111/gcb.16612

Holsman, K.K., Hazen, E.L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S.J., Samhouri, J.F., Aydin, K., 2019. Towards climate resiliency in fisheries management. ICES Journal of Marine Science.

Hop, H., Vihtakari, M., Bluhm, B.A., Assmy, P., Poulin, M., Gradinger, R., Peeken, I., von Quillfeldt, C., Olsen, L.M., Zhitina, L., Melnikov, I.A., 2020. Changes in Sea-Ice Protist Diversity With Declining Sea Ice in the Arctic Ocean From the 1980s to 2010s. Frontiers in Marine Science 7.

Hordoir, R., Axell, L., Höglund, A., Dieterich, C., Fransner, F., Gröger, M., Liu, Y., Schimanke, S., Andersson, H., Ljungemyr, P., Nygren, P., Falahat, S., Nord, A., Jönsson, A., Lake, I., Döös, K., Hieronymus, M., Dietze, H., Löptien, U., Haapala, J., 2019. Nemo-Nordic 1.0: A NEMO-based ocean model for the Baltic and North seas - Research and operational applications. Geoscientific Model Development 12, 363–386. https://doi.org/10.5194/gmd-12-363-2019

Hordoir, R., Skagseth, Ø., Ingvaldsen, R.B., Sandø, A.B., Löptien, U., Dietze, H., Gierisch, A.M.U., Assmann, K.M., Lundesgaard, Ø., Lind, S., 2022. Changes in Arctic Stratification and Mixed Layer Depth Cycle: A Modeling Analysis. Journal of Geophysical Research: Oceans 127, 2021JC017270. https://doi.org/10.1029/2021JC017270

Hyder, K., a, A., b, J., Austen, M., c, R., d, H., e, P., Blanchard, J., Burrows, M., Defriez, E., Dorrington, T., Edwards, K., García-Carreras, B., Heath, M., i, D., Heymans, J., Lowe, J., Houlem, J., Jennings, S., Paterson, D., 2015. Making modelling count - increasing the contribution of shelf-seas community and ecosystem models to policy development and management. Marine Policy 61, 291–302. https://doi.org/10.1016/j.marpol.2015.07.015

Ianelli, J., Holsman, K.K., Punt, A.E., Aydin, K., 2016. Multi-model inference for incorporating trophic and climate uncertainty into stock assessments. Deep Sea Research Part II: Topical Studies in Oceanography, Understanding Ecosystem Processes in the Eastern Bering Sea IV 134, 379–389. https://doi.org/10.1016/j.dsr2.2015.04.002

ICES, 2021. Arctic Fisheries Working Group (AFWG). ICES Scientific Reports. 3:58, 817 pp. https://doi.org/10.17895/ices.pub.8196

ICES, 2020. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 2:82, 1019 pp. https://doi.org/10.17895/ices.pub.7475

IPCC, 2022. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Isaksen, K., Nordli, Ø., Ivanov, B., Køltzow, M.A.Ø., Aaboe, S., Gjelten, H.M., Mezghani, A., Eastwood, S., Førland, E., Benestad, R.E., Hanssen-Bauer, I., Brækkan, R., Sviashchennikov, P., Demin, V., Revina, A., Karandasheva, T., 2022. Exceptional warming over the Barents area. Sci Rep 12, 9371. https://doi.org/10.1038/s41598-022-13568-5

Ives, A.R., Dennis, B., Cottingham, K.L., Carpenter, S.R., 2003. Estimating Community Stability and Ecological Interactions from Time-Series Data. Ecological Monographs 73, 301–330. https://doi.org/10.1890/0012-9615(2003)073[0301:ECSAEI]2.0.CO;2

Jakobsen, T., Ozhigin, V.K., 2012. The Barents Sea: ecosystem, resources, management: half a century of Russian-Norwegian cooperation. Tapir academic press Trondheim.

Kaplan, I.C., Francis, T.B., Punt, A.E., Koehn, L.E., Curchitser, E., Hurtado-Ferro, F., Johnson, K.F., Lluch-Cota, S.E., Sydeman, W.J., Essington, T.E., Taylor, N., Holsman, K., MacCall, A.D., Levin, P.S., 2019. A multi-model approach to understanding the role of Pacific sardine in the California Current food web. Marine Ecology Progress Series 617–618, 307–321. https://doi.org/10.3354/meps12504

Kaplan, I.C., Horne, P.J., Levin, P.S., 2012. Screening California Current fishery management scenarios using the Atlantis end-to-end ecosystem model. Progress in Oceanography, End-to-End Modeling: Toward Comparative Analysis of Marine Ecosystem Organization 102, 5–18. https://doi.org/10.1016/j.pocean.2012.03.009

Kaplan, I.C., Levin, P.S., Burden, M., Fulton, E.A., 2010. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Can. J. Fish. Aquat. Sci. 67, 1968–1982. https://doi.org/10.1139/F10-118

Karp, M.A., Peterson, J.O., Lynch, P.D., Griffis, R.B., Adams, C.F., Arnold, W.S., Barnett, L.A.K., deReynier, Y., DiCosimo, J., Fenske, K.H., Gaichas, S.K., Hollowed, A., Holsman, K., Karnauskas, M., Kobayashi, D., Leising, A., Manderson, J.P., McClure, M., Morrison, W.E., Schnettler, E., Thompson, A., Thorson, J.T., Walter, J.F., III, Yau, A.J., Methot, R.D., Link, J.S., 2019. Accounting for shifting distributions and changing productivity in the development of scientific advice for fishery management. ICES Journal of Marine Science 76, 1305–1315. https://doi.org/10.1093/icesjms/fsz048

Kirby, R.R., Beaugrand, G., 2009. Trophic amplification of climate warming. Proceedings of the Royal Society B: Biological Sciences 276, 4095–4103. https://doi.org/10.1098/rspb.2009.1320

Kirtman, B.P., Bitz, C., Bryan, F., Collins, W., Dennis, J., Hearn, N., Kinter, J.L., Loft, R., Rousset, C., Siqueira, L., Stan, C., Tomas, R., Vertenstein, M., 2012. Impact of ocean model resolution on CCSM climate simulations. Clim Dyn 39, 1303–1328. https://doi.org/10.1007/s00382-012-1500-3

Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D.M., Skjæraasen, J.E., 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. PNAS 111, 3478–3483. https://doi.org/10.1073/pnas.1316342111

Kjesbu, O.S., Sundby, S., Sandø, A.B., Alix, M., Hjøllo, S.S., Tiedemann, M., Skern-Mauritzen, M., Junge, C., Fossheim, M., Thorsen Broms, C., Søvik, G., Zimmermann, F., Nedreaas, K., Eriksen, E., Höffle, H., Hjelset, A.M., Kvamme, C., Reecht, Y., Knutsen, H., Aglen, A., Albert, O.T., Berg, E., Bogstad, B., Durif, C., Halvorsen, K.T., Høines, Å., Hvingel, C., Johannesen, E., Johnsen, E., Moland, E., Skuggedal Myksvoll, M., Nøttestad, L., Olsen, E., Skaret, G., Skjæraasen, J.E., Slotte, A., Staby, A., Stenevik, E.K., Stiansen, J.E., Stiasny, M., Sundet, J.H., Vikebø, F., Huse, G., 2021. Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic. Fish and Fisheries 23, 601–615. https://doi.org/10.1111/faf.12635

Knutti, R., 2010. The end of model democracy? Climatic Change 102, 395–404. https://doi.org/10.1007/s10584-010-9800-2

Kooijman, B., 2009. Dynamic Energy Budget Theory for Metabolic Organisation, 3rd ed. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511805400

Kuzmin, S.A., Akhtarin, S.M., Menis, D.T., 1999. The first finding of the snow crab Chionoecetes opilio (Fabricius) (Decapoda: Majidae) in the Barents Sea. Canadian translation of Fisheries and Aquatic Sciences 5.

Laird, A.K., 1964. Dynamics of Tumour Growth. Br J Cancer 18, 490–502.

Langangen, Ø., Stige, L.C., Yaragina, N.A., Ottersen, G., Vikebø, F.B., Stenseth, N.Chr., 2014. Spatial variations in mortality in pelagic early life stages of a marine fish (Gadus morhua). Progress in Oceanography 127, 96–107. https://doi.org/10.1016/j.pocean.2014.06.003

Langehaug, H.R., Sandø, A.B., Årthun, M., Ilıcak, M., 2019. Variability along the Atlantic water pathway in the forced Norwegian Earth System Model. Clim Dyn 52, 1211–1230. https://doi.org/10.1007/s00382-018-4184-5

Law, A.M., 1991. Simulation-models level of detail determines effectiveness. Industrial engineering 23, 16.

Levins, R., 1966. The strategy of model building in population biology. American Scientist 54, 421–431.

Lien, V.S., Hjøllo, S.S., Skogen, M.D., Svendsen, E., Wehde, H., Bertino, L., Counillon, F., Chevallier, M., Garric, G., 2016. An assessment of the added value from data assimilation on modelled Nordic Seas hydrography and ocean transports. Ocean Modelling 99, 43–59. https://doi.org/10.1016/j.ocemod.2015.12.010

Lindstrøm, U., Smout, S., Howell, D., Bogstad, B., 2009. Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. Deep Sea Research Part II: Topical Studies in Oceanography, The Proceedings of the ECONORTH Symposium on Ecosystem Dynamics in the Norwegian Sea and Barents Sea 56, 2068–2079. https://doi.org/10.1016/j.dsr2.2008.11.017

Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., Eddy, T.D., Cheung, W.W.L., Galbraith, E.D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J.L., Bopp, L., Büchner, M., Bulman, C.M., Carozza, D.A., Christensen, V., Coll, M., Dunne, J.P., Fulton, E.A., Jennings, S., Jones, M.C., Mackinson, S., Maury, O., Niiranen, S., Oliveros-Ramos, R., Roy, T., Fernandes, J.A., Schewe, J., Shin, Y.-J., Silva, T.A.M., Steenbeek, J., Stock, C.A., Verley, P., Volkholz, J., Walker, N.D., Worm, B., 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. Proceedings of the National Academy of Sciences 116, 12907–12912. https://doi.org/10.1073/pnas.1900194116

Melsom, A., Lien, V.S., Budgell, W.P., 2009. Using the Regional Ocean Modeling System (ROMS) to improve the ocean circulation from a GCM 20th century simulation. Ocean Dynamics 59, 969–981. https://doi.org/10.1007/s10236-009-0222-5

Moloney, C.L., St John, M.A., Denman, K.L., Karl, D.M., Köster, F.W., Sundby, S., Wilson, R.P., 2011. Weaving marine food webs from end to end under global change. Journal of Marine Systems 84, 106–116. https://doi.org/10.1016/j.jmarsys.2010.06.012

Mueter, F.J., Planque, B., Hunt, G.L., Jr, Alabia, I.D., Hirawake, T., Eisner, L., Dalpadado, P., Chierici, M., Drinkwater, K.F., Harada, N., Arneberg, P., Saitoh, S.-I., 2021. Possible future scenarios in the gateways to the Arctic for Subarctic and Arctic marine systems: II. prey resources, food webs, fish, and fisheries. ICES Journal of Marine Science 78, 3017–3045. https://doi.org/10.1093/icesjms/fsab122

Nilsen, I., Hansen, C., Kaplan, I., Holmes, E., Langangen, Ø., 2022. Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach. Fish and Fisheries 1–16. https://doi.org/10.1111/faf.12671

Nilsen, I., Kolding, J., Hansen, C., Howell, D., 2020. Exploring Balanced Harvesting by Using an Atlantis Ecosystem Model for the Nordic and Barents Seas. Frontiers in Marine Science 7. https://doi.org/10.3389/fmars.2020.00070

Øien, N., 2009. Distribution and abundance of large whales in Norwegian and adjacent waters based on ship surveys 1995-2001. NAMMCO Scientific Publications 7, 31–47. https://doi.org/10.7557/3.2704

Olsen, E., Aanes, S., Mehl, S., Holst, J.C., Aglen, A., Gjøsæter, H., 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES J Mar Sci 67, 87–101. https://doi.org/10.1093/icesjms/fsp229

Olsen, E., Hansen, C., Nilsen, I., Perryman, H., Vikebø, F., 2019. Ecological Effects and Ecosystem Shifts Caused by Mass Mortality Events on Early Life Stages of Fish. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00669

Olsen, E., Kaplan, I.C., Ainsworth, C., Fay, G., Gaichas, S., Gamble, R., Girardin, R., Eide, C.H., Ihde, T.F., Morzaria-Luna, H.N., Johnson, K.F., Savina-Rolland, M., Townsend, H., Weijerman, M., Fulton, E.A., Link, J.S., 2018. Ocean Futures Under Ocean Acidification, Marine Protection, and Changing Fishing Pressures Explored Using a Worldwide Suite of Ecosystem Models. Frontiers in Marine Science 5, 64. https://doi.org/10.3389/fmars.2018.00064

Onarheim, I.H., Årthun, M., 2017. Toward an ice-free Barents Sea. Geophysical Research Letters 44, 8387–8395. https://doi.org/10.1002/2017GL074304

Onarheim, I.H., Eldevik, T., Smedsrud, L.H., Stroeve, J.C., 2018. Seasonal and Regional Manifestation of Arctic Sea Ice Loss. Journal of Climate 31, 4917–4932. https://doi.org/10.1175/JCLI-D-17-0427.1

O'Neill, B.C., Tebaldi, C., van Vuuren, D.P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J.-F., Lowe, J., Meehl, G.A., Moss, R., Riahi, K., Sanderson, B.M., 2016. The Scenario Model Intercomparison Project

(ScenarioMIP) for CMIP6. Geoscientific Model Development 9, 3461–3482. https://doi.org/10.5194/gmd-9-3461-2016

Ortega-Cisneros, K., Cochrane, K.L., Fulton, E.A., Gorton, R., Popova, E., 2018. Evaluating the effects of climate change in the southern Benguela upwelling system using the Atlantis modelling framework. Fisheries Oceanography 27, 489–503. https://doi.org/10.1111/fog.12268

Oziel, L., Baudena, A., Ardyna, M., Massicotte, P., Randelhoff, A., Sallée, J.-B., Ingvaldsen, R.B., Devred, E., Babin, M., 2020. Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean. Nat Commun 11, 1705. https://doi.org/10.1038/s41467-020-15485-5

Paasche, Ø., Österblom, H., Neuenfeldt, S., Bonsdorff, E., Brander, K., Conley, D.J., Durant, J.M., Eikeset, A.M., Goksøyr, A., Jónsson, S., Kjesbu, O.S., Kuparinen, A., Stenseth, N.C., 2015. Connecting the Seas of Norden. Nature Clim Change 5, 89–92. https://doi.org/10.1038/nclimate2471

Payne, M.R., Kudahl, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K., 2021. Climate risk to European fisheries and coastal communities. Proceedings of the National Academy of Sciences 118, e2018086118. https://doi.org/10.1073/pnas.2018086118

Peck, M., Pinnegar, J., 2018. Impacts of climate change on fisheries and aquaculture Synthesis of current knowledge, adaptation and mitigation options.

Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P.E., Nascimento, M.C., Blanchet, M.-A., Ellingsen, I.H., Jørgensen, L.L., Blanchet, H., 2021. Overexploitation, Recovery, and Warming of the Barents Sea Ecosystem During 1950–2013. Frontiers in Marine Science 8.

Plagányi, É.E., 2007. Models for an Ecosystem Approach to Fisheries. FAO Fisheries Technical Paper. 108p. https://doi.org/10.25607/OBP-392

Planque, B., Favreau, A., Husson, B., Mousing, E.A., Hansen, C., Broms, C., Lindstrøm, U., Sivel, E., 2022. Quantification of trophic interactions in the Norwegian Sea pelagic food-web over multiple decades. ICES Journal of Marine Science 79, 1815–1830. https://doi.org/10.1093/icesjms/fsac111

Planque, B., Lindstrøm, U., Subbey, S., 2014. Non-Deterministic Modelling of Food-Web Dynamics. PLOS ONE 9, e108243. https://doi.org/10.1371/journal.pone.0108243

Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology 77, 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

Qu, B., Liu, X., 2020. The effect of wind and temperature to phytoplankton biomass during blooming season in Barents Sea. Dynamics of Atmospheres and Oceans 91, 101157. https://doi.org/10.1016/j.dynatmoce.2020.101157

Reid, P.C., Fischer, A.C., Lewis-Brown, E., Meredith, M.P., Sparrow, M., Andersson, A.J., Antia, A., Bates, N.R., Bathmann, U., Beaugrand, G., Brix, H., Dye, S., Edwards, M., Furevik, T., Gangstø, R., Hátún, H., Hopcroft, R.R., Kendall, M., Kasten, S., Keeling, R., Le Quéré, C., Mackenzie, F.T., Malin, G., Mauritzen, C., Ólafsson, J., Paull, C., Rignot, E., Shimada, K., Vogt, M., Wallace, C., Wang, Z., Washington, R., 2009. Chapter 1 Impacts of the Oceans on Climate Change, in: Advances in Marine Biology, Advances in Marine Biology. Academic Press, pp. 1–150. https://doi.org/10.1016/S0065-2881(09)56001-4

Reum, J.C.P., Townsend, H., Gaichas, S., Sagarese, S., Kaplan, I.C., Grüss, A., 2021. It's Not the Destination, It's the Journey: Multispecies Model Ensembles for Ecosystem Approaches to Fisheries Management. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.631839

Riahi, K., van Vuuren, D.P., Kriegler, E., Edmonds, J., O'Neill, B.C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J.C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., Ebi, K., Hasegawa, T., Havlik, P., Humpenöder, F., Da Silva, L.A., Smith, S., Stehfest, E., Bosetti, V., Eom, J., Gernaat, D., Masui, T., Rogelj, J., Strefler, J., Drouet, L., Krey, V., Luderer, G., Harmsen, M., Takahashi, K., Baumstark, L., Doelman, J.C., Kainuma, M., Klimont, Z., Marangoni, G., Lotze-Campen, H., Obersteiner, M., Tabeau, A., Tavoni, M., 2017. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Global Environmental Change 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Sætre, R., 2007. The Norwegian coastal current, 1st ed. Institute of marine research.

Sakshaug, E., Johnsen, G.H., Kovacs, K.M., 2009. Ecosystem Barents Sea. Tapir Academic Press.

Sandø, A.B., Hjøllo, S.S., Hansen, C., Skogen, M.D., Hordoir, R., Sundby, S., 2022. Risikoanalyse for de norske havområdene om direkte og indirekte virkninger av klimaendringer på marine økosystemer under ulike utslippsscenarier.

Sandø, A.B., Melsom, A., Budgell, W.P., 2014. Downscaling IPCC control run and future scenario with focus on the Barents Sea. Ocean Dynamics 64, 927–949. https://doi.org/10.1007/s10236-014-0731-8

Seland, Ø., Bentsen, M., Olivié, D., Toniazzo, T., Gjermundsen, A., Graff, L.S., Debernard, J.B., Gupta, A.K., He, Y.-C., Kirkevåg, A., Schwinger, J., Tjiputra, J., Aas, K.S., Bethke, I., Fan, Y., Griesfeller, J., Grini, A., Guo, C., Ilicak, M., Karset, I.H.H., Landgren, O., Liakka, J., Moseid, K.O., Nummelin, A., Spensberger, C., Tang, H., Zhang, Z., Heinze, C., Iversen, T., Schulz, M., 2020. Overview of the Norwegian Earth System Model (NorESM2) and key climate response of CMIP6 DECK, historical, and scenario simulations. Geoscientific Model Development 13, 6165–6200. https://doi.org/10.5194/gmd-13-6165-2020

Semenov, M.A., Stratonovitch, P., 2010. Use of multi-model ensembles from global climate models for assessment of climate change impacts. Climate Research 41, 1–14. https://doi.org/10.3354/cr00836

Shchepetkin, A.F., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean modelling 9, 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schön, P.-J., Sims, D.W., Genner, M.J., 2011. Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea. Current Biology 21, 1565–1570. https://doi.org/10.1016/j.cub.2011.08.016

Skagseth, Ø., Eldevik, T., Årthun, M., Asbjørnsen, H., Lien, V.S., Smedsrud, L.H., 2020. Reduced efficiency of the Barents Sea cooling machine. Nat. Clim. Chang. 10, 661–666. https://doi.org/10.1038/s41558-020-0772-6

Skogen, M., Ji, R., Akimova, A., Daewel, U., Hansen, C., Hjøllo, S., van Leeuwen, S., Maar, M., Macias, D., Mousing, E., Almroth-Rosell, E., Sailley, S., Spence, M., Troost, T., de Wolfshaar, K., 2020. Disclosing the truth: are models better than observations? Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps13574

Skogen, M.D., Hjøllo, S.S., Sandø, A.B., Tjiputra, J., 2018. Future ecosystem changes in the Northeast Atlantic: a comparison between a global and a regional model system. ICES J Mar Sci 75, 2355–2369. https://doi.org/10.1093/icesjms/fsy088

Smedsrud, L.H., Esau, I., Ingvaldsen, R.B., Eldevik, T., Haugan, P.M., Li, C., Lien, V.S., Olsen, A., Omar, A.M., Otterå, O.H., Risebrobakken, B., Sandø, A.B., Semenov, V.A., Sorokina, S.A., 2013. The Role of the Barents Sea in the Arctic Climate System. Reviews of Geophysics 51, 415–449. https://doi.org/10.1002/rog.20017

Spence, M.A., Blanchard, J.L., Rossberg, A.G., Heath, M.R., Heymans, J.J., Mackinson, S., Serpetti, N., Speirs, D.C., Thorpe, R.B., Blackwell, P.G., 2018. A general framework for combining ecosystem models. Fish and Fisheries 19, 1031–1042. https://doi.org/10.1111/faf.12310

Steinacher, M., Joos, F., Frölicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S.C., Gehlen, M., Lindsay, K., Moore, J.K., Schneider, B., Segschneider, J., 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences 7, 979–1005. https://doi.org/10.5194/bg-7-979-2010

Stige, L.C., Eriksen, E., Dalpadado, P., Ono, K., 2019. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsz063

Stige, L.C., Kvile, K.Ø., Bogstad, B., Langangen, Ø., 2018. Predator-prey interactions cause apparent competition between marine zooplankton groups. Ecology 99, 632–641. https://doi.org/10.1002/ecy.2126

Stockwell, J.D., Doubek, J.P., Adrian, R., Anneville, O., Carey, C.C., Carvalho, L., De Senerpont Domis, L.N., Dur, G., Frassl, M.A., Grossart, H.-P., Ibelings, B.W., Lajeunesse, M.J., Lewandowska, A.M., Llames, M.E., Matsuzaki, S.-I.S., Nodine, E.R., Nõges, P., Patil, V.P., Pomati, F., Rinke, K., Rudstam, L.G., Rusak, J.A., Salmaso, N., Seltmann, C.T., Straile, D., Thackeray, S.J., Thiery, W., Urrutia-Cordero, P., Venail, P., Verburg, P., Woolway, R.I., Zohary, T., Andersen, M.R., Bhattacharya, R., Hejzlar, J., Janatian, N., Kpodonu, A.T.N.K., Williamson, T.J., Wilson, H.L., 2020. Storm impacts on phytoplankton community dynamics in lakes. Global Change Biology 26, 2756–2784. https://doi.org/10.1111/gcb.15033

Tebaldi, C., Knutti, R., 2007. The use of the multi-model ensemble in probabilistic climate projections. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 365, 2053–2075. https://doi.org/10.1098/rsta.2007.2076

Tittensor, D.P., Beger, M., Boerder, K., Boyce, D.G., Cavanagh, R.D., Cosandey-Godin, A., Crespo, G.O., Dunn, D.C., Ghiffary, W., Grant, S.M., Hannah, L., Halpin, P.N., Harfoot, M., Heaslip, S.G., Jeffery, N.W., Kingston, N., Lotze, H.K., McGowan, J., McLeod, E., McOwen, C.J., O'Leary, B.C., Schiller, L., Stanley, R.R.E., Westhead, M., Wilson, K.L., Worm, B., 2019. Integrating climate adaptation and biodiversity conservation in the global ocean. Science Advances 5, eaay9969. https://doi.org/10.1126/sciadv.aay9969

Tittensor, D.P., Eddy, T.D., Lotze, H.K., Galbraith, E.D., Cheung, W., Barange, M., Blanchard, J.L., Bopp, L., Bryndum-Buchholz, A., Büchner, M., Bulman, C., Carozza, D.A., Christensen, V., Coll, M., Dunne, J.P., Fernandes, J.A., Fulton, E.A., Hobday, A.J., Huber, V., Jennings, S., Jones, M., Lehodey, P., Link, J.S., Mackinson, S., Maury, O., Niiranen, S., Oliveros-Ramos, R., Roy, T., Schewe, J., Shin, Y.-J., Silva, T., Stock, C.A., Steenbeek, J., Underwood, P.J., Volkholz, J., Watson, J.R., Walker, N.D., 2018. A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1.0. Geoscientific Model Development 11, 1421–1442. https://doi.org/10.5194/gmd-11-1421-2018

Tittensor, D.P., Novaglio, C., Harrison, C.S., Heneghan, R.F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G.L., Büchner, M., Cheung, W.W.L., Christensen, V., Coll, M., Dunne, J.P., Eddy, T.D., Everett, J.D., Fernandes-Salvador, J.A., Fulton, E.A., Galbraith, E.D., Gascuel, D., Guiet, J., John, J.G., Link, J.S., Lotze, H.K., Maury, O., Ortega-Cisneros, K., Palacios-Abrantes, J., Petrik, C.M., du Pontavice, H., Rault, J., Richardson, A.J., Shannon, L., Shin, Y.-J., Steenbeek, J., Stock, C.A., Blanchard, J.L., 2021. Next-generation ensemble projections reveal higher climate risks for marine ecosystems. Nat. Clim. Chang. 11, 973–981. https://doi.org/10.1038/s41558-021-01173-9

Tjiputra, J.F., Schwinger, J., Bentsen, M., Morée, A.L., Gao, S., Bethke, I., Heinze, C., Goris, N., Gupta, A., He, Y.-C., Olivié, D., Seland, Ø., Schulz, M., 2020. Ocean biogeochemistry in the Norwegian Earth System Model version 2 (NorESM2). Geoscientific Model Development 13, 2393–2431. https://doi.org/10.5194/gmd-13-2393-2020

Tracton, M.S., Kalnay, E., 1993. Operational Ensemble Prediction at the National Meteorological Center: Practical Aspects. Weather and Forecasting 8, 379–398. https://doi.org/10.1175/1520-0434(1993)008<0379:OEPATN>2.0.CO;2

Tsubouchi, T., Våge, K., Hansen, B., Larsen, K.M.H., Østerhus, S., Johnson, C., Jónsson, S., Valdimarsson, H., 2021. Increased ocean heat transport into the Nordic Seas and Arctic Ocean over the period 1993–2016. Nat. Clim. Chang. 11, 21–26. https://doi.org/10.1038/s41558-020-00941-3

United Nations, 2022. Day of 8 Billion [WWW Document]. United Nations. URL https://www.un.org/development/desa/dpad/publication/un-desa-policy-brief-no-140-a-world-of-8-billion/ (accessed 12.8.22).

United Nations, 2015. Sustainable development goals - United Nations [WWW Document]. URL https://sustainabledevelopment.un.org (accessed 1.31.18).

Vaghi, C., Rodallec, A., Fanciullino, R., Ciccolini, J., Mochel, J.P., Mastri, M., Poignard, C., Ebos, J.M.L., Benzekry, S., 2020. Population modeling of tumor growth curves and the reduced Gompertz model improve prediction of the age of experimental tumors. PLoS Comput Biol 16. https://doi.org/10.1371/journal.pcbi.1007178

van Denderen, D., Gislason, H., van den Heuvel, J., Andersen, K.H., 2020. Global analysis of fish growth rates shows weaker responses to temperature than metabolic predictions. Global Ecology and Biogeography 29, 2203–2213. https://doi.org/10.1111/geb.13189

Winsor, C.P., 1932. The Gompertz Curve as a Growth Curve. Proc Natl Acad Sci U S A 18, 1–8.

Wolfe, A.M., Allen, S.E., Hodal, M., Pawlowicz, R., Hunt, B.P.V., Tommasi, D., 2016. Impact of advection loss due to wind and estuarine circulation on the timing of the spring phytoplankton bloom in a fjord. ICES Journal of Marine Science 73, 1589–1609. https://doi.org/10.1093/icesjms/fsv151

Zhou, B., Du, J., 2010. Fog Prediction from a Multimodel Mesoscale Ensemble Prediction System. Weather and Forecasting 25, 303–322. https://doi.org/10.1175/2009WAF2222289.1

Zwietering, M.H., Jongenburger, I., Rombouts, F.M., Riet, K. van ’t, 1990. Modeling of the Bacterial Growth Curve. Appl. Environ. Microbiol. 56, 1875–1881.

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5. Papers

This chapter contains the papers that constitute this thesis, listed below in progressive order:

Paper I:

Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach

Ina Nilsen, Cecilie Hansen, Isaac Kaplan, Elizabeth Holmes and Øystein Langangen*

Fish and fisheries (2022)

Paper II:

Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas

Ina Nilsen, Filippa Fransner, Are Olsen, Jerry Tjiputra, Robinson Hordoir and Cecilie Hansen*

In Review at Fisheries Oceanography

Paper III:

A shifting chessboard: projections of prawn, capelin, mesopelagic fish, zooplankton, and their Nordic and Barents Seas foodweb under climate change

Ina Nilsen, Isaac Kaplan and Cecilie Hansen*

Manuscript ready for submission

Paper I:

Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach

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PAPER I

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ORIGINAL ARTICLE
WILEY
FISH and FISHERIES

Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach

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Abstract

It is commonly accepted that no ecosystem model is the 'best', but rather that ecosystem models should be used in ensembles. This is also the case for the Barents Sea ecosystem, where we have used two different ecosystem models to explore the role of the top-predator Northeast Arctic (NEA) stock of Atlantic cod (*Gadus morhua*, Gadidae) in the food web. The two models differ in complexity; Gompertz being less complex in terms of food web (7 components) and processes compared to the complex Nordic and Barents Seas Atlantis model (53 components). On the other hand, Gompertz provides thousands of stochastic realizations for each scenario, whereas Atlantis provides only one deterministic simulation. To compare the response to changes in NEA cod on two key prey species, capelin (*Mallotus villosus*, Osmeridae) and polar cod (*Boreogadus saida*, Gadidae), we perturbed the historical fishing pressure by ±50% and used the same NEA cod biomass in both models. Even though the links between NEA cod and the prey species are similar in the two models, the results from the study reveal that indirect effects through other food-web components might be as important as direct predator–prey interactions. Differences in spatial structure and overlap between species also influence the species response to the perturbations. In this study, we focus on the mechanisms that drives the changes in the models, and advise on potential consequences for fisheries management. The two models can complement each other, and the differences between them point to areas where more knowledge is needed.

KEYWORDS
EBFM, ecosystem models, fisheries management, foodweb, model comparison, trophic flows

1 | INTRODUCTION

All fish species are part of complex communities of interacting species, typically including predators and prey as well as competitors. Therefore, a change in the abundance or biomass in one species may propagate to others. In addition, abiotic factors, such as climate warming, may play an important role in the dynamics of marine ecosystems, for instance by affecting recruitment of fish (Ottersen et al., 2013). As a result, ecosystem-based fisheries management (EBFM) which recognizes the interactions within an ecosystem has been advocated for decades (Botsford et al., 1997; May et al., 1979). Yet, EBFM is rarely implemented in tactical management (Skern-Mauritzen et al., 2016).

One reason for this is the level of uncertainty associated with the response of marine ecosystems to management actions, which includes process, observational and model uncertainty as well as uncertainty associated with human behaviour (Harwood & Stokes, 2003). Model uncertainty is often used interchangeably with structural uncertainty (Geary et al., 2020; Hill et al., 2007) and describes the uncertainty that is introduced by assuming a certain model structure over any other.

Structural differences may lead to different models giving different projections under the same scenarios. For ecosystem models, this is further complicated by the fact that the models may not run with the same set of species or functional groups, the same spatial structure or at the same time scale (Spence et al., 2018). Another problem is selecting the appropriate level of detail for a model (Levins, 1966), which is often considered one of the most difficult aspects of the modelling process (Brooks & Tobias, 1996; Law, 1991). However, parts of these uncertainties can be addressed by basing decisions on multiple independent models (e.g. Fulton et al., 2015; Hill et al., 2007), that is a multi-model approach.

Multi-model approaches are already widely used for climatic predictions at a global scale (Gregory et al., 2005; IPCC, 2013), where similar-yet-different Earth System Models are used to draw possible trajectories of global temperature under different emission scenarios, thus integrating model uncertainty into the projections. Such multi-modelling approaches rely on addressing a single question with common scenarios and applying them to different models. Because models have different assumptions about system dynamics, a multi-model approach can highlight key areas of uncertainty in ways that support decision-making (Ianelli et al., 2016; Jacobsen et al., 2016; Marasco et al., 2007; Thorpe et al., 2015). A multi-model approach can also facilitate collaboration among modellers and provide a common interpretation of available information (Fulton et al., 2015).

Inevitably, marine ecosystem models are often tailored to specific ecosystems, time periods and geographies, and are time-consuming and costly to develop and standardize. Even models of the same marine ecosystem may differ significantly, both in terms of taxonomy, age groups, density independence, species interactions and linear vs non-linear responses, as well as environmental forcing, human impacts, and spatial and temporal resolution. The practice of considering model uncertainty in implemented ecosystem models therefore appears to be relatively rare. Several recent efforts have largely focused on uncertainty in parameter values, initial conditions and the process uncertainty that arises from natural variation (Bracis et al., 2020; Hansen et al., 2019; McGregor et al., 2020), whereas uncertainties about model structure have received less attention (Geary et al., 2020; Hill et al., 2007; Wildermuth et al., 2018).

Still, studies have emphasized that EBFM often benefits from a suite of ecosystem models that span a broad range of objectives. For instance, some models are useful for data organization and as catalysts for subsequent efforts, some may allow full exploration of parameter uncertainty within a limited number of species, and others may trace ecological impacts through a broader set of drivers and species (Fulton et al., 2015; Kaplan et al., 2019). In this study, we will address model uncertainty by testing fisheries management scenarios in two ecosystem models of varying complexity representing the same geographical area.

The Barents Sea ecosystem, situated in the Arctic region north of Norway and Russia, offers an ideal opportunity to understand further aspects of model uncertainty. This opportunity arises because current modelling efforts in this region include a minimalistic multispecies model (the Gompertz model), and one of the most complex (Atlantis). Both model types are fitted and tested using best practices (see below for details), but with important structural differences. The Barents Sea is also a great study area because the ecosystem dynamics and model behaviour can be focused on relatively few abundant fish stocks of high ecological and socio-economic importance (Olsen et al., 2010) as well as several key species at lower trophic levels, including krill and *Calanus* species. In particular, the Barents Sea holds the largest Atlantic cod (*Gadus morhua*, Gadidae) stock in the world (Kjesbu et al., 2014) the Northeast Arctic (NEA) cod. NEA cod play a dominant role in the Barents Sea ecosystem as important predators due to their high abundance, wide distribution, long migrations and generalist feeding habits, which influence practically all trophic links (Link et al., 2009). NEA cod also consume a very wide range of food items and can switch to prey that are more abundant in a given season and area (Jakobsen & Ozhigin, 2011). Therefore, predictions regarding the ecological role and effects of NEA cod are of clear interest, as is understanding how these predictions vary across models.

In this study we focus on the effect of NEA cod on other species, in particular forage fish species: capelin (*Mallotus villosus*, Osmeridae) and polar cod (*Boreogadus saida*, Gadidae). We use two different ecosystem models of varying complexity (Gompertz and Atlantis) to address the ecological role of NEA cod under different fisheries management scenarios, and investigate consistent results across models, and as well as divergence in model projections. We adopt this detailed analysis to better understand the ecosystem dynamics in the Barents Sea and the role of structural uncertainty in the models used. Rather than trying to select a 'best' model, we compare the models mechanistically by exploring the strengths of each of the models, while learning from the differences between them.

2 | MODELS AND METHOD

Two different ecosystem models were chosen to explore how changes in NEA cod abundance would impact the Barents Sea ecosystem: Gompertz (Stige et al., 2019) and NoBa Atlantis (Hansen et al., 2019a). These two models differ in complexity, number of species and the amount of time required to run and build them. However, both models were comparable in terms of spatial and temporal scale as well as having common species included.

2.1 | The Gompertz model

The Gompertz model is widely used in many aspects of biology (Tjørve & Tjørve, 2017). It has been used to describe the growth of animals and plants (Paine et al., 2012; Winsor, 1932), as well as multi-species dynamics (Hampton et al., 2013; Ives et al., 2003; Langangen et al., 2017; Stige et al., 2018) and growth of bacteria and cancer cells (Laird, 1964; Vaghi et al., 2020; Zwietering et al., 1990). In this study, a state-space version of the Gompertz model was used and analysed (Stige et al., 2019). This model was originally developed to study the direct and indirect effects of sea ice cover on the major zooplankton groups and planktivorous fish in the northern Barents Sea. The model can be regarded as a minimalistic ecosystem model and will hereafter be referred to just as 'Gompertz'.

In short, our Gompertz model focus on five species or groups of species that are modelled dynamically: capelin, polar cod, krill, amphipods and copepods. In addition to these, two key predators, that is NEA cod and herring (*Clupea harengus*, Clupeidae), are included, as well as impacts from fishery and ice cover. To limit model complexity, the NEA cod, which is included as a covariate based on time series of observed biomass, is only allowed to affect the dynamics of capelin and polar cod biomasses. Herring is also included as a covariate that affects capelin, mainly through predation on capelin larvae.

Climate is represented through time series of annual sea ice cover during wintertime, while fishing is given as a fraction of biomass removed. Fishing is only applied to capelin as it is the only dynamic species that was significantly harvested historically during the period with available data (1980–2015).

The model is fitted in a Bayesian state-space framework, where the species and processes are described by a set of state variables and equations referred to as the 'process model'. The process model consists of five equations to describe the dynamics of copepods, krill, amphipods, capelin and polar cod. The five equations describing the log-transformed biomass dynamics are presented below in a compact form (Equation 1) and as a matrix (Equation 2).

The general compact form:

$$x_t = a + bx_{T-1} + c\,z_{T-1} + \delta T \qquad (1)$$

More specifically for our case:

$$\begin{vmatrix} x_{1T} \\ x_{2T} \\ x_{3T} \\ x_{4T} \\ x_{5T} \end{vmatrix} = \begin{vmatrix} c_{10} \\ c_{20} \\ c_{30} \\ c_{40} \\ c_{50} \end{vmatrix} + \begin{vmatrix} c_{11} & 0 & c_{13} & c_{14} & c_{15} \\ 0 & c_{22} & 0 & c_{24} & 0 \\ c_{31} & 0 & c_{33} & 0 & c_{35} \\ c_{41} & c_{42} & 0 & c_{44} & 0 \\ c_{51} & 0 & c_{53} & 0 & c_{55} \end{vmatrix} \times \begin{vmatrix} x_{1T-1} \\ x_{2T-1} \\ x_{3T-1} \\ x_{4T-1} \\ x_{5T-1} \end{vmatrix} + \begin{vmatrix} c_{16} & 0 & 0 & 0 \\ c_{26} & 0 & 0 & 0 \\ c_{36} & 0 & 0 & 0 \\ c_{46} & c_{47} & c_{48} & c_{49} \\ c_{56} & c_{57} & 0 & 0 \end{vmatrix} \times \begin{vmatrix} z_{1T-1} \\ z_{2T-1} \\ z_{3T-1} \\ z_{4T-1} \end{vmatrix} + \begin{vmatrix} \delta_{1T} \\ \delta_{2T} \\ \delta_{3T} \\ \delta_{4T} \\ \delta_{5T} \end{vmatrix} \qquad (2)$$

In these equations, the state variable x_i represents the biomass of the five dynamically modelled species on log scale: x_1 is copepod biomass, x_2 is krill biomass, x_3 is amphipod biomass, x_4 is capelin biomass and x_5 is polar cod biomass, while z_1–z_4 represents the covariates ice, NEA cod, herring and fishing respectively. The subscript T symbolizes the year (1980–2015) while the c coefficients represent the productivity (c_{i0}), density dependence (c_{ii}) and biotic and abiotic effects (c_{ij}).

In addition, process error (*8*) for all of the five species was included. The process errors, which account for environmental factors not included in the model (Ives et al., 2003), were assumed to be independent in time and were jointly estimated from a multivariate normal distribution that accounts for the potential correlation structure (Stige et al., 2019).

With the Bayesian state-space approach, the process model is linked to data by an observation model. The observation model explicitly accounts for uncertainties about biological processes and observation noise (Clark & Bjørnstad, 2004). The output of the Bayesian state-space model is the posterior distributions of the model parameters, which can be used to quantify uncertainty in the ecosystem dynamics (Langangen et al., 2017). We use 2000 estimated parameter posterior samples to simulate the biomasses of capelin, polar cod, krill, amphipods and copepods from 1980 to 2015. A schematic representation of the species and the covariates and the interactions between them is given in Figure 1. The

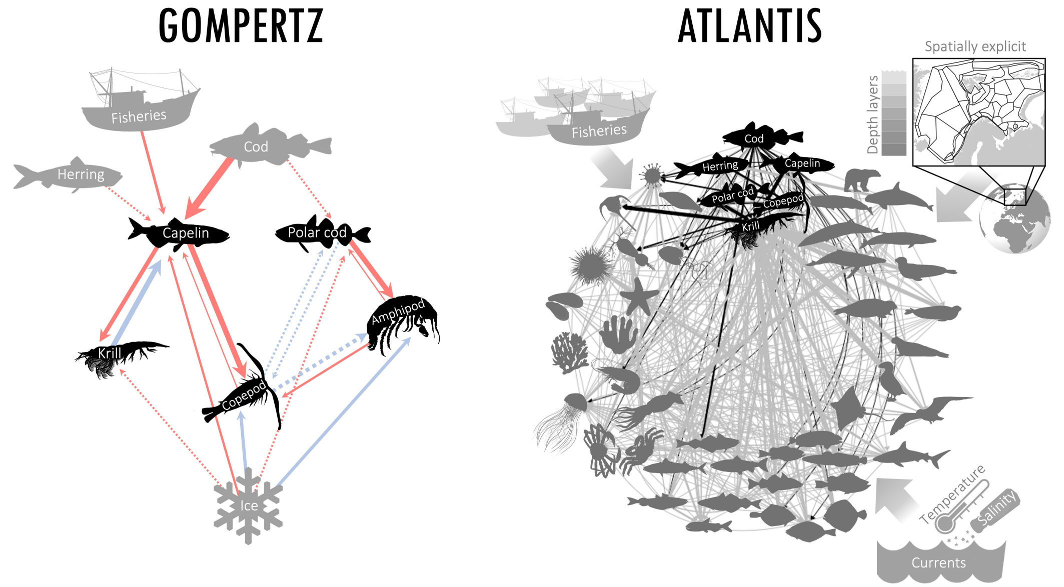

FIGURE 1 Schematic representation of both models. (a) Gompertz model where the black figures represent the dynamically modelled species, while grey figures represent other key abiotic or biotic variables. Arrows symbolize interactions where thickness is approximately proportional to mean estimated effect sizes (posterior means of c-values) while red and blue color indicates positive or negative interaction. Note that not all interactions shown were statistically significant, as whole lines indicates 95% c.i. (Stige et al., 2019). (b) Atlantis model where the black figures and arrows represent the species included in both models and their interactions with other species. Grey figures and arrows show the species and interactions not included in Gompertz. Multiple fishing fleets, physical forcing through temperature, salinity and currents, and spatially specific aspects are also included

strength of the interactions between the species was estimated from the mean of the posterior samples and is illustrated by the colour and widths of the arrows (Stige et al., 2019). Note that not all the interactions were statistically significant (dotted lines). To estimate the magnitude of the interactions throughout the simulation, we multiplied the c_{ij} -values with the biomass at the previous timestep. For example, the direct effect of NEA cod on capelin would then be c_{47} (NEA cod effect on capelin) multiplied with the biomass of cod at the previous timestep (z_{4T-1}) as the direct effect is both determined by the c_{ij} -value and the biomass. For the comparison between the two models, we analyse the median output of the Gompertz model.

2.2 | The Atlantis model

The Atlantis modelling framework (Audzijonyte et al., 2019; Fulton et al., 2011) is one of the most complex marine end-to-end ecosystems models in the world (Plagányi, 2007). It combines oceanography, population dynamics, spatial distributions, nutrient cycling, fisheries and species interactions in a spatially explicit domain. Most species are modelled as individual species or aggregated into functional groups with species of similar life history and ecological characteristics. The version implemented in the Nordic and Barents Seas (NoBa) (Hansen et al., 2016, 2019a) is the version that will be used in this study and will hereafter be referred to as 'Atlantis'.

Atlantis includes all trophic levels from phytoplankton to marine mammals, represented by 53 species and functional groups. These species are connected through a diet matrix where the proportion of prey in the predator´s diet is defined (Figure 1). The availability of prey also depends on spatial and temporal overlap, as well as the gape size limit, that is the size of the prey compared to the predator. The harvest sub-model allows for multiple fishing fleets with its own set of features like gear selectivity, target species and management structures. In the base run set up prior to this study, fisheries of the 12 main commercially important stocks were set up and harvested close to historical fishing levels (Hansen et al., 2019b). The model is forced bottom-up by daily inputs of temperature, salinity and currents from a Regional Ocean Modelling system (ROMS: Shchepetkin & McWilliams, 2005) covering the Northeast Atlantic (Skogen et al., 2007). Some of the key aspects of the model are summarized in Table 1.

There is a high taxonomic resolution in Atlantis, especially for species that are harvested, vulnerable and/or economically important. Lower trophic levels are also represented but are to a larger degree aggregated into groups based on size. Zooplankton, for example, are split into large, medium, small and gelatinous groups. This means that the amphipods and krill, which are simulated individually

TABLE 1 Comparison of the structural differences in the models

	Gompertz	Atlantis
Species and functional groups	5 (+2)	53
Spatial resolution	None	60 polygons, 7 depth layers
Model type	Statistical state-space	Deterministic end-to-end
Includes process error	Yes	No
Number of model realizations	2000	1
Dynamic (i.e. project through time)	Yes	Yes
Trophic interaction	Two-way coupling +one way	Two-way coupling
Number of links between all species	8	423
Number of links: Capelin	6	23
Number of links: Polar cod	5	19
Representation of harvest	Timeseries of landings data of capelin at the stock level	Varying fishing mortality rates on commercially harvested species
Representation of physics	Yearly ice cover given in %	Daily input of physical forcing through temperature, salinity and currents
Representation of life stages	None	All vertebrates separated into age groups, while some invertebrates (prawn, squid) are separated into juvenile/adults

in Gompertz, are gathered into one broader group of 'large zooplankton' in Atlantis. Capelin and polar cod, on the other hand, are modelled as individual species in both models, and the 'Medium zooplankton' group in Atlantis corresponds to the 'Copepods' as both groups are based on data and characteristics of *Calanus finmarchicus* (Hansen et al., 2016, 2019a; Stige et al., 2019). Another difference is that all vertebrate groups in Atlantis are age structured in up to 10 age classes, which is not the case in Gompertz, where all age classes for a given species are aggregated.

NEA cod and herring are also included in both models. However, in Atlantis both species are dynamically modelled, while in Gompertz they are represented as covariates based on forced time series. This means that NEA cod and herring are unaffected by fluctuations in climate and other species abundance in Gompertz, while this is not the case in Atlantis. The number of species also differ greatly between the two models, as Atlantis includes more than ten times more species and functional groups than Gompertz. This is also reflected by the number of trophic links included in the models.

2.3 | Comparison of model structure

Each of these ecosystem models have pros and cons associated with their use in providing projections. The Gompertz model is by design limited to a narrow taxonomic scope and simple representations of predator effects on forage fish, but this simplicity facilitates larger numbers of model projections and inclusion of both process and observational error. The Atlantis framework, in contrast, is limited in terms of replicates by slow simulation time and therefore lacks the stochasticity and uncertainty handled by the Gompertz model, but in exchange it includes a broader representation of the whole food web and encompasses additional important species and interactions (with the exception of large zooplankton which had a more detailed representation in Gompertz). Atlantis is however more difficult to link directly to data. Atlantis models can be calibrated to historical time series (Hansen et al., 2019b) and can be tested via extensive sensitivity analysis (Hansen et al., 2019a) and skill assessment (Olsen et al., 2016), but statistically fitting to data, as is done with the Gompertz model, is precluded by the long simulation times. Atlantis also includes age structure and spatial dynamics, which are lacking in Gompertz. These aspects tend to make models like Atlantis less responsive to perturbations than models like Gompertz (Walters et al., 2016). Using these two independently derived models with distinctive assumptions and trade-offs could highlight key areas of uncertainty and help address complex ecosystem management issues. Analysing models of different complexity might also help us understand how much resolution of space, species and sizes is needed to address complex ecosystem questions. In Table 1, we compare some of the key aspects of these ecosystem modelling approaches.

2.4 | Scenarios

To compare the two models, we took a hindcasting approach where historical time-series covering the years 1980–2015 were used. This was done to avoid typical problems associated with forecasting, such as potential large uncertainties and over-confidence in model forecasting (Brander et al., 2013). Since the models differed in several aspects, it was necessary to define a common baseline to compare the outputs. Atlantis simulates NEA cod biomass, while Gompertz uses forced time series as input. Consequently, the simulated NEA cod biomass from Atlantis was used as input in Gompertz, as the two time-series were quite similar (grey and black line, Figure 2). With this approach, it was possible to compare the ecosystem response in the two models while NEA cod biomass was the same. For species other than NEA cod, parameters and forcing were left unchanged, to investigate the isolated effects of NEA cod.

A base run in Atlantis set up with historic fishing levels was used as the control run in the two models. The NEA cod biomass from this scenario was found to be significantly correlated with observations ($r = 0.97$, $p = 0$) (Figure 2). The NEA cod biomass was then perturbed by changing the fishing regimes on NEA cod in Atlantis. First, the historic fishing pressure was reduced by 50%, and then the fishing pressure was increased by 50%. The three scenarios used for analysis are summarized in Table 2 along with the mean fishing mortality throughout the simulated period. The historic fishing pressure applied in Atlantis was based on the reported values (ICES, 2018, 2019).

2.5 | Elimination of unstable runs

Our application of the Gompertz model involved replacing the original NEA cod time series (which itself was based on fishery survey observations) with Atlantis NEA cod trends. This resulted in some of the 2000 posterior samples from the Gompertz model indicating unstable dynamics. Investigation of the instability indicated that it was largely driven by the parameters of density dependence for capelin (c_{44}) and polar cod (c_{55}) being larger than 1 for some of the posteriors. Figure S3 demonstrates the effect of density dependence on capelin and polar cod and how values above 1 could lead to unstable dynamics.

The range of parameters describing density dependence (c_{ii}) were not restricted below 1 in the original model parameter estimation (Supplementary materials; Stige et al., 2019), and we therefore attempted to stabilize the model by constraining c_{44} and c_{55} to be below 1 (Figure S4). This reduced the number of unstable runs to some extent, but it did not solve the problem completely.

Since the samples had extreme values that would not be realistic in real ecosystems, it was decided to remove them from the analysis. Based on Ives et al. (2003), unstable posteriors were classified by analysing the eigenvalues of the B-matrix of the interaction strengths. The B-matrix is formed by the *c* values with 0s where there is no interaction between species (matrix in Equation 1). All the *c* values for the 2000 runs were assembled into B-matrices at a 10 × 10 form, and the largest eigenvalue was computed for those matrices. The posterior samples where the B-matrix had an eigenvalue larger than 1 (i.e. unstable dynamics) were then excluded from the analysis.

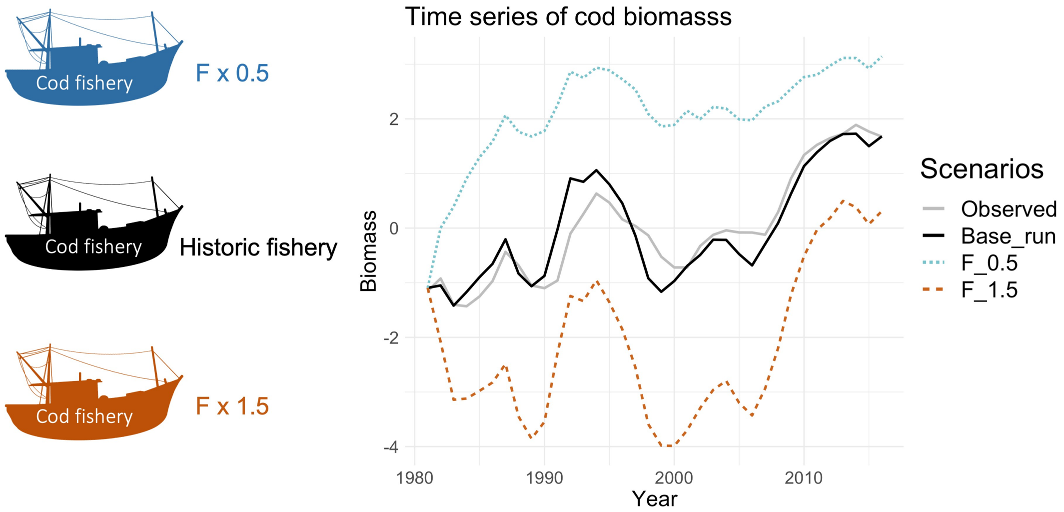

FIGURE 2 Biomass of NEA cod in both models normalised to zero mean and unit standard deviation. Black line shows simulated biomass from Atlantis used as the base case in both models, while the grey line shows observed biomass used in the original Gompertz model. Dotted lines show scenarios from Atlantis where the fishing mortality on NEA cod was reduced (blue) or increased (orange) by 50%

TABLE 2 Scenarios set up in Atlantis and used as input in Gompertz. The base run represents historical fishing levels, while in F_0.5 and F_1.5 the historical fishing pressure for NEA cod was changed by ±50%, respectively.

Scenario	Description	Mean F ± sd
Base_run	Historic NEA cod fishery	0.32 ± 0.12
F_0.5	Historic NEA cod fishery multiplied by 0.5	0.16 ± 0.06
F_1.5	Historic NEA cod fishery multiplied by 1.5	0.47 ± 0.18

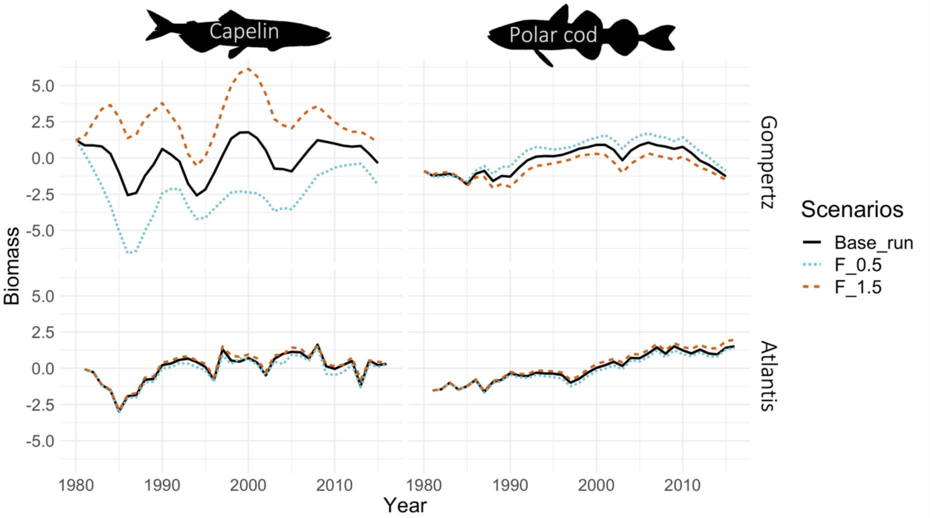

FIGURE 3 Simulated biomass of capelin and polar cod in both models normalised to zero mean and unit standard deviation. Black line shows the base run scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue) or increased (orange) by 50%

We found that the model preformed consistently across different ways of treating the instabilities, especially when focusing on the median as we do here. Nevertheless, the instability of the Gompertz model for some of the posterior samples was not optimal and this must be kept in mind when interpreting the results.

3 | RESULTS

In the results, we study the impacts of NEA cod by concentrating on how capelin and polar cod responded to the NEA cod perturbations in the two models. Then we try to understand why the two species responded the way they did by investigating the underlying mechanisms of the models, first in Gompertz and then in Atlantis. All biomass outputs were normalized to zero mean and unit standard deviation to facilitate comparison. Since Atlantis produced one model realization per simulation while Gompertz produced 2000, the median of the Gompertz samples was used for comparison. The median was calculated after 605 (~30%) unstable runs were removed based on the calculated eigenvalue. The fact that the median was used should be kept in mind when interpreting the results, as this excludes the uncertainty of the Gompertz results. For those interested, a figure including the uncertainty of the Gompertz results can be found in the Figure S2. All plotting was carried out through 'R studio' (R Studio Team, 2020) under version 4.1.2.

First, we had to find out how the perturbated fishing scenarios affected the NEA cod biomass and how the simulated NEA cod from Atlantis compared to the observed time series in Gompertz (Figure 2). The NEA cod stock in Atlantis (black line) corresponded well with the observed biomass (grey line), and most of the variability in the model originated from variation in catch over time. For the perturbated scenarios, the biomass of NEA cod was, as expected, higher when the fishery was reduced, and lower when the fishery increased. These biomass projections of NEA cod from the three scenarios were then used as time series input in the Gompertz model.

3.1 | Northeast Arctic cod effect on capelin and polar cod

The NEA cod harvesting regimes affected capelin and polar cod differently in the two models (Figure 3). One of the most apparent differences between them was the magnitude of the response: both capelin and polar cod were less affected by the NEA cod perturbations in Atlantis compared to Gompertz. This was especially true for capelin, which was noticeably affected by cod in Gompertz, but hardly affected at all in Atlantis. In terms of the direction of the response, both the Gompertz and Atlantis models projected that a higher biomass of NEA cod would have negative effects on capelin. On the other hand, the direction of the response of polar cod differed between the two models. While polar cod was slightly negatively affected by higher levels of NEA cod in Atlantis, higher levels of NEA cod resulted in more polar cod in Gompertz. Still, it should be noted that when accounting for the uncertainty (Figure S2), the effects of higher versus lower NEA cod on polar cod were largely overlapping for the Gompertz model, and the results should therefore be considered uncertain.

To understand why the species responded differently to NEA cod perturbations in the two models, we further analysed the results of each model separately by looking at the underlying mechanisms, as detailed below.

3.2 | Effects of Northeast Arctic cod in Gompertz

As depicted for the Gompertz model in Figure 1, the direct effects of cod on both capelin and polar cod were expected to be negative, via predation. However, the Gompertz model projections suggested that cod would have a negative effect on capelin, but a positive effect on polar cod. We therefore investigated if NEA cod could affect polar cod indirectly through other species. The structure of the Gompertz model allowed us to visualize this directly from the estimated species interaction coefficients in Equation 1. Two different pathways were explored (Figure 4), where the magnitude of the *c* coefficient was multiplied with the change in biomass for that particulate species. Figure 4a illustrates the direct effect of NEA cod on capelin as well as the indirect effect on polar cod through capelin and copepods. Figure 4b shows the pathway in the opposite direction where NEA cod affects polar cod directly and then capelin indirectly through polar cod and copepods.

The results confirmed that the dominating effect on capelin was the direct negative effect of NEA cod (Figure 4a). Polar cod, on the other hand, was both affected by NEA cod directly and indirectly through capelin and copepods, where the latter seemed to be the most dominant. The negative effect on capelin due to higher NEA cod abundance had a positive effect on copepods which then had a positive effect on polar cod (Figure 4a). This indirect effect was stronger than the negative direct effect of NEA cod on polar cod (Figure 4b), which explains why polar cod responded positively to increased NEA cod biomass.

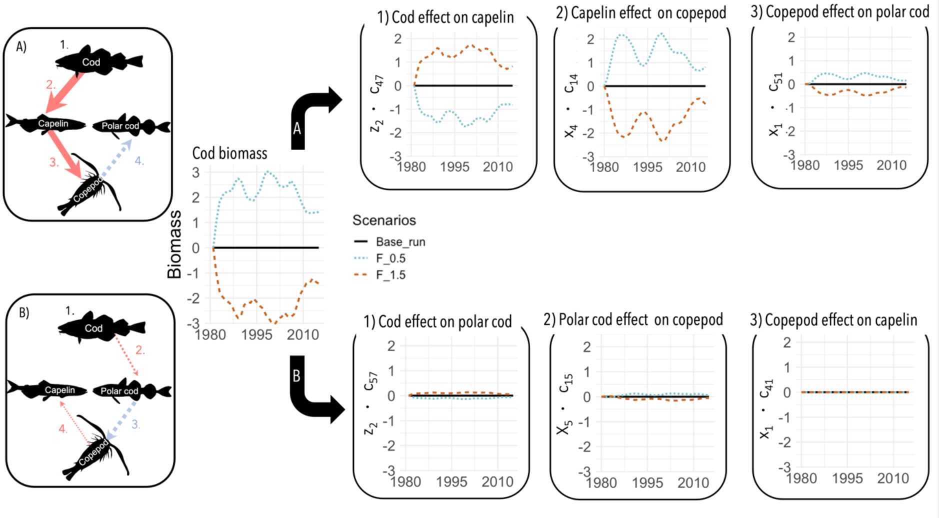

FIGURE 4 Direct and indirect effects of NEA cod in the Gompertz model. The two pathways of how capelin and polar cod and affected are presented to the left with arrows showing the strength of the interaction (thickness) and whether the effect is positive (blue) or negative (red). Note that the arrows directly correspond to interaction *c* coefficients in Gompertz, Equation 1. Not all interactions shown were statistically significant, as solid lines indicate significance based on the 95% CI, and dashed lines are not significant based on 95% CI (Stige et al., 2019). (a) Direct effect on capelin and indirect effect on polar cod through capelin and copepods. (b) Direct effect on polar cod and indirect effect on capelin through polar cod and copepods. Black line shows the base line scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue) or increased (orange) by 50%. The total effect of species x on species y was estimated by multiplying the biomass of species x with the c coefficient determining the strength of x´s effect on y.

In addition to the direct and indirect effects of NEA cod, there was also an effect caused by the density dependent parameters. As mentioned, the c_{ii} parameters govern the strength of the density dependence in the Gompertz model. As c_{ii} increases, the compensatory effect of density dependence decreases, and when $c_{ii} = 1$ no density dependence occurs (Ives et al., 2003). This means that a population with high density dependence (c_{ii} close to 0) will be more robust against predation as the predation will be partly compensated for, while populations with low density dependence (c_{ii} close to 1) are likely to respond more strongly to altered predation pressure. Comparing the density dependent parameters for capelin and polar cod also indicated that capelin had more runs with low density dependence, which most likely contributes to the stronger response to NEA cod seen in capelin biomass (Figure S3).

3.3 | Effects of Northeast Arctic cod in Atlantis

To get a better overview of the Atlantis results, we plotted the biomass as change in percentage for NEA cod, capelin and polar cod (Figure 5). We also examined the direct effect of NEA cod on capelin and polar cod by investigating the change in NEA cod predation under the two scenarios. Both capelin and polar cod experienced changes in predation pressure from NEA cod under the two scenarios, indicating a direct link between the two species and NEA cod. Still, the change in capelin and polar cod biomass was almost negligible compared to the changes in NEA cod biomass and predation mortality, as the mean change in biomass was <10% for capelin and <5% for polar cod.

To investigate why the response to NEA cod was so weak, the total mortality from all predators was plotted (Figure 6). Although NEA cod accounts for a significant portion of the total predation on capelin and polar cod, the figure also introduced other predators and showed how the mortality increased and decreased in the two scenarios with varying NEA cod abundance.

Most of the reduction in NEA cod predation seemed to be replaced by increased predation from other species. When predation from NEA cod was reduced, capelin and polar cod experienced a higher predation pressure from species such as herring and blue whiting (for capelin) and skates (for polar cod). This effect was the opposite when the NEA cod predation increased. Still, the total predation pressure (black line, Figure 6) slightly increased in the scenario with 50% lower fishing pressure on NEA cod and decreased in the scenario with 50% higher fishing pressure, indicating that the responses in capelin and polar cod in large part was caused by a direct effect from NEA cod.

The spatial overlap between NEA cod, capelin and polar cod in Atlantis was also investigated (Figure S6). This spatio-temporal overlap of prey and predators is explicitly represented in the Atlantis model, and the overlap could therefore be studied. NEA cod and capelin were in the same areas throughout the entire course of a year. The overlap between NEA cod and polar cod, on the other hand, was present throughout the year, but mainly prominent during fall and wintertime in the Southeastern Barents Sea, when polar cod migrates further south.

Since Atlantis models a wide range of species, we also included a figure of how all species in Atlantis responded to the various cod scenarios (Figure S7). Results showed that the response to the altered NEA cod stock was negligible for most species in the early period of the simulation (1985–1990), but slightly stronger towards the end (2010–2015). Another visible overall trend was that most species responded positively to less NEA cod and were negatively affected by more NEA cod. Multiple species responded to the altered fishing regime, including prawns, herring, long rough dab and large demersal fish. The strongest response was seen in haddock and the planktonic groups. However, the plankton groups in Atlantis are highly variable, and haddock depends strongly on the plankton biomass for recruitment, so these results are highly uncertain and were not used for further interpretation.

Overall, the results revealed that the prey communities in the two ecosystem models responded differently to the same NEA cod abundance. Capelin responded negatively to NEA cod in both models but had a stronger negative response in Gompertz. Polar cod, on the other hand, reacted opposite in the two models: positive to NEA cod in Gompertz and slightly negatively in Atlantis. Even though NEA cod had negative direct effects on capelin and polar cod in both models, this negative effect was overshadowed by an indirect positive effect through capelin and copepods in the Gompertz model. This indirect effect could not be identified in Atlantis, which resulted in the two models projecting different responses in polar cod. Even though the polar cod response in the Gompertz model was non-significant (Figure S2), the results still provided a good contrast to the Atlantis result and emphasize the uncertainty regarding this species' responses to changes in cod fishery exploitation.

4 | DISCUSSION

To understand why the models responded differently we take a closer look at the structural differences between the models, focusing on the food web complexity and the fact that Atlantis included additional features like age structure and horizontal grid resolution. We also discuss our results in the broader context of best practices for handling structural uncertainty in multi-model approaches and consider how this can be used for living marine resource management purposes.

4.1 | Food web complexity and age structure

The main difference between the responses in the two models was that Gompertz projected a stronger response to the NEA cod perturbations than Atlantis. These results seemed to emerge from a combination of weaker direct effects in Atlantis compared to Gompertz, in addition to the differences in taxonomic resolution, as Atlantis includes nearly 10 times as many species and a higher

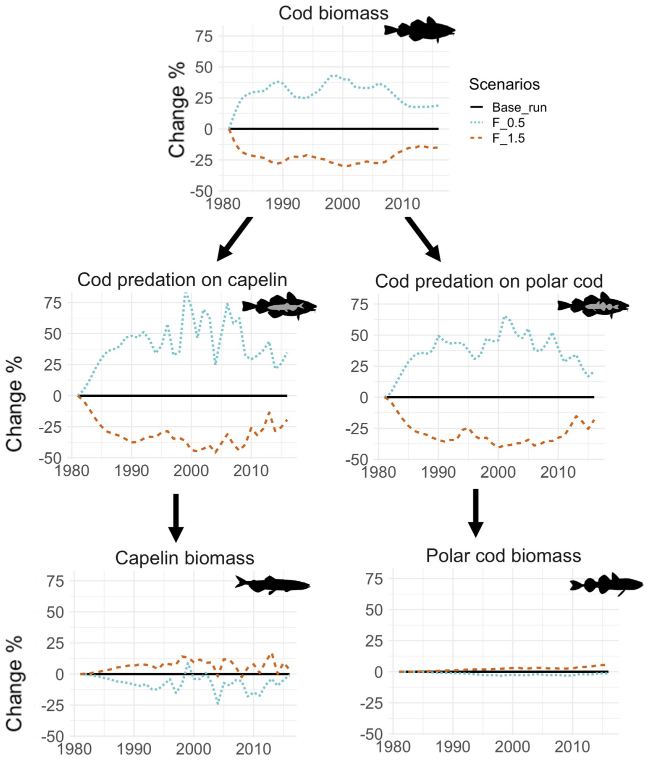

FIGURE 5 The effect of NEA cod on capelin and polar cod explained through changes in NEA cod predation in the Atlantis model. Black line shows the base line scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue dotted lines) or increased (orange dashed lines) by 50%

number of links between the species. This structural difference led to NEA cod predation in Atlantis being largely compensated for by other species, and capelin and polar cod was therefore less affected in Atlantis than in Gompertz. These results are consistent with previous studies of how various models of the same ecosystem can produce different outcomes, as both Smith et al. (2011) and Kaplan et al. (2013) found that models including fewer species (EwE, OSMOSE) projected stronger impacts compared to Atlantis with its high taxonomic resolution.

Still, we also highlighted the significance of other species in the Gompertz model. Even though Gompertz included few species, the indirect effects from other species on polar cod were more important for its response to the perturbations compared to direct predation effects. Note that these results were based on mean posterior samples and not all effects were statistically significant (Figure S2). Previous studies have shown similar results of how indirect effects may lead to unforeseen responses, such as Kaplan et al. (2017), which saw a positive effects of reduced sardine abundance on zooplankton and small forage fish. However, these indirect effects on polar cod through copepods were not easy to verify through field data. Studies have indicated that warmer temperatures may increase overlap between capelin and polar cod causing increased competition for copepods (McNicholl et al., 2016; Orlova et al., 2002, 2009). Hence, one could assume that cod affecting capelin positively or negatively could result in the opposite effect on polar cod due to increased competition for copepods.

In Atlantis, polar cod was directly affected by NEA cod, but the response was partly compensated for by other species such as skates and long rough dab. Stomach content data indicates that polar cod is a part of skate's diet in the Barents Sea (Dolgov, 2005), but the exact strength of the link is hard to identify due to lack of data. This response was not accounted for in the Gompertz model and raises the question to whether skates should be included when modelling polar cod, or if the link is so uncertain that it should be excluded. Still, using the two models emphasized different links that could potentially play a part in polar cod responses to changes in NEA cod abundance.

In addition to taxonomy, Atlantis also includes life history traits in the form of age structure. The inclusion of age structure could be partially responsible for the speed with which different species responded to the perturbations; this differs from the Gompertz

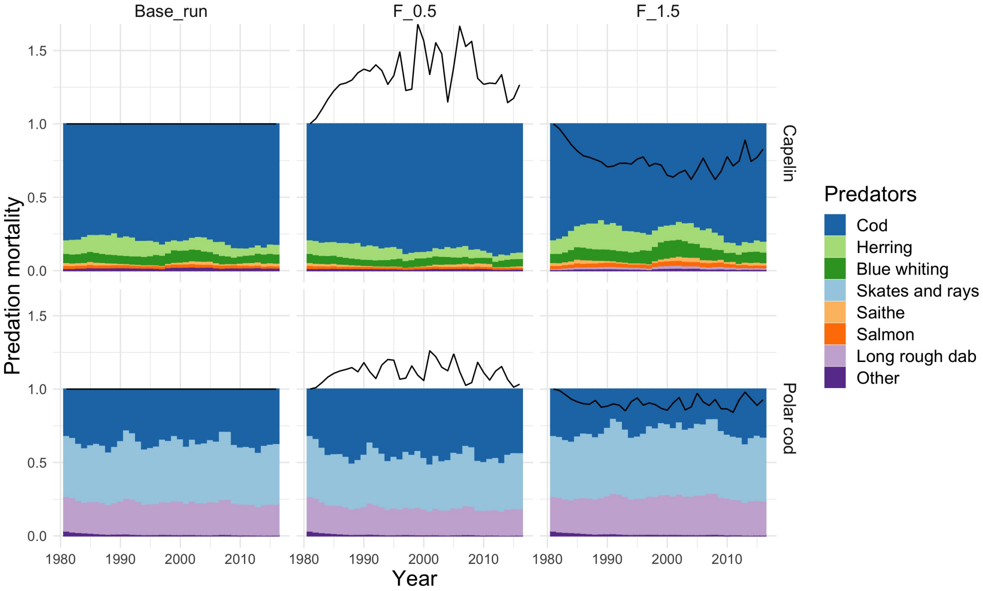

FIGURE 6 The portions of predation mortality for capelin and polar cod caused by various predators in Atlantis for the three scenarios. Black lines show how the total predation mortality varied between the scenarios

model, which omits age structure. Results showed that the species biomasses were quicker to respond to the change in NEA cod in Gompertz compared to Atlantis. This response was most evident for polar cod where Gompertz allowed for a relatively large percent change in biomass over the first 10 years of the simulations, while polar cod was hardly affected at all in Atlantis. In return, the response in polar cod in Atlantis steadily increased throughout the simulation and could potentially have proved to be greater than the effect on capelin if a longer simulation time was applied instead of a hindcast. This could be caused by the fact that capelin has a faster life history than polar cod in the Atlantis model, as the life span of polar cod is set to 10 years while it is set to only 5 years for capelin.

4.2 | Spatial complexity

Another important difference between the two models was that Atlantis included a spatial aspect, while Gompertz did not. Spatial resolution is an important issue when considering the dynamics of ecosystems. Enhanced spatial resolution generally increases model complexity and requires more data for model construction, parameterization, calibration and validation, and may lead to great increases in computing time. However, without spatial structure, competitors and predators are effectively 'everywhere' and encounter rates are not related to abundance as they are in nature (Fulton et al., 2004).

Non-spatial models may also underrepresent seasonal dynamics in cases where spatial complexity involves seasonal movement or migration by one or more key consumers. Fulton et al. (2004) studied the effect of reducing spatial resolution in models and found that simpler models did not capture the effects of changes in nutrient loads or fishing pressure as well as more complex models. An alternative could be to add an implied spatial structure to more simple models (like Strath E2E2, Heath et al., 2020).

In a spatially explicit model like Atlantis, the interactions between species are determined by spatial and temporal overlap. The degree to which species overlap in time and space will therefore largely determine the strength of the interactions between the species. In Gompertz, these interactions are governed by the c_{ij} parameters, which are constant throughout the run, but vary between the 2000 model realizations. However, the input data were selected to represent the central and northern Barents Sea, which partly accounts for the spatial overlap (Stige et al., 2019).

Looking at the spatial distribution of the NEA cod, capelin and polar cod in Atlantis, results imply that the slightly stronger direct effect on capelin could be explained by a greater spatial overlap with NEA cod. We also saw that NEA cod represents a stronger part of the predation mortality applied to capelin compared to polar cod.

The geographical distribution of polar cod in the Barents Sea is not as well-known as capelin, as the current knowledge is mostly based on surveys that primarily targeted capelin, and areas north and east of the usual distribution of capelin have thus not been covered (Gjøsæter et al., 2020). Stomach data from 1984 to 2016 does not identify polar cod as a big part (occurrence in less than 10% of the samples) of NEA cod diet (Holt et al., 2019), which supports the assumptions made in Gompertz. However, Barents Sea field observations have shown that since the early 2000s, warmer temperatures have led to an expansion of NEA cod feeding grounds towards the northern Barents Sea (Fall et al., 2018), resulting in a greater overlap with polar cod. In these areas the NEA cod consumption of polar cod increased, with evidence of polar cod practically replacing capelin in the NEA cod diet in some local areas (Orlova et al., 2009). This indicates that the link between NEA cod and polar cod might be increasingly strong. Climate change and shifts in distribution might therefore call for spatial resolution, or at least some implicit modelling of overlap functions through time. While the Gompertz model is built for a specific area, it does not capture the dynamics in species distribution. This can only be modelled in spatially explicit models such as Atlantis.

4.3 | Model uncertainty

Our approach here has been to understand how structural differences between the two models lead to divergent responses of species such as polar cod; however we have neither formally created a model ensemble, nor have we weighted or ranked the models.

Structural uncertainty and resulting divergence in predicted responses are common in complex ecosystem models (Geary et al., 2020). Unlike physical ocean models that generally share a common set of state variables and governing equations, ecosystem models often differ in model structure and components, complicating efforts to formally combine predictions across models (Spence et al., 2018). Methods of combining outputs for different ecosystem models have previously been proposed, though applications of these methods are more rare. One method is to use a 'democracy' of simulators (Knutti, 2010; Payne et al., 2015) where each model gets one vote, regardless of how well it represents the true ecosystem, and a distribution of possible outputs is derived from this. Alternative approaches are to find the 'best' model based on fits to historical data, or to apply Bayesian model averaging, again based on model fits to data (such as Ianelli et al., 2016). Another novel approach, developed by Spence et al. (2018), is to construct a flexible statistical meta-model of the relationships between a collection of mechanistic models and their biases or discrepancies. This is particularly appealing because even when an individual model omits a species, the method statistically predicts behaviour of that species based upon interspecies relationships that can be obtained from other models in the ensemble, and ultimately this gap filling allows quantitative comparison across an ensemble of somewhat dissimilar models. Overall, our exploration of structural uncertainty is a step towards 'mingling models' (Reum et al., 2021; Townsend et al., 2014), not fully achieving formal ensembles but nonetheless using multiple models to strengthen inference and qualitatively compare predictions from models that span a range of complexity. This study also has the strength of being able to look at model responses mechanistically, which might be hidden by a statistical ensemble.

4.4 | Consequences of model complexity for ecosystem-based fisheries management

Incorporating ecosystem considerations requires moving from the single-species models used in stock assessments to more complex models that include species interactions, environmental drivers and human consequences. Model uncertainty generally increases with the number of assumptions made, which often increases with the complexity of the system of interest since more processes can be represented (Hill et al., 2007). With this increasing complexity, model fit can improve, but parameter uncertainty increases. Overly simple models, on the other hand, may not be able to represent important aspects of ecosystem dynamics and can thus have large model bias (Collie et al., 2016). Our study applied two models of very different complexity that illustrate these trade-offs, where the models are potentially on each side of the complexity scale.

The complexity of the Gompertz model is relatively low, while the opposite is true for the Atlantis model (Plagányi, 2007). This large difference in complexity between the models is likely to lead to a relatively high risk of model bias in the Gompertz model while Atlantis may be prone to higher risk of parameter uncertainty (Collie et al., 2016). Neglecting model uncertainty can lead to underrepresentation of uncertainty in model predictions, with important implications for management (Hill et al., 2007), as also indicated by our analysis of the underlying mechanisms of the ecosystem response to changed fishing pressure in cod in the two contrasting models. It is important to use the ecosystem models for what they are designed for, among other purposes as an important tool to explore trade-offs from changes in management strategies (Link et al., 2012). The consequences for management of our analysis depend on the credibility of the two models. We summarize the possible interpretations and consequences of the different combinations of model credibility in Table 3.

The perturbation of the NEA cod fishery by 50% was regarded as extreme and we consider it a relatively unlikely scenario. Still, the results could provide valuable information for future management of capelin and polar cod in the Barents Sea. For capelin, both models projected that increased harvesting of NEA cod was associated with a higher capelin biomass. However, the magnitude of the increase was quite different between the two models, which indicates the role of model uncertainty caused by the structural differences in the models. The management of capelin and NEA cod is currently one of the few examples of EBFM in the world, as the importance of capelin as food for cod has been considered in the capelin fishery since 1991 (Skern-Mauritzen et al., 2016). These results thereby support the current management strategy that capelin and NEA cod should be considered together.

TABLE 3 Possible interpretation of the credibility of the models

Possible Interpretation	Discussion & Consequences
Atlantis is more credible than Gompertz	Spatial and age resolution are essential to understand foodweb dynamics, suggesting that models which lack such resolution should be given less priority. Given the relatively long-run times of Atlantis, incorporating uncertainty analysis in this should be high on the agenda rather than obtaining large samples sized from running overly simplistic models. We may need standards for the 'minimum requirements' for a model to be considered credible for foodweb response evaluation.
Gompertz is more credible than Atlantis	This implies that we should focus more on computational speed and ensemble size of projections to estimate uncertainty, rather than formulating a single model including a large range of mechanisms with less certainty on parameter values. Interaction strengths of Gompertz is more likely to be correct with implications for fisheries management of fewer but stronger foodweb links. The Gompertz model is also much more tractable for quantifying parameter and process uncertainty.
Both Gompertz and Atlantis are equally credible	We can have higher confidence in the responses that are common to both models, while we remain uncertain about the sensitivity of key links in the foodweb to the cod fishery where the responses differ between the two models. It is also uncertain how much spatial structure and taxonomic structure is necessary to characterize the foodweb response. Based on Collie et al., we may gain important insights from Models of intermediate complexity (MICE, Plagányi et al., 2014) that are more complex than Gompertz, but simpler than Atlantis.
Neither models are credible	We may need to consider more models before being able to meaningfully inform fisheries management. Based on perceived failings of a model, we might gain some information on lacking mechanisms and potential large parameter uncertainties. Ensemble methods (Spence et al., 2018) may help maximize the information we can get from available models and help with credibility issue.

For polar cod, the situation was somewhat different. The perturbations did not affect polar cod strongly in Atlantis, and Gompertz model, there was an indirect positive effect on polar cod, but this was quite uncertain (Figure S2). This indicates that a smaller change in NEA cod management would be unlikely to have catastrophic effects on this species. The results indicate that NEA cod and polar cod are quite independent, and a classical single species management approach would not differ extensively from a multispecies approach.

However, Atlantis results (Figure S5) displayed the impacts of NEA cod on other parts of the ecosystem that one might have missed with a single-species model, or even a simpler ecosystem model like Gompertz. Results showed similar responses as capelin and polar cod on additional species, such as prawns and herring that are important prey for NEA cod, as well as long rough dab and large demersal fish that compete with NEA cod for the same type of prey. Even though the changes in these species were not dramatic, the results emphasize the benefits of models including multiple species to capture a broad range of ecosystem responses.

5 | CONCLUSIONS

Our study emphasized the value of using multiple models to study ecosystems, both to better understand the models, and to provide useful information in terms of connections we are uncertain about and areas that need more research. Similar to earlier studies (Fulton et al., 2015; Kaplan et al., 2019), we find that a suite of models can be valuable in a collaborative context. By applying a multi-model approach to investigate the role of NEA cod in the Barents Sea, we draw the following conclusions:

- Including similar food webs for a selected set of species in the Barents Sea, the results from two ecosystem models are consistent in terms of the direction of effects on capelin, an important prey group, even though the magnitude varied.
- In both ecosystem models, indirect food web effects can be as important as direct effects.
- As illustrated by the case of polar cod, differences in horizontal model grid resolution are in part responsible for different responses to the same perturbations, due to changes in overlap between the top predator and its prey. This could potentially be important for models used in management, as these usually does not take into account neither other species nor have a spatial resolution. Applying models both with and without a spatial resolution could help identify the size of this uncertainty.
- The two models complement each other, and used in a management context they can guide the actions on different species, for instance using the strong cod-capelin interactions of the Gompertz model to explore potential management trade-offs between those species. The Atlantis model can be used to understand broader impacts of cod across a full suite of species ranging from prawns to larger demersal fish.

Our study supported the idea that fisheries management strategies could benefit from using multiple models of varying complexity, rather than relying on single models to assess ecosystem impacts of management and predator abundance. The results also illustrated the importance of trophic effects that would not be incorporated in single-species fisheries management, and which potentially could have impact on other parts of the ecosystem.

Although NEA cod is considered to be sustainably managed (Kjesbu et al., 2014), EBFM encourages consideration of trophic links and other drivers, to strengthen and coordinate management across not only this target species but also co-occurring species such as polar cod and capelin. This study shows that ecosystem models are useful tools to improve and support this more holistic management approach.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting the results in the paper will be available upon request.

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REFERENCES

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., & Fulton, E. A. (2019). Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. *Methods in Ecology and Evolution*, *10*, 1814–1819. https://doi.org/10.1111/2041-210X.13272

Botsford, L. W., Castilla, J. C., & Peterson, C. H. (1997). The management of fisheries and marine ecosystems. *Science*, *277*, 509–515. https://doi.org/10.1126/science.277.5325.509

Bracis, C., Lehuta, S., Savina-Rolland, M., Travers-Trolet, M., & Girardin, R. (2020). Improving confidence in complex ecosystem models: The sensitivity analysis of an Atlantis ecosystem model. *Ecological Modelling*, *431*, 109133. https://doi.org/10.1016/j.ecolmodel.2020.109133

Brander, K., Neuheimer, A., Andersen, K. H., & Hartvig, M. (2013). Overconfidence in model projections. *ICES Journal of Marine Science*, *70*, 1065–1068. https://doi.org/10.1093/icesjms/fst055

Brooks, R. J., & Tobias, A. M. (1996). Choosing the best model: Level of detail, complexity, and model performance. *Mathematical and Computer Modelling*, *24*, 1–14. https://doi.org/10.1016/0895-7177(96)00103-3

Clark, J. S., & Bjørnstad, O. N. (2004). Population time series: Process variability, observation errors, missing values, lags, and Hidden States. *Ecology*, *85*, 3140–3150. https://doi.org/10.1890/03-0520

Collie, J. S., Botsford, L. W., Hastings, A., Kaplan, I. C., Largier, J. L., Livingston, P. A., Plagányi, É., Rose, K. A., Wells, B. K., & Werner, F. E. (2016). Ecosystem models for fisheries management: Finding the sweet spot. *Fish and Fisheries*, *17*, 101–125. https://doi.org/10.1111/faf.12093

Dolgov, A. (2005). Feeding and Food Consumption by the Barents Sea Skates. *Journal of Northwest Atlantic Fishery Science*, *37*, 495–503. https://doi.org/10.2960/J.v35.m523

Fall, J., Ciannelli, L., Skaret, G., & Johannesen, E. (2018). Seasonal dynamics of spatial distributions and overlap between Northeast Arctic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in the Barents Sea. *PLoS One*, *13*(10), e0205921. https://doi.org/10.1371/journal.pone.0205921

Fulton, E. A., Boschetti, F., Sporcic, M., Jones, T., Little, L. R., Dambacher, J. M., Gray, R., Scott, R., & Gorton, R. (2015). A multi-model approach to engaging stakeholder and modellers in complex environmental problems. *Environmental Science & Policy*, *48*, 44–56. https://doi.org/10.1016/j.envsci.2014.12.006

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R. J., Smith, A. D. M., & Smith, D. C. (2011). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries*, *12*, 171–188. https://doi.org/10.1111/j.1467-2979.2011.00412.x

Fulton, E. A., Smith, A. D. M., & Johnson, C. R. (2004). Effects of spatial resolution on the performance and interpretation of marine ecosystem models. *Ecological Modelling*, *176*, 27–42. https://doi.org/10.1016/j.ecolmodel.2003.10.026

Geary, W. L., Bode, M., Doherty, T. S., Fulton, E. A., Nimmo, D. G., Tulloch, A. I. T., Tulloch, V. J. D., & Ritchie, E. G. (2020). A guide to ecosystem models and their environmental applications. *Nature Ecology & Evolution*, *4*, 1459–1471. https://doi.org/10.1038/s41559-020-01298-8

Gjøsæter, H., Huserbråten, M., Vikebø, F., & Eriksen, E. (2020). Key processes regulating the early life history of Barents Sea polar cod. *Polar Biology*, *43*, 1015–1027. https://doi.org/10.1007/s00300-020-02656-9

Gregory, J. M., Dixon, K. W., Stouffer, R. J., Weaver, A. J., Driesschaert, E., Eby, M., Fichefet, T., Hasumi, H., Hu, A., Jungclaus, J. H., Kamenkovich, I. V., Levermann, A., Montoya, M., Murakami, S., Nawrath, S., Oka, A., Sokolov, A. P., & Thorpe, R. B. (2005). A model intercomparison of changes in the Atlantic thermohaline circulation in response to increasing atmospheric CO2 concentration. *Geophysical Research Letters*, *32*, https://doi.org/10.1029/2005GL023209

Hampton, S., Holmes, E., Scheef, L., Scheuerell, M., Katz, S., & Pendleton, D. (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, *94*, 2663–2669. https://doi.org/10.1890/13-0996.1

Hansen, C., Drinkwater, K. F., Jähkel, A., Fulton, E. A., Gorton, R., & Skern-Mauritzen, M. (2019a). Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. *PLoS One*, *14*, e0210419. https://doi.org/10.1371/journal.pone.0210419

Hansen, C., Nash, R. D. M., Drinkwater, K. F., & Hjøllo, S. S. (2019b). Management scenarios under climate change – A study of the nordic and barents seas. *Frontiers in Marine Science*, *6*, 1–13. https://doi.org/10.3389/fmars.2019.00668

Hansen, C., Skern-Mauritzen, M., van der Meeren, G., Jähkel, A., & Drinkwater, K. (2016). Set-up of the nordic and barents seas (NoBa)

Atlantis model. https://doi.org/10.13140/RG.2.1.3339.9929

Harwood, J., & Stokes, K. (2003). Coping with uncertainty in ecological advice: Lessons from fisheries. *Trends in Ecology & Evolution*, *18*, 617–622. https://doi.org/10.1016/j.tree.2003.08.001

Heath, M., Speirs, D., Thurlbeck, I., & Wilson, R. (2020). S trath E2E2: An r package for modelling the dynamics of marine food webs and fisheries. *Methods in Ecology and Evolution*, *12*, 280–287. https://doi.org/10.1111/2041-210X.13510

Hill, S. L., Watters, G. M., Punt, A. E., McAllister, M. K., Quéré, C. L., & Turner, J. (2007). Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries*, *8*, 315–336. https://doi.org/10.1111/j.1467-2979.2007.00257.x

Holt, R. E., Bogstad, B., Durant, J. M., Dolgov, A. V., & Ottersen, G. (2019). Barents Sea cod (*Gadus morhua*) diet composition: Long- term interannual, seasonal, and ontogenetic patterns. *ICES Journal of Marine Science*, *11*, 45–12. https://doi.org/10.1093/ icesjms/fsz082

Ianelli, J., Holsman, K. K., Punt, A. E., & Aydin, K. (2016). Multi-model inference for incorporating trophic and climate uncertainty into stock assessments. *Deep Sea Research Part II: Topical Studies in Oceanography, Understanding Ecosystem Processes in the Eastern Bering Sea IV*, *134*, 379–389. https://doi.org/10.1016/j.dsr2.2015.04.002

ICES. (2018). Report of the Working Group on Widely Distributed Stocks (WGWIDE) 28 August- 3 September 2018. Torshavn, Faroe Islands 488. ICES CM 2018/ACOM

ICES (2019). Arctic Fisheries Working Group (AFWG). Cod (Gadus morhua) in subareas 1 and 2 (Northeast Arctic). Report of the ICES Advisory Committee. https://doi.org/https://doi.org/10.17895/ices.pub.4412

IPCC. (2013). *The physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

Ives, A. R., Dennis, B., Cottingham, K. L., & Carpenter, S. R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, *73*, 301–330.

Jacobsen, N. S., Essington, T. E., & Andersen, K. H. (2016). Comparing model predictions for ecosystem-based management. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(4), 666–676. https://doi.org/10.1139/cjfas-2014-0561

Jakobsen, T., & Ozhigin, V. K. (2011). *The Barents Sea: ecosystem, resources, management: half a century of Russian-Norwegian cooperation*. Tapir academic press Trondheim.

Kaplan, I. C., Brown, C. J., Fulton, E. A., Gray, I. A., Field, J. C., & Smith, A. D. (2013). Impacts of depleting forage species in the California Current. *Environmental Conservation*, *40*(4), 380–393. https://doi.org/10.1017/S0376892913000052

Kaplan, I. C., Francis, T. B., Punt, A. E., Koehn, L. E., Curchitser, E., Hurtado-Ferro, F., Johnson, K. F., Lluch-Cota, S. E., Sydeman, W. J., Essington, T. E., Taylor, N., Holsman, K., MacCall, A. D., & Levin, P. S. (2019). A multi-model approach to understanding the role of Pacific sardine in the California Current food web. *Marine Ecology Progress Series*, *617–618*, 307–321. https://doi.org/10.3354/meps12504

Kaplan, I. C., Koehn, L. E., Hodgson, E. E., Marshall, K. N., & Essington, T. E. (2017). Modeling food web effects of low sardine and anchovy abundance in the California Current. *Ecological Modelling*, *359*, 1–24. https://doi.org/10.1016/j.ecolmodel.2017.05.007

Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsæter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D., & Skjæraasen, J. E. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences*, *111*, 3478–3483. https://doi.org/10.1073/pnas.1316342111

Knutti, R. (2010). The end of model democracy? *Climate Change*, *102*, 395–404. https://doi.org/10.1007/s10584-010-9800-2

Laird, A. K. (1964). Dynamics of tumour growth. *British Journal of Cancer*, *18*, 490–502. https://doi.org/10.1038/bjc.1964.55

Langangen, Ø., Ohlberger, J., Stige, L. C., Durant, J. M., Ravagnan, E., Stenseth, N. C., & Hjermann, D. Ø. (2017). Cascading effects of mass mortality events in Arctic marine communities. *Global Change Biology*, *23*, 283–292. https://doi.org/10.1111/gcb.13344

Law, A. M. (1991). Simulation-models level of detail determines effectiveness. *Industrial Engineering*, *23*, 16.

Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, *54*, 421–431.

Link, J. S., Bogstad, B., Sparholt, H., & Lilly, G. R. (2009). Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries*, *10*, 58–87. https://doi.org/10.1111/j.1467-2979.2008.00295.x

Link, J. S., Ihde, T. F., Harvey, C. J., Gaichas, S. K., Field, J. C., Brodziak, J. K. T., Townsend, H. M., & Peterman, R. M. (2012). Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management. *Progress in Oceanography*, *102*, 102–114. https://doi.org/10.1016/j.pocean.2012.03.008

Marasco, R. J., Goodman, D., Grimes, C. B., Lawson, P. W., Punt, A. E., & Quinn II, T. J. (2007). Ecosystem-based fisheries management: some practical suggestions. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(6), 928–939. https://doi.org/10.1139/f07-062

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J., & Laws, R. M. (1979). Management of multispecies fisheries. *Science*, *205*, 267–277. https://doi.org/10.1126/science.205.4403.267

McGregor, V. L., Fulton, E. A., & Dunn, M. R. (2020). Addressing initialisation uncertainty for end-to-end ecosystem models: Application to the chatham rise Atlantis model. *PeerJ*, *8*, e9254. https://doi.org/10.7717/peerj.9254

McNicholl, D., Walkusz, W., Davoren, G., Majewski, A., & Reist, J. (2016). Dietary characteristics of co-occurring polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) in the Canadian Arctic, Dietary Bay. *Polar Biology*, *39*(6), 1099–1108. https://doi.org/10.1007/s00300-015-1834-5

Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A., & Gjøsæter, H. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES Journal of Marine Science*, *67*, 87–101. https://doi.org/10.1093/icesjms/fsp229

Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., & Link, J. S. (2016). Ecosystem model skill assessment. Yes we can! *PLoS One*, *11*, e0146467. https://doi.org/10.1371/journal.pone.0146467

Orlova, E. L., Dolgov, A. V., Rudneva, G. B., Oganin, I. A., & Konstantinova, L. L. (2009). Trophic relations of capelin Mallotus villosus and polar cod Boreogadus saida in the Barents Sea as a factor of impact on the ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography, the Proceedings of the ECONORTH Symposium on Ecosystem Dynamics in the Norwegian Sea and Barents Sea*, *56*, 2054–2067. https://doi.org/10.1016/j.dsr2.2008.11.016

Orlova, E. L., Ushakov, N. G., Nesterova, V. N., & Boitsov, V. D. (2002). Food supply and feeding of capelin (Mallotus villosus) of different size in the central latitudinal zone of the Barents Sea during intermediate and warm years. *ICES Journal of Marine Science*, *59*, 968–975. https://doi.org/10.1006/jmsc.2002.1255

Ottersen, G., Stige, L. C., Durant, J. M., Chan, K.-S., Rouyer, T. A., Drinkwater, K. F., & Stenseth, N. C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Marine Ecology Progress Series*, *480*, 205–225. https://doi.org/10.3354/meps10249

Paine, C. E. T., Marthews, T. R., Vogt, D. R., Purves, D., Rees, M., Hector, A., & Turnbull, L. A. (2012). How to fit nonlinear plant growth models and calculate growth rates: An update for ecolo- gists. *Methods in Ecology and Evolution*, *3*, 245–256. https://doi. org/10.1111/j.2041-210X.2011.00155.x

Payne, M. R., Barange, M., Cheung, W. W. L., MacKenzie, B. R., Batchelder, H. P., Cormon, X., & Paula, J. (2015). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES Journal of Marine Science: Journal Du Conseil*, *73*(5), 1272–1282. https://doi.org/10.1093/icesjms/fsv231

Plagányi, É. E. (2007). Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. 108p.

Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T., Pillans, R. D., Thorson, J. T., Fulton, E. A., Smith, A. D. M., Smith, F., Bayliss, P., Haywood, M., Lyne, V., & Rothlisberg, P. C. (2014).Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries*, *15*, 1–22. https://doi.org/10.1111/j.1467-2979.2012.00488.x

Reum, J. C. P., Townsend, H., Gaichas, S., Sagarese, S., Kaplan, I. C., & Grüss, A. (2021). It's not the destination, it's the journey: Multispecies model ensembles for ecosystem approaches to fish- eries management. *Frontiers in Marine Science*, *8*, 1–14. https://doi.org/10.3389/fmars.2021.631839

RStudio Team (2020). *RStudio: Integrated Development for R*. RStudio. http://www.rstudio.com/

Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, *9*, 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., & Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*, *17*, 165–175. https://doi.org/10.1111/faf.12111

Skogen, M. D., Budgell, W. P., & Rey, F. (2007). Interannual variability in Nordic seas primary production. *ICES Journal of Marine Science*, *64*, 889–898. https://doi.org/10.1093/icesjms/fsm063

Smith, A. D., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L. J., & Shin, Y. J. (2011). Impacts of fishing low–trophic level species on marine ecosystems. *Science*, *333*(6046), 1147–1150.

Spence, M. A., Blanchard, J. L., Rossberg, A. G., Heath, M. R., Heymans, J. J., Mackinson, S., Serpetti, N., Speirs, D. C., Thorpe, R. B., & Blackwell, P. G. (2018). A general framework for combining ecosystem models. *Fish and Fisheries*, *19*, 1031–1042. https://doi.org/10.1111/faf.12310

Stige, L. C., Eriksen, E., Dalpadado, P., & Ono, K. (2019). Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. *ICES Journal of Marine Science*, *76*(Supplement_1), i24–i36. https://doi.org/10.1093/icesjms/fsz063

Stige, L. C., Kvile, K. Ø., Bogstad, B., & Langangen, Ø. (2018). Predator-prey interactions cause apparent competition between marine zooplankton groups. *Ecology*, *99*, 632–641. https://doi.org/10.1002/ecy.2126

Thorpe, R. B., Quesne, W. J. F. L., Luxford, F., Collie, J. S., & Jennings, S. (2015). Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing. *Methods in Ecology and Evolution*, *6*, 49–58. https://doi.org/10.1111/2041-210X.12292

Tjørve, K. M. C., & Tjørve, E. (2017). The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the Unified-Richards family. *PLoS One*, *12*, e0178691. https://doi.org/10.1371/journal.pone.0178691

Townsend, H., Harvey, C. J., Aydin, K., Gamble, R., Gruss, A., Levin, P. S., Link, J. S., Osgood, K. E., Polovina, J., Schirripa, M. J., & Wells, B. (2014). *Report of the 3rd national ecosystem modeling workshop (NEMoW 3): Mingling models for marine resource management – multiple model inference*. NOAA Technical Memorandum.

Vaghi, C., Rodallec, A., Fanciullino, R., Ciccolini, J., Mochel, J. P., Mastri, M., Poignard, C., Ebos, J. M. L., & Benzekry, S. (2020). Population modeling of tumor growth curves and the reduced Gompertz model improve prediction of the age of experimental tumors. *PLoS Computational Biology*, *16*(2), e1007178. https://doi.org/10.1371/journal.pcbi.1007178

Walters, C., Christensen, V., Fulton, B., Smith, A. D. M., & Hilborn, R. (2016). Predictions from simple predator-prey theory about im- pacts of harvesting forage fishes. *Ecological Modelling*, *337*, 272–280. https://doi.org/10.1016/j.ecolmodel.2016.07.014 Wildermuth, R. P., Fay, G., & Gaichas, S. (2018). Structural uncertainty in qualitative models for ecosystem-based management of Georges Bank. *Canadian Journal of Fisheries and Aquatic Science*, *75*, 1635–1643. https://doi.org/10.1139/cjfas-2017-0149

Winsor, C. P. (1932). The gompertz curve as a growth curve. *Proceedings of the National Academy of Sciences*, *18*, 1–8. https://doi.org/10.1073/pnas.18.1.1

Zwietering, M. H., Jongenburger, I., Rombouts, F. M., & van't Riet, K. (1990). Modeling of the bacterial growth curve. *Applied and Environment Microbiology*, *56*, 1875–1881. https://doi.org/10.1128/aem.56.6.1875-1881.1990

SUPPORTING INFORMATION

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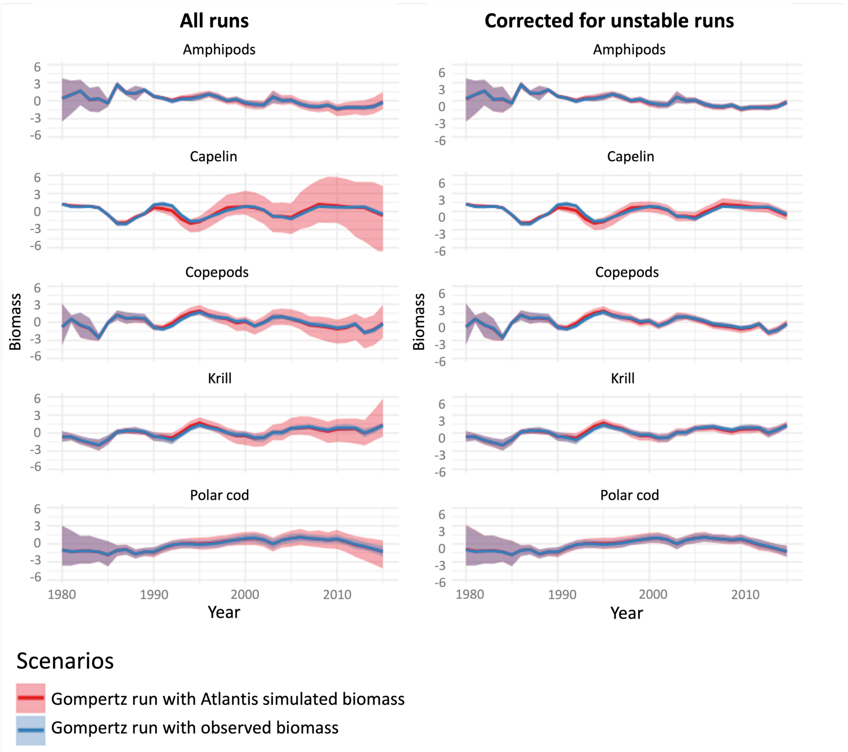
Supplementary materials for:
Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach

Figure S1 shows how removing unstable runs using eigenvalue greatly reduced the uncertainty of the Gompertz output, without affecting the mean. Panel a) plots all the runs compared to after unstable posteriors (identified by calculation the eigenvalue) was removed. The red lines show Gompertz with Atlantis cod biomass, while the blue line show the original Gompertz outputs. We see that removing unstable runs using eigenvalue greatly reduced the uncertainty of the results, mainly for capelin, but also for the other species. In panel b) we investigated how removing unstable runs affected the confidence interval and the median. Here the red line displays the results before removing unstable runs, while the blue lines show after. We see that removing unstable runs greatly affected the confidence interval but only impacted the median of the runs marginally.

a)



b)

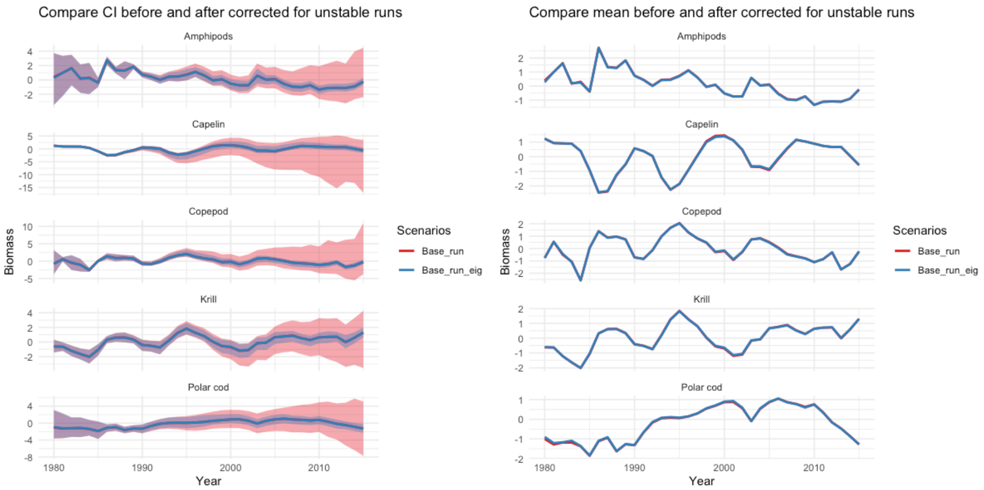


__Figure S1.__ A) All posterior samples from Gompertz using observed NEA cod biomass (blue) and Atlantis simulated biomass (red) before and after removing unstable runs. Solid line shows the median while shaded area represents the 95 % confidence interval. B) A comparison of the posterior samples before (red) and after (blue) correcting for unstable runs. This shows how the uncertainty was reduced, while the median of the runs only changed marginally.

Figure S2 show the results in Figure 3, but with the uncertainty included of the Gompertz results included. The uncertainty bands indicate that there is a great uncertainty of the results. For capelin the effects of cod could be more extreme than what the median of the results indicated, but there is little overlap between the two scenarios. For polar cod there is a big overlap of the two scenarios which indicates that the effect of NEA cod on polar cod was more uncertain.

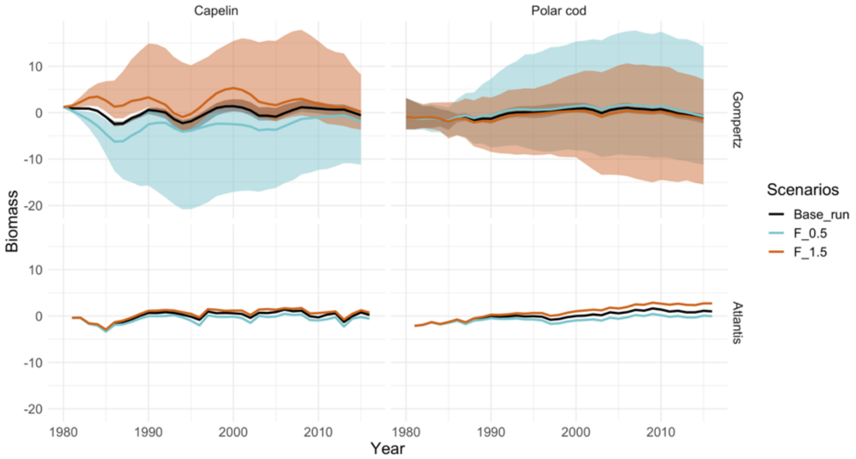


__Figure S2.__ Results of simulations with uncertainty of Gompertz results included. The black line shows the base line scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue) or increased (orange) by 50%. Solid lines show the median while shaded areas show 95 % confidence intervals.

Figure S3 demonstrates the effect of density dependence on capelin and polar cod. Two posterior samples were selected for capelin and polar cod where the density dependent parameters were either high or low, while the other parameters (c-values) were kept relatively constant. This was done to study the effect of density dependence alone and how it impacted the results. In Figure S3 we see how low-density dependence in the Gompertz model caused a stronger response to NEA cod perturbations for both capelin and polar cod. We also see that the number of runs with low density dependence ($c_{ii} > 1$) was higher for capelin than polar cod, which contributes to the stronger response to NEA cod perturbations in capelin biomass. Note that the figure show all of the runs before the unstable ones were removed.

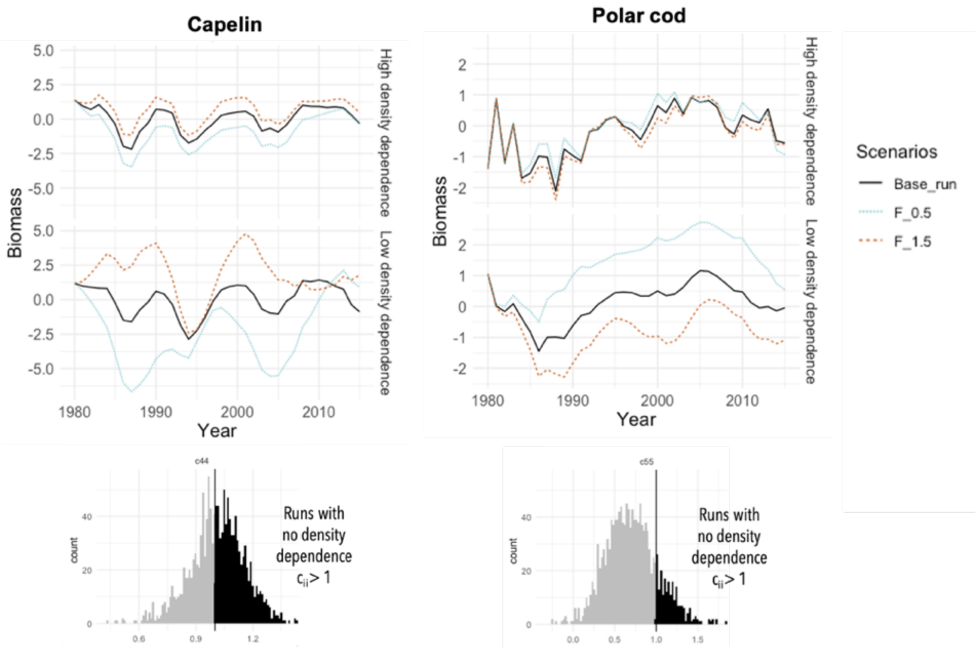


Figure S3. *Two different posterior samples with varying density dependence for capelin and polar cod in the Gompertz model. The effect of NEA cod was kept constant between the two samples for each of the species to investigate the effect of density dependence alone. The black line shows the baseline scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue) or increased (orange) by 50%. The figure also displays how many of the runs that had the density dependence above 1 where we see that this was the case for a higher fraction of the cii values for capelin compared to polar cod.*

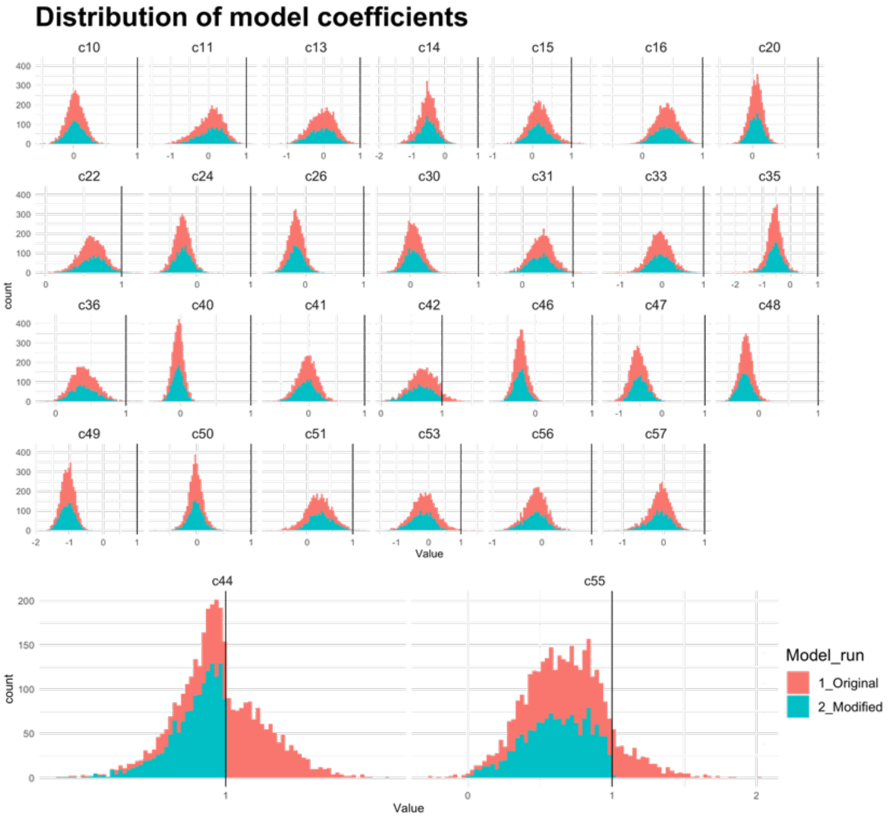


__Figure S4.__ The distribution of the model parameters before and after the density dependent coefficients for capelin and polar cod (c_{44} and c_{55}) was constrained to be below 1.

Figure S4 show the distribution of the model parameters before and after the density dependent coefficients for capelin and polar cod (c44 and c55) were constrained to be below 1. This was done in an attempt to fix the problem with unstable runs. This reduced the number of unstable runs (from 30 % to 15 %), but it did not solve the problem completely. Note that we reran the model with only 3 chains for timesaving reasons, which causes the frequency to be lower at the modified version.

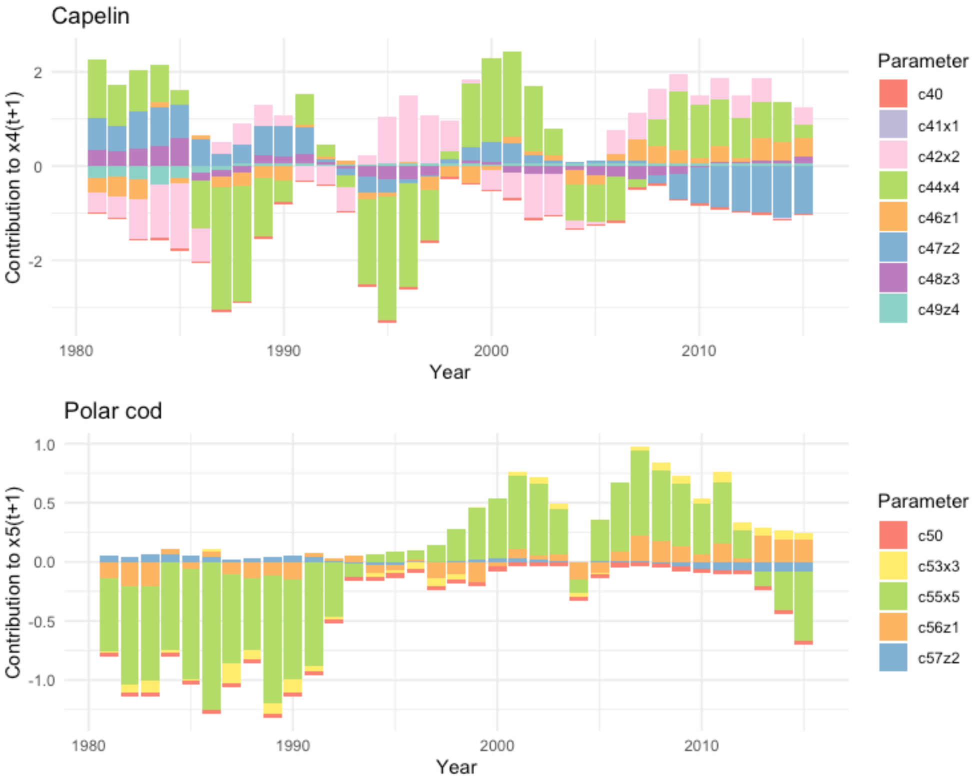


Figure S5. *The contribution to the variation in capelin and polar cod biomass in the Gompertz base run. The density dependence (green,* $c_{44}x_4$ *and* $c_{55}x_5$*) seemed to have a big impact on both species. We also see that the impact of cod (blue,* $c_{47}z_2$ *and* $c_{57}z_2$*) was greater on capelin than polar cod.*

In figure S5 we attempt to show how much the parameters contributed to the variation in capelin and polar cod biomass. We see clearly that the density dependent parameters (c44x4 and c55x5, green) had a great impact on both species. We also see that the direct effect of cod was greater on capelin compared to polar cod (c47z2 and c57z2, blue).

Figure S6 show the spatial distributions of NEA cod and polar cod in Atlantis during the course of a year, and the percentage of the capelin or polar cod stock overlapping with NEA cod. Capelin seems to have a greater overlap with NEA cod compared to polar cod, as the overlap with NEA cod is relatively high throughout most of the year. Polar cod is mainly distributed further north, but during wintertime when polar cod migrates to the South-eastern Barents Sea, the overlap with NEA cod increases.

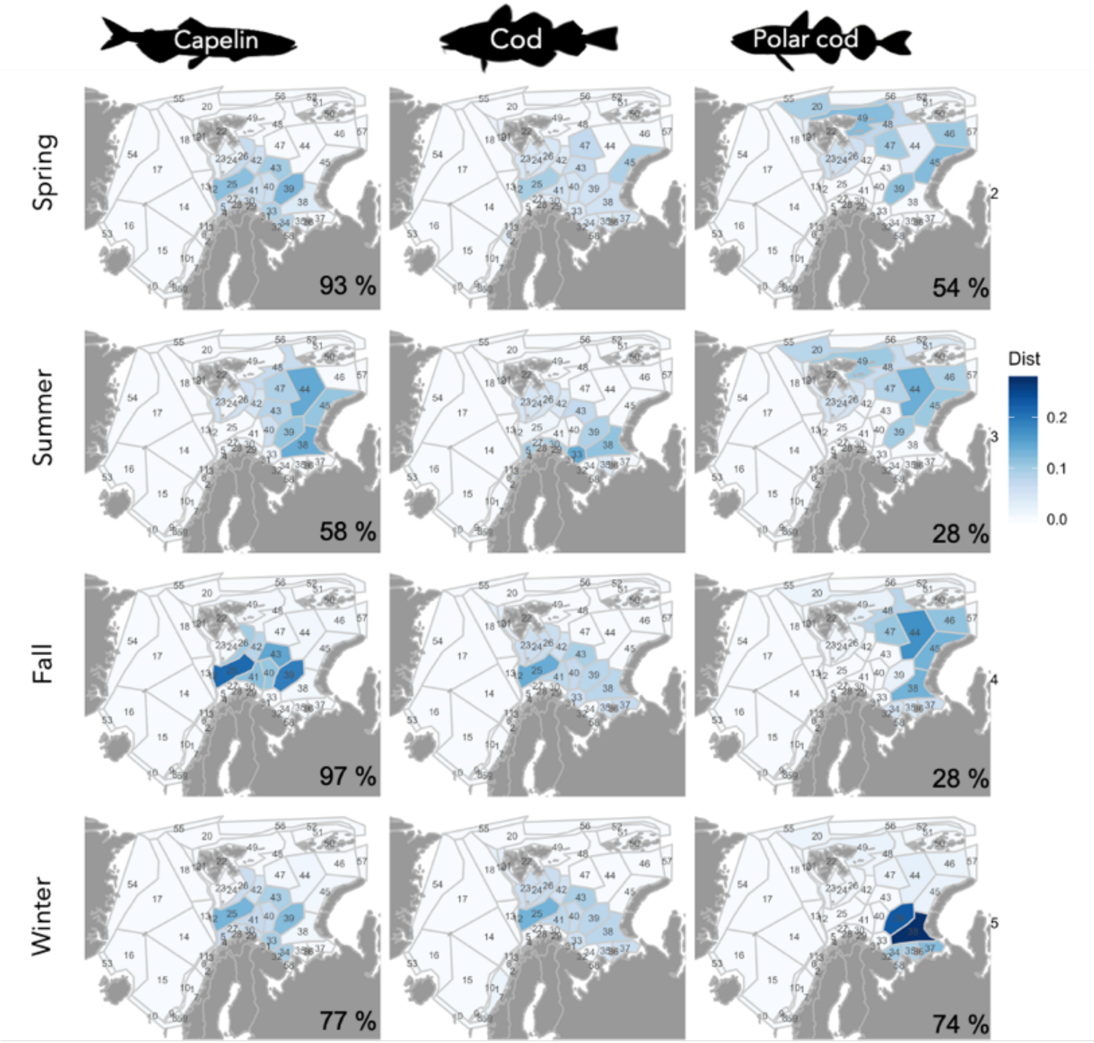


Figure S6. *The geographical distribution of NEA cod and polar cod in Atlantis throughout the course of a year. The figure shows how the biomass (given as a portion of the total biomass) is distributed throughout the polygons, as well as the percentage of the capelin and polar cod stock overlapping with NEA cod.*

Atlantis includes more species than Gompertz, which makes it possible to look at how the perturbated cod fisheries affected the entire ecosystem. Figure S7 shows how the other species responded in the scenarios in terms of percentage change in biomass. The change in biomass was calculated from the mean of a five-year period during the early stage of the simulation (1985-1990) and by the end of the simulation (2005-2010).

The species that were most affected by NEA cod was haddock and the planktonic groups. However, these results should be treated with caution as the plankton groups are highly variable, and haddock depends strongly on plankton for recruitment. Other species groups that responded to the change in NEA cod were prawns and herring, that were positively affected by less NEA cod, and long rough dab and large demersal fish that were negatively affected by more NEA cod and positively affected by less NEA cod. The most noticeable effect was that while cod responded strongly during the early period, the response of most other species was stronger during the later period of the simulation. Another overall trend in the results was that most species reacted negatively to more cod, and positively to less cod, the same as what was seen in capelin and polar cod.

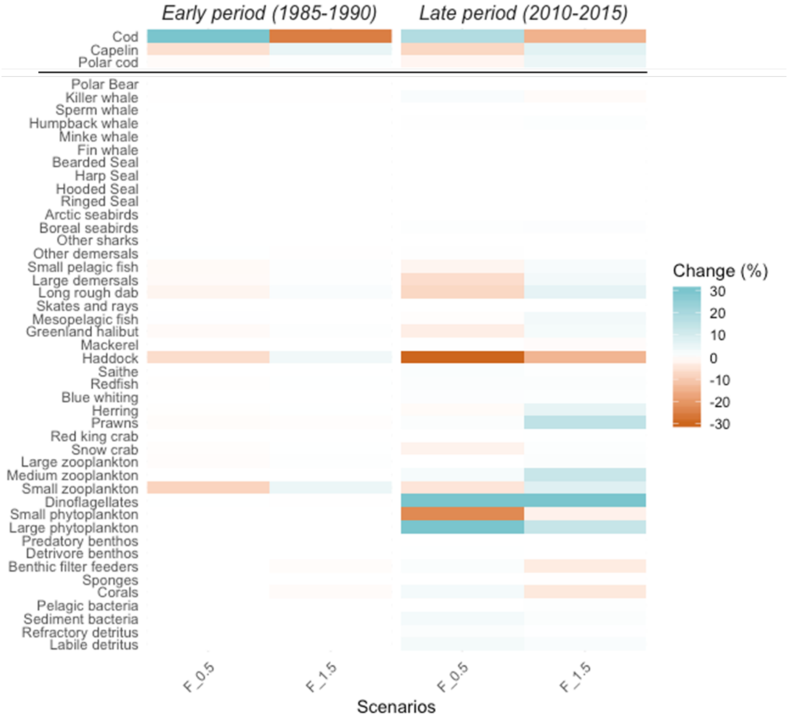


Figure S7. *An overview of how all the other species in Atlantis responded to the perturbed cod fisheries in terms of change in biomass. The mean change in biomass during a five-year period was calculated first in the early stage of the simulation (1985-1990) and then in the late period towards the end of the simulation (2010-2015). Dark blue/orange areas are changes above or below 30%.*

PAPER I

Paper II:

Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas

Ina Nilsen, Filippa Fransner, Are Olsen, Jerry Tjiputra, Robinson Hordoir and Cecilie Hansen*

In Review at Fisheries Oceanography

Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas

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Abstract

Downscaling physical forcing from global climate models is both time consuming and labor demanding and can delay or limit the physical forcing available for regional marine ecosystem modelers. Earlier studies have shown that downscaled physics is necessary for capturing the dynamics of primary production and lower trophic levels, however, it is not clear how higher trophic levels respond to the coarse resolution physics of global models. Here, we apply the Nordic and Barents Seas Atlantis ecosystem model (NoBa) to study the consequences of using physical forcing from global climate models versus using that from regional models. The study is therefore (i) a comparison between a regional model and its driving global model to investigate the extent to which a global climate model can be used for regional ecosystem predictions, and (ii) a study of the impact of future climate change in the Nordic and Barents Seas. We found that few higher trophic level species were affected by using forcing from a global versus a regional model, and there was a general agreement in future biomass trends and distribution patterns. However, the slight difference in temperature between the models dramatically impacted Northeast Arctic cod (*Gadus morhua*), which highlights how species projection uncertainty could arise from poor physical representation of the physical forcing, in addition to uncertainty in the ecosystem model parameterization.

Keywords: *Atlantis, Barents Sea, Climate change, Downscaling, Ecosystem modeling, Northeast Arctic cod*

1. Introduction

Global warming is already causing large-scale impacts in sub-Arctic and Arctic Ocean regions, with temperatures quickly rising and sea ice receding (Comiso, 2011; Smedsrud et al., 2013). These changes are altering the ecosystem by displacing southern, boreal species further north, while arctic species are retreating and declining (Fossheim et al., 2015; Frainer et al., 2017; Kjesbu et al., 2021, 2014). With the increasing number of marine environmental stressors (Henson et al., 2017), there is an urgent need to understand how marine ecosystems will respond to these changes (Fagundes et al., 2020).

The only process-based tools available to study the implications of future climate change are models. To study potential responses in ecosystem function and structure to climate change, output from climate models is often used as forcing for ecosystem models (Lotze et al., 2019; Tittensor et al., 2021). Over the past few years, the Intergovernmental Panel on Climate Change (IPCC) has developed five SSP narratives to describe alternative pathways for future society (IPCC, 2022). The SSPs contain a range of baseline scenarios spanning between 1.9 and 8.5 W/m2 of radiative forcing by 2100 and play an important role in facilitating integrated research across multiple climate modeling communities (O'Neill et al., 2016).

Global climate models, such as those used in the IPCC reports (IPCC, 2022), are generally capable of reproducing the observed long-term trends at a global scale. However, due to their global coverage, even with increasing computational power, their spatial resolution and parameterizations remain insufficient at regional scales that are relevant for marine ecosystems (Melsom et al., 2009; Tjiputra et al., 2007). This can lead to biases relative to observational data and inaccuracies in regional details (Skogen et al., 2018).

A way to improve such biases is through downscaling, where a high-resolution regional ocean circulation model is initiated from, and/or nested into, a global climate model (Skogen et al., 2018). This is done to translate coarse global information into finer scale resolution in order to simulate more accurate regional processes and obtain climate information on scales that are relevant to society (Ekström et al., 2015). Regional models also have the advantage of better-calibrated parameterizations targeted for the study regions (Hordoir et al., 2022).

Previous studies have explored the impact of increased model resolution and found that higher-resolution physical forcing produces results closer to observations and provides a better representation of ocean dynamics and variability. Increased resolution has been found to improve the representation of physical processes such as the northward transport of heat and salt (Langehaug et al., 2019), frontal regions (Kirtman et al., 2012), and deep convection (Busecke et al., 2019). Improving these processes results in temperatures and salinity closer to observations (Melsom et al., 2009; Sandø et al., 2014; Skogen et al., 2018) and improves the timing of spring bloom and estimates of net primary production (Hansen and Samuelsen, 2009; Skogen et al., 2018).

However, the process of downscaling physical forcing from global models is both time consuming and labor demanding, which can delay or limit the physical forcing available for ecosystem modelers. Some ecosystem models have coarse resolution grids with few or only one grid cell. Examples for the Nordic and Barents seas include Ecopath with Ecosim (Pedersen et al., 2021), Gompertz (Nilsen et al., 2022; Stige et al., 2019), NDND (Planque et al., 2014), RCaN (Planque et al., 2022), Gadget (Lindstrøm et al., 2009) and NoBa Atlantis (Hansen et al., 2016), where only the last one has more than two grid cells. The coarse resolution will cause these models to lose the details provided by the high-resolution models. However, differences in physics might still be reflected in the mean values used as forcing. If this is the case, how large are these differences, and would they impact not only the lower trophic levels, but also higher?

Several studies have used ecosystem models to study how species in the Nordic and Barents Seas might respond to future climate changes, from lower trophic levels to complex systems including several trophic levels. Skogen et al. (2018) used physical forcing from climate models of various resolution, and found no trends in future nutrient levels or primary production. Hansen et al. (2019b) studied the effect of changes in management strategies in combination with climate changes, and found an increased vulnerability in pelagic and demersal functional groups when harvesting a higher number of species. Cheung et al. (2010) showed that high-latitude areas such as the Norwegian and Barents Seas are likely to experience an increase in total catch potential in the future, based on calculations of future primary production, trophic level, and geographic range. This is supported by observations from the Barents Sea over the last decades, where increasing temperatures have been beneficial for e.g., Northeast Arctic cod (*Gadus morhua*) (Kjesbu et al., 2021, 2014).

In this study, we aim to focus on the higher trophic level species, and the goal is twofold: 1) study how much we gain, if anything, when applying downscaled forcing compared to forcing from a global climate model in a coarse resolution end-to-end ecosystem model simulation, and 2) to evaluate expected ecosystem changes in the Nordic and Barents Seas under the future climate changes with the two different types of forcing.

2. Models and simulations

To investigate how much we gain from downscaling, we study ecosystem responses to applying physical forcing from a global circulation model and from a downscaled regional model in the Nordic and Barents Seas Atlantis model. We will also investigate how sensitive the projections of the Barents Sea ecosystem are to the underlying physical forcing.

2.1 Models

We use physical forcing taken directly from the ocean component of a global climate model (NorESM2) and as downscaled with a regional ocean circulation model (Nemo-NAA10km) and apply them to an ecosystem model (NoBa Atlantis). The concept is illustrated in Figure 1 and a short description of the two oceanographic models and the ecosystem model follows below. Figure 1 also shows a comparison of the sea surface temperature as projected for the Nordic Seas and parts of the Arctic Ocean by NorESM2 and Nemo-NAA10km. Clearly, the RCM appears to capture spatial aspects in greater detail, including the northward flowing Atlantic Water and circulation along the coasts.

2.1.1 NorESM2

The Norwegian Earth System Model version 2 (NorESM2-MM; Seland et al., 2020; Tjiputra et al., 2020) is a fully coupled Earth system Model developed in Norway in collaboration with the National Center for Atmospheric Research (NCAR) in the United States. The model is an important tool for Norwegian climate researchers in the study of the past, present and future climate, and was recently updated from its original version NorESM1 (Bentsen et al., 2013; Tjiputra et al., 2013). The NorESM2-MM has contributed to the Coupled Model Intercomparison Project phase 6 – CMIP6 and to the latest assessment report of IPCC-AR6. It consists of the atmospheric model CAM6-Nor, the ocean physical model BLOM (Bentsen et al., 2020), the ocean biogeochemistry model iHAMOCC (Tjiputra et al., 2020), the sea ice model (CICE5.1.2), land model (CLM5), and river runoff model (MOSART). BLOM has a horizontal resolution of ~1° and 53 vertical isopycnic layers. CAM6-Nor has a horizontal resolution of ~1° on 32 vertical layers. The NorESM2-MM will hereafter be referred to just as “NorESM”, and a full description including an evaluation of its key climatic and biogeochemical features is available in Seland et al. (2020) and Tjiputra et al. (2020).

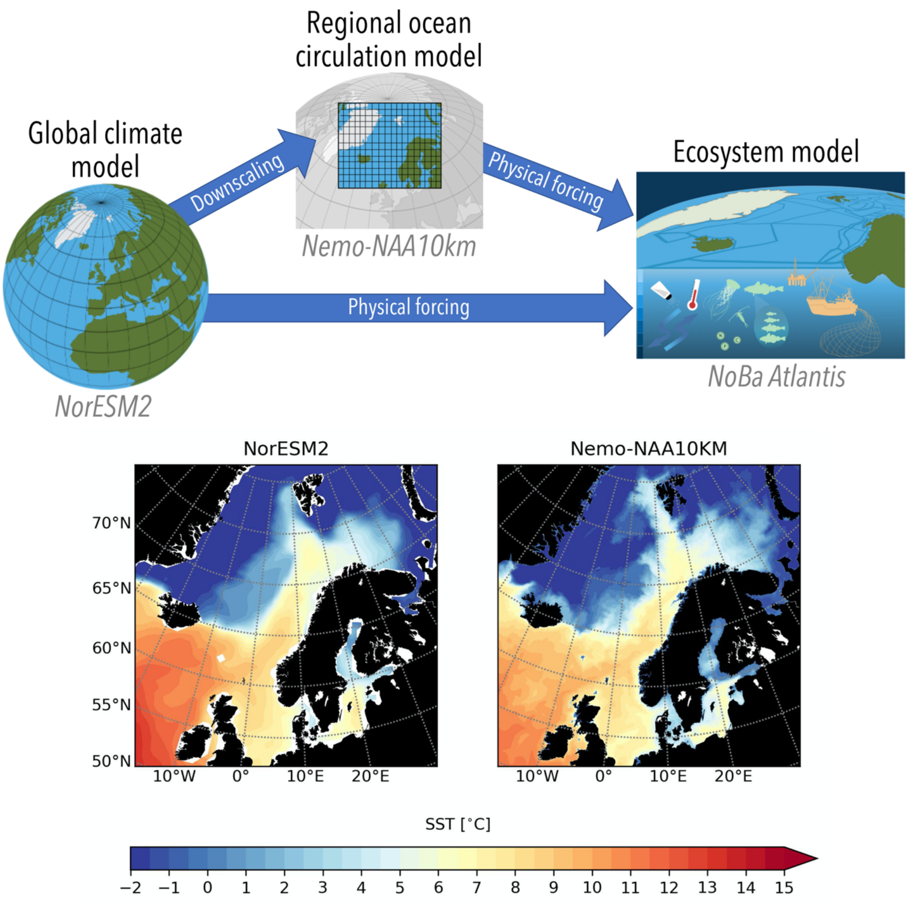

Figure 1. *An overview of the experiment configurations in the study where physical forcing from a global climate model and from a regional ocean circulation model are applied to an ecosystem model. Note that the regional extent of Nemo does not correspond to the one in the figure. The lower part of the figure illustrates the effects of downscaling, here visualized by showing projected mean sea surface temperatures (SST) from January 2000 directly from NorESM2 and as downscaled by Nemo-NAA10km.*

2.1.2 Nemo-NAA10km downscaling

The Norwegian Institute of Marine Research's regional ocean model Nemo-NAA10km (Hordoir et al., 2022) covers a major part of the North Atlantic and of the Arctic Oceans. This model is used for studying ocean processes in a changing climate, it is based on the NEMO ocean engine for both representing ocean and sea ice dynamics. The model works in forced mode at its surface and open boundary conditions. The model can be forced either by an atmospheric/oceanic reanalysis such as the ERA5 reanalysis (Hersbach et al., 2020) for the atmosphere, or the GLORYS reanalysis (Egbert and Erofeeva, 2002) for the ocean. The model can also be forced by a climate model both for the atmosphere and the ocean (climate downscaling), which allows for a better representation of ocean processes than that represented in climate models due to the higher resolution available. Nemo-NAA10km has been forced by the NorESM2 climate model for several emission scenarios (including SSP5-8.5 which is applied here).

Nemo-NAA10km is a forced model but runs without any kind of restoring in salinity nor in temperature. This enables a representation of the inter-annual variability of the thermohaline structure of the ocean. More information about this can be found in the supplementary materials and in Hordoir et al. (2022)

2.1.3 NoBa Atlantis (ecosystem model)

The Atlantis modeling framework (Audzijonyte et al., 2019; Fulton et al., 2011) is one of the most complex marine end-to-end ecosystem models in the world (Plagányi, 2007). In this study, the version implemented in the Nordic and Barents Seas (hereafter NoBa) (Hansen et al., 2019a, 2016) will be used.

The NoBa model contains 53 key species and functional groups (hereafter components) that are connected through a diet matrix. Most vertebrate species are age-structured while invertebrates are gathered into biomass pools. The model simulates spatial variation and is divided into 60 polygons with up to 7 depth layers depending on total water column depth (Hansen et al., 2016). The species can move between polygons and layers either actively through swimming or passively transported by currents (e.g., plankton, egg, larvae, nutrients). The majority of the vertebrate species have forced migration to ensure seasonal movement patterns throughout the year. The species are however free to distribute themselves (e.g., based on food availability, temperature preference, etc.) within these given polygons. A thorough description of the updates of this version of the NoBa model following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2020, 2006) is included in the Supplementary material.

2.2 Forcing

NoBa is forced by daily inputs of temperature, salinity, sea ice in each polygon, and also the net transport of water (m^3s^{-1}) between the polygons. In this study, monthly output from NorESM2 or 5-day mean forcing from Nemo-NAA10km was used to create the physical forcing for NoBa. To create the forcing files, an average value (of temperature, salinity, or sea ice concentration) was calculated over all grid cells (either Nemo-NAA10km or NorESM2) included in each of the 60 polygons of NoBa Atlantis. In the vertical, the average was calculated over the layers from the physical models which were within the depth levels of NoBa. Net transport was calculated across each face of the polygons (253 in total) for all depth levels. Linear interpolation was used to create daily fields from the monthly and 5-day means from NorESM2 and Nemo-NAA10km, respectively.

NoBa explicitly simulates concentrations of nutrients through nitrate which depends on primary production, remineralization (Murray and Parslow, 1997), horizontal transport, and vertical exchange between layers and sediments. Light is also calculated within the model for each of the polygons. Primary production is determined by a maximum growth rate and by limiting factors such as nutrients, light, and an eddy scalar (to facilitate vertical mixing between the layers). After the forcing from NorESM2 and Nemo-NAA10km was fitted to the NoBa grid we refer to the simulations using the two various sets of forcing as just “NorESM” and “Nemo” respectively to avoid confusion.

2.3 Simulations

Following the application of new forcing, the commercially exploited species in NoBa had to be calibrated to fit better to observations. This was done in order to ensure that the biomasses and the catches would be at observed levels and thereby represent the current situation. The same tuning was applied for both simulations i.e., Nemo-NAA10km and NorESM2 forced (Table S1), and the model was initiated from year 1980 and included a 24-year spin-up period where the same physical state of the year 1980 was repeated. The change in forcing started after the spin-up. Historical fishing levels were applied for the hindcast period (year 1980-2020) using assessment catches and total stock biomass data (ICES, 2021, 2020). After this, the fishing mortality in the last year (year 2020) was applied and maintained throughout the rest of the simulation. More information about the parameters that were tuned, and the results of the tuning can be found in the supplementary materials (Table S1, Figure S1).

In this study, we use the SSP5-8.5 scenario, which represents the highest emissions no-policy baseline scenario with fossil-fueled development and a growing economy. Although the SSP5-8.5 is the "worst-case scenario" and might not represent the most realistic future (Mohr et al., 2015; Wang et al., 2017) we decided to use this high-end baseline scenario to explore what 'could' happen, as it offers the largest signal-to-noise ratio, which was of interest in our study.

To compare the impact of physical forcing from the two models, eight simulations were set up (Table 1). In these simulations, we used forcing from either Nemo-NAA10km or NorESM2 (Nemo_ref, NorESM_ref), and then turned on the thermal niche of the species (Nemo_temp, NorESM_temp), included ice as forcing (Nemo_ice, NorESM_ice), or included both ice as forcing and the thermal niche (Nemo_ice_t, NorESM_ice_t). These scenarios were set up to study how the distinct parameter settings affected the species.

Table 1. Overview of the NoBa simulations conducted in this study

NO	NAME	DESCRIPTION
1	*Nemo_ref*	Forcing from Nemo-NAA10km
2	*NorESM_ref*	Forcing from NorESM2
3	*Nemo_temp*	Forcing from Nemo-NAA10km, thermal niche turned on
4	*NorESM_temp*	Forcing from NorESM2, thermal niche turned on
5	*Nemo_ice*	Forcing from Nemo-NAA10km, including ice forcing
6	*NorESM_ice*	Forcing from NorESM2, including ice forcing
7	*Nemo_ice_t*	Forcing from Nemo-NAA10km, including ice forcing and thermal niche turned on
8	*NorESM_ice_t*	Forcing from NorESM2, including ice forcing and thermal niche turned on

Turning on the thermal niche restricts the species to spawn or reside in polygons within their tolerated temperature range. Hence, if the temperature in the polygon is below or above the species´ temperature range, the species cannot inhabit or spawn in that polygon when the thermal niche is turned on. However, the temperature still affects the species when the thermal niche is turned off as it is included in both growth and consumption equations (Audzijonyte et al., 2017). The temperature ranges set in NoBa were based on literature (Hansen et al., 2016).

Using ice as forcing was important since the Barents Sea is largely covered by ice during winter and early spring. Including ice also affects the distribution of the species, as some species don´t tolerate being under ice, while others thrive being on, in or under the ice. The ice cover also affects the primary production by limiting the availability of light in the water underneath it.

2.4 Data analysis

To compare both the forcing from the models and the results from the NoBa simulations, two different periods of 15 years: an early (year 2005-2020) and a late (year 2085-2100) were chosen. These periods were used to examine the trends throughout the simulation and compare potential future levels to the present. The temperature, salinity and ice of the entire model area were estimated by accounting for the area and depth of the polygons and layers. For temperature and salinity, the median values over all polygons were used for comparison since the distribution of values was somewhat skewed and had some clear outliers. Total ice cover was estimated by summarizing the areas covered with ice concentration > 30 %. Monthly and yearly means of the physical forcing were calculated based on snapshots taken every 5th day throughout the year.

To study the effects of the physical forcing on the ecosystem, the difference in biomass (%) in NorESM simulations compared to Nemo was used. We considered any difference exceeding 15 % to be significant based on uncertainty limits used in the ICES reports (ICES, 2021). The biomass estimates were based on five snapshots throughout the year to capture seasonal variation, and a yearly mean was calculated based on this. It should be noted that haddock (*Melanogrammus aeglefinus*), snow crab (*Chionoecetes opilio*) and king crab (*Paralithodes camtschaticus*) were removed from the results, as these species are either collapsing or increasing to unrealistically high levels. There is no obvious reason to believe this would happen in the real world, such that this behavior is in all likelihood a consequence of model artifacts. The species were sorted by trophic levels (Fishbase, 2022) to investigate the effect of the physical forcing on the different parts of the food chain. Species with trophic levels > 3 were considered high trophic level species (Pauly and Watson, 2005).

When studying the sensitivity to future climate changes in NoBa, all species and groups were gathered into 11 categories (Table S2). The biomasses of the species within each category were summarized to study how the total biomass varied compared to the mean biomass in the early period (year 2005-2020) in the scenarios. The groups of bacteria and benthos were not plotted for these future studies as these contain large functional groups and the parameterization of these is more uncertain.

The spatial distribution of the commercial species was also investigated to evaluate how it is affected by the difference in physical forcing. This was calculated by estimating the center of gravity of the distribution, based on the mean longitude and latitude coordinates where the greatest portion of the stock resides throughout the seasons. We then explored the change in this point, either between the scenarios with different physical forcing, or from early period to late period. To evaluate the change, we decided that the change in distribution point was considered significant when the distance was equal to or more than 10 km, which is a relatively small distance compared to observed changes in distribution, but due to the coarse resolution of the model and the fact that it was based on mean changes over a 15-year period, it would still provide insight into projected movement.

All figures were created using “R studio” (RStudio Team, 2020), version 4.1.2.

3. Results

The results are separated into three sections. The first summarizes how the physics from the two oceanographic models differed after being fitted to the NoBa polygons, the second evaluates the sensitivity of the NoBa Atlantis ecosystem simulations to the difference in physics, and the third uses the different scenarios and forcings to study impacts of future climate change on the Nordic and Barents Sea ecosystem.

3.1 Differences in temperature, salinity and ice cover

The monthly climatology of temperature and salinity from Nemo and NorESM above and below 150 meters for the early (year 2005-2020) and late (year 2085-2100) periods were compared after being fitted to the NoBa grid (Figure 2). For temperature, the difference largely depended on what part of the water column we compared. In the upper 150 meters, Nemo projected a higher overall median temperature throughout the year, both for the early- (3.3 °C compared to 3.0 °C) and the late period (5.0 °C compared to 4.6 °C; Figure 2a). Below 150 meters however, Nemo projected lower temperatures, both for the early (1.9 °C compared to 2.2 °C) and the late period (2.9 °C compared to 3.2 °C; Figure 2a). While Nemo projected warmer temperatures in the shallower parts of the water column mainly around Svalbard and in the Barents Sea, NorESM projected warmer temperatures in the deeper layers of the Norwegian Sea (Figure S2). Accounting for the volume of the polygons the overall temperature was higher in NorESM, but the greatest differences between the two models were observed in the sea surface layer where Nemo was warmest (up to 6 °C). The difference in the upper layers was highest in September (> 1 °C) for both periods, while for the lower part of the water column the difference was more or less the same throughout the year. Between 2005-2020 and 2085-2100, the median temperatures throughout the entire water column increased by 1.4 and 1.2 °C in NorESM and Nemo, respectively. The overall difference between the two also increased as the median difference went from 0.3°C to 0.5 °C.

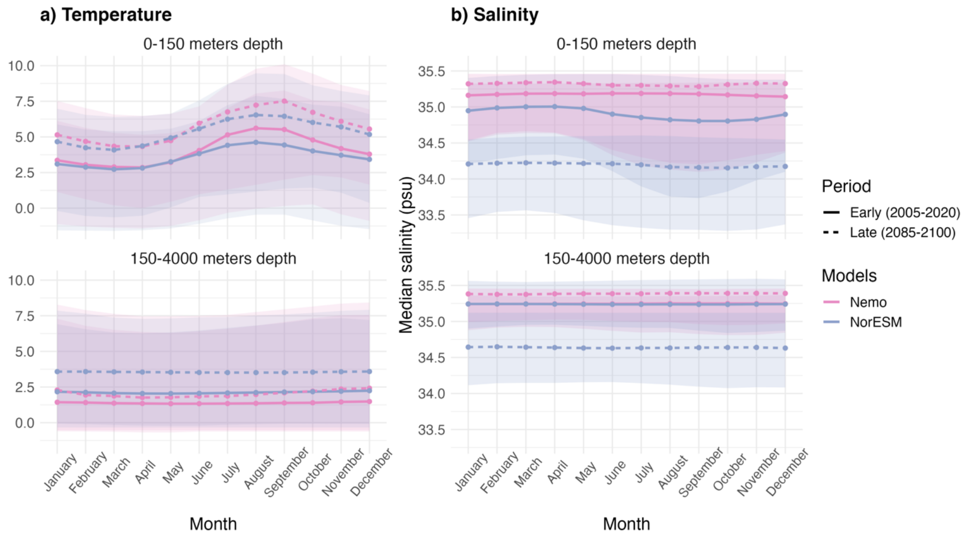

Figure 2. Monthly climatology of temperature and salinity above and below 150 meters of the water column throughout the entire model when using Nemo (pink) or NorESM (purple) as forcing. The solid lines show the early period (2005-2020), while dotted lines show the late period (2085-2100), and the shaded bands shows the 95 % confidence interval.

For salinity, the situation was somewhat different (Figure 2b). The difference in salinity was uniformly distributed across all polygons and layers (but with a slightly greater difference in the layers closest to the surface for the early period) (Figure S3). The biggest difference here was temporal rather than spatial as NorESM projected a clear decline in the salinity throughout the simulation, while Nemo was quite stable and slightly increasing. For the early period, NorESM projected marginally lower salinity than Nemo (median -0.1 compared to Nemo), while towards the end of the simulation the salinity was substantially lower (median -0.93 compared to Nemo). From the early period to the late, NorESM projected a decrease in median salinity from 35.1 to 34.4, while Nemo had a slight increase from 35.2 to 35.4. The difference in salinity was largest in the upper 150 meters of the water column in both periods.

The NoBa-fitted sea ice cover from Nemo and NorESM was compared, focusing on the area with sea ice concentration > 30%. The seasonal ice cover was calculated as a mean and compared for the early- and late periods. The results showed a consistent decrease in ice concentration from the early to the late period in both models. In Nemo the ice cover extended further southward along eastern Greenland, compared to NorESM where the ice cover was mostly confined to the northeastern Barents Sea (Figure 3).

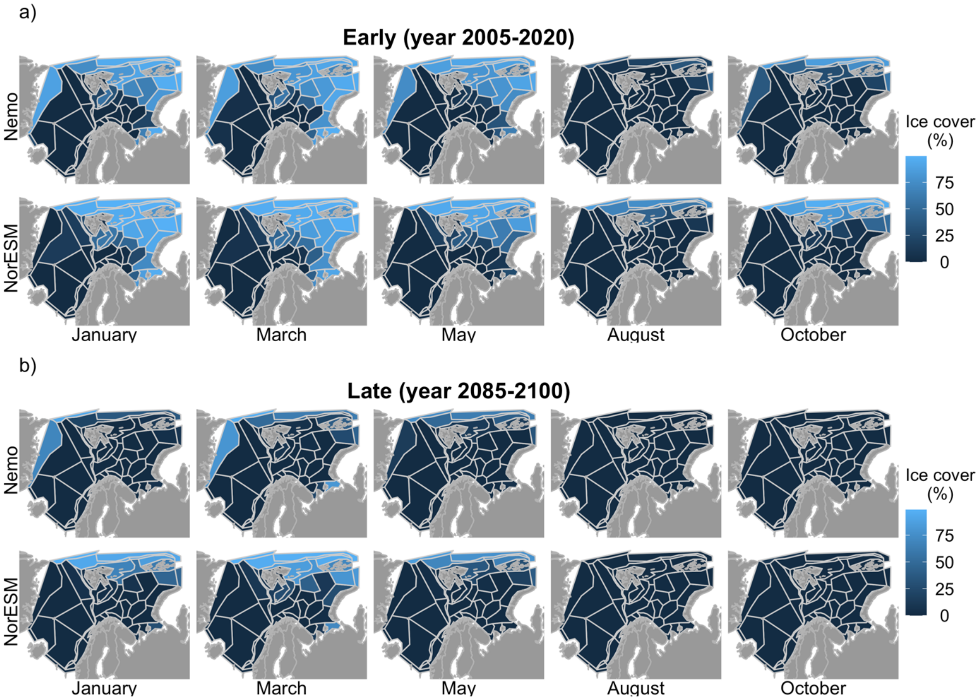

Figure 3. Mean seasonal sea ice cover [%] from Nemo and NorESM and how they varied throughout the year, when interpolated into NoBa grids (polygon outlines). The sea ice cover was given as concentration averaged over the a) early (year 2005-2020) and b) late (year 2085-2100) periods.

The total area covered with ice throughout the entire year was approximately the same for Nemo and NorESM in the early period, while in the late period the area was slightly greater (20 %) in NorESM compared to Nemo. When comparing the monthly sea ice cover (Figure S4) for the early period, Nemo projected more ice in the spring (February-May), while NorESM projected more during the rest of the year, especially in the late summer (July-September). In the late period NorESM projected more ice than Nemo in all months except April and December.

3.2 Species responses to forcing from Nemo or NorESM

The biomasses of all components in NoBa were compared to explore how they responded to the two sets of physical forcing (Figure 4). This was done for the two 15-year periods defined as early and late, which allowed for comparison between the two physical forcings and how this difference varied through time. The components were sorted by trophic levels to investigate the effect of the physical forcing on the different parts of the food chain.

Figure 4. *Difference in biomass for the components in NoBa when using physics from NorESM compared to Nemo. The difference in mean biomass for two 15-year periods were compared; an early- (year 2005-2020) and a late period (year 2085-2100). Green cells indicate a higher biomass in NorESM compared to Nemo, while red cells indicate a lower biomass in NorESM, and differences > 15 % are given as values.*

The majority of the species in the model were not notably impacted by using NorESM as physical forcing instead of Nemo. The species and groups that were most impacted were lower trophic levels species such as the phyto- and zooplankton groups, prawns, and mesopelagic fish.

However, some higher trophic level species were also impacted in the simulations, in particular long rough dab (*Hippoglossoides platessoides*) and Greenland halibut (*Reinhardtius hippoglossoides*). Both species responded when turning on the thermal niche, and the difference was the same whether ice was included as forcing or not, indicating that the thermal niche was the main driver for this response. The biomass of long rough dab was reduced in NorESM compared to Nemo both in the early (-18 %) and late (-20%) periods. The reduction in biomass was caused by a reduction in numbers rather than weight and occurred first in age class 1 at the start of the simulation indicating a reduction in recruitment. Greenland halibut, on the other hand, increased in biomass (by 22 %) in NorESM compared to Nemo in the late period when the thermal niche was turned on. The increase in biomass was also here caused by a higher abundance and occurred in the first age class.

When comparing the early period to the late, it was evident that the difference in biomass between the NorESM and Nemo simulations was apparent for more species in the late period compared to the early. Another tendency was that higher trophic level species also responded more strongly to the difference in physical forcing when the thermal niche was turned on.

We also investigated which traits might the influence stability of biomass to environmental change (Supplementary materials, Figure S5). The changes in biomass in NorESM compared to Nemo from figure 4 were converted to absolute values as a measure of variability. This variability was plotted for all species and separately only for vertebrates, against trophic level, lifespan (a proxy for population growth rate or population productivity), temperature sensitivity (the width of the thermal niche) and core area (size of occupied habitat at model initialization for vertebrates). Results showed a negative correlation between variability and trophic level and lifespan. When focusing only on vertebrates there was also a significant negative correlation between variability and thermal niche, as well as the area occupied area at model initialization.

How the different sets of physical forcing affected the distribution of the commercial species was also studied. The distributions were not notably altered when using different physical forcing (i.e Nemo vs NorESM). The only changes were observed when the thermal niche was turned on, and occurred in herring, which was displaced between 24-11 km (depending on the seasons) to the East in NorESM compared to

Nemo in the late period, and Northeast Arctic cod (*Gadus morhua*), hereafter cod, which was relocated 18 km southwest in NorESM in the spring. However, these displacements were relatively small compared to the size of the polygons and were considered negligible.

3.3 Species responses to future climate changes

Using two sets of physical forcing and various temperature and ice sensitivity settings offered the opportunity to include uncertainty in the projections when studying the ecosystem responses to climate changes. The species in NoBa were grouped into categories, and the change in total biomass within each category throughout the simulation was plotted (Figure 5).

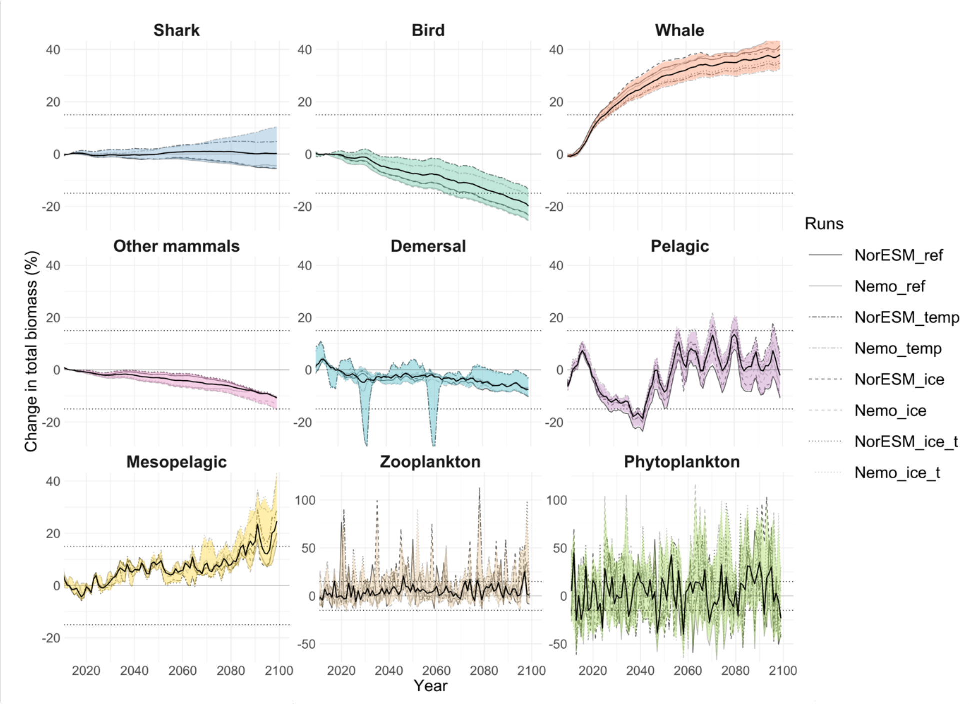

Figure 5. *Projected changes in total biomass for various species groups. Grey lines represent the projected biomass from the different simulations, while black solid line shows median and shaded area shows the 95 % confidence interval. Horizontal dotted lines indicate changes greater than 15 %. Please note that the number of species within each category varies and that the y-axes for the zoo- and phytoplankton groups differ from the others.*

For most of the categories the overall trend was the same for all simulations, while the biomass levels varied slightly. The groups of whales and mesopelagic species had positive biomass trends and increased by 30-40 % towards year 2100, while other mammals and seabirds decreased by 10-20 %. The pelagic species first decreased and then increased before stabilizing. The zoo- and phytoplankton groups were highly variable, but the overall level was stable throughout the run. The sharks and the demersal species had a stable mean, but the various simulations projected different trends. For sharks, the simulations with the thermal niche turned on projected a slight positive increase of 5-10 % towards the end of the simulation, while the runs without the thermal niche projected a slight decrease of ~5 %.

The most striking effect of climate change was in the demersal group where projections displayed two big drops in biomass depending on the different scenarios. Investigating the species within this group revealed that cod was causing most of this variation (Figure 6). The cod stock experienced two severe declines in biomass in year 2032 and 2060, happening only in the scenarios where NorESM was used as forcing and the thermal niche was turned on (NorESM_ temp and NorESM_ice_t). The biomass in these years was reduced by ~60 % with catches reduced to ~50 % compared to current levels (year 2005-2020).

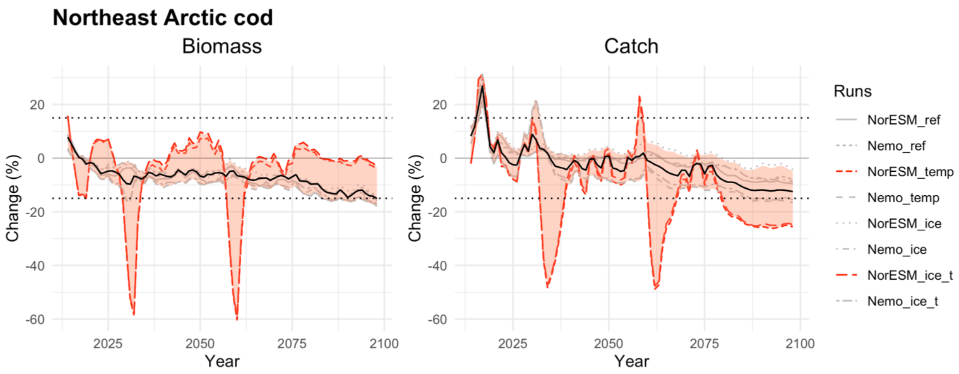

Figure 6. *Projected changes in Northeast Arctic cod biomass and annual catches in scenarios with various physical forcing and parameter settings showed several drops in biomass. Grey lines represent the projected biomass from the different scenarios with the two projections resulting in collapse marked as red. The black solid line shows median biomass and shaded area shows the 95 % confidence interval. Lines indicating changes greater than 15 % was marked as horizontal dotted lines.*

Investigating the collapses further revealed that the temperatures in the spawning areas of cod were lower in NorESM compared to Nemo. The minimum spawning temperature of cod was set to 4 °C based on literature (Bergstad et al., 1987; Höffle et al., 2014; Langangen et al., 2019; Righton et al., 2010; Sandø et al., 2020), and temperature in NorESM was thereby below the tolerated temperature for cod to spawn, resulting in recruitment failure. This could clearly be observed as intermittent declines in temperature in the spawning area were followed by stock collapses and occurred when NorESM had particularly low temperatures. Although the temperatures from Nemo also occasionally dropped below 4 °C, the durations of these events were generally much shorter. The individual species within each category were investigated separately to reveal if this was happening in any of the other species as well (Figure S6), but this mainly occurred with cod.

Comparing the early period to the late period showed that both models projected notable changes in distribution for the different commercial species, especially for herring (*Clupea harengus*), saithe (*Pollachius virens*), cod, golden redfish (*Sebastes norvegicus*) and Greenland halibut. All these species moved in a northeastern direction, with the exception of saithe, which moved northwest. Turning on the thermal niche slightly increased the change in distribution, but the overall results were more or less the same for all the scenarios. The change in distribution also appeared gradually for these species, as opposed to a sudden shift in distribution. A summary of the distance between the early and the late period can be found in table S3.

4. Discussion

In this study we had two objectives. First, to study how much we gain when applying downscaled forcing compared to forcing from a global climate model in a coarse resolution end-to-end ecosystem model simulation. And second, to evaluate expected ecosystem changes in the Nordic and Barents Seas under future climate changes with the two different types of forcing.

What we gain from downscaled physics was interpreted at the resolution of our ecosystem model, NoBa, and therefore the translation from Nemo-NAA10km and NorESM2 onto NoBa was critical. Comparing the physical forcing in Nemo and NorESM revealed that the temperature and ice cover varied between the two models even after being converted to the coarse NoBa grid. Nemo projected higher temperatures in the upper water column around Svalbard, while NorESM projected higher temperatures below 150 meters in the Norwegian Sea (Figure 2a). The temperature difference slightly increased throughout the simulation. The sea ice cover in terms of area with ice concentration > 30 % was similar in the two models for the early period, while in the late period Nemo projected less ice than NorESM. The distributions of the sea ice cover also differed between the models with Nemo projecting more ice east of Greenland compared to NorESM (Figure 3).

A large part of the differences between NorESM and Nemo was most likely a result of the different horizontal resolutions of NorESM2 and Nemo-NAA10km. It is well known that the representation of currents, fronts, and sites of deep convection, are improved with an increased horizontal resolution of ocean models (Busecke et al., 2019; Kirtman et al., 2012; Langehaug et al., 2019). In the Nordic and Barents seas, increased resolution typically leads to an increased northward transport of heat and salt (Langehaug et al., 2019), which brings the simulated temperature and salinity closer to the observed. NorESM2 and Nemo-NAA10km further have different vertical coordinate systems, vertical resolution, and physical parameterizations, which all have an impact on the representation of vertical mixing and the bottom boundary currents. Also, the river forcing and the sea ice modules differ between the models, which can give rise to differences in the freshwater budget. To get around problems with biases in the physical forcing, adopting an anomaly approach could be a possible solution, i.e., where the ecosystem model is forced with modeled changes from present climatology, instead of the modeled full field hydrography. Similar approaches are used for example in data assimilation (Bethke et al., 2021), and in acidification studies (Fransner et al., 2022), and could be applied to future ecosystem studies. A detailed investigation of the inter-model differences would require an extensive analysis of the simulated ocean dynamics and additional sensitivity runs and is beyond the scope of this paper.

The lower trophic levels in NoBa responded quickly to changes in physics and were generally more variable than the higher trophic levels. The results of the study were therefore in line with the findings that the lower trophic levels were more sensitive to the resolution of the physical forcing (Hansen and Samuelsen, 2009; Lee et al., 2016; Skogen et al., 2018), although a direct comparison is not easy as NoBa has a coarse resolution and is better at capturing the dynamics of higher trophic level species. While variable, the projected lower trophic level biomass showed no clear trend with time in the various simulations. This could be due to the fact that the planktonic groups in NoBa are divided based on size rather than species, where the size classes have wide temperature ranges and will therefore not be constricted by the thermal niche. Generally, high-latitude spring-bloom ecosystems should benefit from higher temperatures giving increased production, but other factors like changes in mixed-layer-depth may alter this (Skogen et al., 2018). Other recent papers have also found uncertainty in projections of future trends in plankton and net primary production, but more agreement across models and stronger impacts regarding the effects of climate change on higher trophic levels (Heneghan et al., 2021; Lotze et al., 2019; Skogen et al., 2018; Tittensor et al., 2021).

Generally, few species responded differently to using forcing from NorESM2 compared to Nemo-NAA10km (Figure 4). The high trophic level species that stood out in our results were cod, long rough dab and Greenland halibut, where all three had in common that they responded in the simulations where the thermal niche was turned on. Cod had the most dramatic response where events of massive recruitment failure occurred in NorESM, leading to collapses in total biomass and greatly reduced catches (Figure 6). This was due to the temperature in NorESM occasionally falling below the tolerated spawning temperature of cod. Investigating the temperature in the polygons where the adult long rough dab spawned revealed that, similar to cod, the temperature in NorESM was occasionally below their tolerated spawning temperature in several of the polygons, leading to a reduced recruitment. Greenland halibut, on the other hand, responded positively in the NorESM scenario as opposed to the other two. This response was due to the reduction in long rough dab (and partly cod) as these prey on the same species and overlap in distribution.

Investigating which traits might influence stability showed that species with short lifespans were more variable in the model. Lower trophic level species and species with narrower thermal niches experienced higher variability, although the significance of this correlation depended on whether all species were studied or just vertebrates were included. Vertebrate species also experienced higher variability when occupying a smaller habitat at model initialization. Lower trophic levels, which consistently responded more strongly to changes in physical forcing, include a temperature correction in the growth rates. The correction is higher for phytoplankton than other species (Hansen et al., 2016) and might lead to stronger responses in phytoplankton-feeding organisms (like zooplankton) which in turn could impact other zooplankton-feeding species (such as prawns). The response to this variability is dampened through the system (Bracis et al., 2020; Hansen et al., 2019; Pantus, 2006). In addition, plankton and other invertebrates use all their energy to grow (in our model formulation), while vertebrates devote energy to reproduction. Furthermore, our results suggest that for vertebrates in particular, traits such as lifespan, thermal niche, and area occupied influence stability.

Turning on the thermal niche had a larger effect on the species when comparing the scenarios, both in terms of how the species responded to the physical forcing from NorESM or Nemo, and their projections in a future warmer climate. The temperature ranges that were set in NoBa were based on literature, but species temperature tolerance is uncertain, and in our model especially for the functional groups and non-commercial species where information is scarce. Even for cod, the tolerated temperature range for spawning grounds has been discussed in several studies (Bergstad et al., 1987; Höffle et al., 2014; Langangen et al., 2019; Righton et al., 2010; Sandø et al., 2020) with minimum temperature ranging from 2.0 – 6.5 °C. The lowest tolerated temperature for cod spawning was set to 4 °C in NoBa, but this divergence reflects the uncertainty regarding the species´ tolerated temperature ranges. Another issue was that due to the coarse spatial resolution of NoBa, the temperature range of several species had to be adjusted to allow them to be in areas where they had been observed historically (Table S1). The thermal niche also affected the species in such a way that if the temperature was outside the species range it could not spawn or inhabit that polygon. Given the coarse resolution of NoBa, future studies might benefit from adjusting this parameter to first *reduce* the spawning or habitat quality before inhibiting it when the temperature is outside the tolerated range.

Adding ice as forcing had a weaker effect on the species compared to the thermal niche, especially for the higher trophic level species discussed above. However, many Arctic species are known to be highly dependent on ice (Kearney et al., 2021). Polar cod (*Boreogadus saida*) is an example of such a species, where the reduction in ice cover projected by the SSP5-8.5 scenario is expected to severely impair their recruitment and habitat conditions. (Gjøsæter et al., 2020; Kjesbu et al., 2021). The fact that polar cod was not negatively affected in our projections suggests that further development of the ice parameters in the NoBa model is needed, as the link between the species and their dependence on ice might be too weak. This was the first attempt at applying ice in an Atlantis model, and for future studies the link between the survival of a species and its dependency on ice should be revised.

There was a Northeastern shift in some species throughout the simulations. The same trends were observed in Nemo and NorESM and occurred independent of whether the various settings were turned on. As most vertebrate species in NoBa are restricted to seasonal migrations, the species cannot move into completely new areas, but how the stock is distributed within the given polygons can change. When the thermal niche is turned off, the distribution depends on migration pattern and food availability. Since the trends were observed in all scenarios this indicates that the Northeastern shift was caused by a change in food availability. The primary production in NoBa is affected by light and nutrients, and the reduced ice coverage in NorESM and Nemo would therefore lead to increased production further north which can explain the shift in distribution. These results are consistent with other studies indicating increased primary production in the Arctic Ocean (Steinacher et al., 2010; Vancoppenolle et al., 2013) and species moving further North (Fossheim et al., 2015; Frainer et al., 2017).

Another trend in response to future climate changes was that whales and mesopelagic species were increasing, while sea birds and other marine mammals were declining. Sea birds are expected to decline under future climate changes (Dias et al., 2019; Mitchell et al., 2020) due to a higher frequency of extreme weather events and lower food supply. Marine mammals that depend on ice (such as polar bear and seals included in the “other mammals” group) are also expected to decline due to habitat loss, while the effects on whales are more uncertain (Kovacs and Lydersen, 2008). Mesopelagic species are less studied, but are expected to be positively impacted based on assessment reports (Kraft et al., 2021). The projected trends are therefore in line with what other studies have suggested.

Overall, most of the higher trophic level species did not respond notably to using physics from the global model compared to the regional. The NoBa simulations also mostly agreed on the sign of future changes with both sets of forcing. Our results therefore indicate that for modelers lacking available downscaled physical forcing, using physics from a global model could be sufficient to study climate effects on higher trophic level species. This is in line with Drenkard et al. (2021) who have suggested a pragmatic approach when considering if downscaling is needed for ecosystem studies. They argue that the primary objective of downscaling should be to resolve ocean features (e.g., mesoscale activity and upwelling (Small et al., 2015)) that are important for the species that are being studied, that are not captured by the global climate model.

The case of cod illustrates such an ocean feature, in this case the temperature at spawning grounds, that must be downscaled properly given what we know about that species and how it is represented in the ecosystem model. The future state of the cod stock and potential consequences for fisheries are uncertain. A warmer climate might increase suitable feeding areas for cod (Kjesbu et al., 2021), while at the same time cause potential negative effects on its prey species (Gjøsæter et al., 2020). However, the collapses of the cod stock in our results were caused by cooler temperatures, not warmer. Although the stock has been at low levels before (ICES, 2021), sudden collapses, like the ones projected in the scenarios using NorESM and turning on the thermal niche, have not been reported and seem rather unlikely.

To analyze the results and determine the effects of the different physical forcing on the species we chose to set certain boundaries. Whether the species were regarded as impacted, or if the change in distribution point was significant depended on the boundaries set prior to the study, as well as the periods that were chosen to study changes throughout the simulation. All of these choices inevitably affect the results and how we interpret them. A crucial uncertainty regarding the results of this study is where we set these limits, as well as the assumptions within the models. The temperature ranges set for the thermal niche, as discussed above, are also uncertain and demonstrate another boundary setting that should be treated with caution. It should also be noted that the species were not parameterized to be affected by the salinity (which differed greatly between Nemo and NorESM) and were only marginally affected by ice. The results could therefore have been entirely different if the dependency on salinity and ice were strengthened. There were also species that were excluded which could have impacted the results, including haddock, snow crab and king crab. The recruitment of haddock strongly depends on variability in lower trophic levels, which results in high variability in biomass and makes it unrealistically sensitive to any perturbations (Olsen et al., 2019). Snow crab larval dispersion was not parameterized correctly in this study which caused it to collapse, while king crab is currently represented as biomass pools instead of individuals which leads to unrealistic behavior, and the group is therefore in the process of being reparametrized as a vertebrate.

Using ensembles of ecosystem models (Heneghan et al., 2021; Lotze et al., 2019; Tittensor et al., 2021) or multiple climate models and projections (IPCC, 2022) to deal with uncertainty is commonly applied, but this study also highlights the benefits of using multiple sets of physical forcing to deal with uncertainty.

5. Conclusions

This study focused on investigating ecosystem changes in the Nordic and Barents Seas under the future climate, as well as how much we gain from applying downscaled forcing compared to forcing from a global model in a coarse resolution ecosystem model. Most commercial species were projected to move further north as a response to future temperature change, which is consistent with previous studies suggesting a borealization of the Arctic Ocean/Barents Sea with climate change (Fossheim et al., 2015; Frainer et al., 2017). Whales and mesopelagic species were increasing, while sea birds and other marine mammals were declining, which is also in line with former studies (Dias et al., 2019; Kovacs and Lydersen, 2008; Mitchell et al., 2020).

Higher trophic levels were generally not particularly impacted by using downscaled physics compared to physics from a global model. This suggests that physical forcing from global models in many cases is sufficient to study higher trophic levels. However, cod illustrates an exception to this, and we demonstrated how even minor differences in temperature may impact the modeled species. The reason behind cod being particularly sensitive was that the temperature in the spawning areas was below the tolerated temperature range. This highlights the need for higher precision when dealing with species with higher sensitivity to the physical environment, in which cases downscaling can become of importance. Without access to the downscaled physical forcing the results would project collapses in the future cod stock, which would be of huge importance as cod is the most valuable stock in the Norwegian economy.

References:

Audzijonyte, A., Gorton, R., Kaplan, I.C., Fulton, E.A., 2017. Atlantis User's Guide Part I: General Overview, Physics & Ecology.

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., Fulton, E.A., 2019. Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. Methods in Ecology and Evolution 10, 1814–1819. https://doi.org/10.1111/2041-210X.13272

Bentsen, M., Bethke, I., Debernard, J.B., Iversen, T., Kirkevåg, A., Seland, Ø., Drange, H., Roelandt, C., Seierstad, I.A., Hoose, C., Kristjánsson, J.E., 2013. The Norwegian Earth System Model, NorESM1-M – Part 1: Description and basic evaluation of the physical climate. Geoscientific Model Development 6, 687–720. https://doi.org/10.5194/gmd-6-687-2013

Bergstad, O.A., Jørgensen, T., Dragesund, O., 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fisheries Research, Comparative biology, assessment, and management of gaboids from the North Pacific and Atlantic Oceans 5, 119–161. https://doi.org/10.1016/0165-7836(87)90037-3

Bethke, I., Wang, Y., Counillon, F., Keenlyside, N., Kimmritz, M., Fransner, F., Samuelsen, A., Langehaug, H., Svendsen, L., Chiu, P.-G., Passos, L., Bentsen, M., Guo, C., Gupta, A., Tjiputra, J., Kirkevåg, A., Olivié, D., Seland, Ø., Solsvik Vågane, J., Fan, Y., Eldevik, T., 2021. NorCPM1 and its contribution to CMIP6 DCPP. Geoscientific Model Development 14, 7073–7116. https://doi.org/10.5194/gmd-14-7073-2021

Busecke, J.J.M., Resplandy, L., Dunne, J.P., 2019. The Equatorial Undercurrent and the Oxygen Minimum Zone in the Pacific. Geophysical Research Letters 46, 6716–6725. https://doi.org/10.1029/2019GL082692

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D., Pauly, D., 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology 16, 24–35. https://doi.org/10.1111/j.1365-2486.2009.01995.x

Comiso, J.C., 2011. Large Decadal Decline of the Arctic Multiyear Ice Cover. J. Climate 25, 1176–1193. https://doi.org/10.1175/JCLI-D-11-00113.1

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: A global assessment. Biological Conservation 237, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Drenkard, E.J., Stock, C., Ross, A.C., Dixon, K.W., Adcroft, A., Alexander, M., Balaji, V., Bograd, S.J., Butenschön, M., Cheng, W., Curchitser, E., Lorenzo, E.D., Dussin, R., Haynie, A.C., Harrison, M., Hermann, A., Hollowed, A., Holsman, K., Holt, J., Jacox, M.G., Jang, C.J., Kearney, K.A., Muhling, B.A., Buil, M.P., Saba, V., Sandø, A.B., Tommasi, D., Wang, M., 2021. Next-generation regional ocean projections for living marine resource management in a changing climate. ICES Journal of Marine Science 78, 1969–1987. https://doi.org/10.1093/icesjms/fsab100

Egbert, G.D., Erofeeva, S.Y., 2002. Efficient Inverse Modeling of Barotropic Ocean Tides. Journal of Atmospheric and Oceanic Technology 19, 183–204. https://doi.org/10.1175/1520-0426(2002)019<0183:EIMOBO>2.0.CO;2

Ekström, M., Grose, M.R., Whetton, P.H., 2015. An appraisal of downscaling methods used in climate change research. WIREs Climate Change 6, 301–319. https://doi.org/10.1002/wcc.339

Fagundes, M., Litvin, S.Y., Micheli, F., De Leo, G., Boch, C.A., Barry, J.P., Omidvar, S., Woodson, C.B., 2020. Downscaling global ocean climate models improves estimates of exposure regimes in coastal environments. Sci Rep 10, 14227. https://doi.org/10.1038/s41598-020-71169-6

Fishbase, 2022. www.fishbase.org. World Wide Web electronic publication.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R., Aschan, M., Dolgov, A., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change 5. https://doi.org/10.1038/nclimate2647

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A.V., Fossheim, M., Aschan, M.M., 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. PNAS 114, 12202–12207. https://doi.org/10.1073/pnas.1706080114

Fransner, F., Fröb, F., Tjiputra, J., Goris, N., Lauvset, S.K., Skjelvan, I., Jeansson, E., Omar, A., Chierici, M., Jones, E., Fransson, A., Ólafsdóttir, S.R., Johannessen, T., Olsen, A., 2022. Acidification of the Nordic Seas. Biogeosciences 19, 979–1012. https://doi.org/10.5194/bg-19-979-2022

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D.M., Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12, 171–188. https://doi.org/10.1111/j.1467-2979.2011.00412.x

Gjøsæter, H., Huserbråten, M., Vikebø, F., Eriksen, E., 2020. Key processes regulating the early life history of Barents Sea polar cod. Polar Biol 43, 1015–1027. https://doi.org/10.1007/s00300-020-02656-9

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198, 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Railsback, S.F., Vincenot, C.E., Berger, U., Gallagher, C., DeAngelis, D.L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A.S.A., Milles, A., Nabe-Nielsen, J., Polhill, J.G., Radchuk, V., Rohwäder, M.-S., Stillman, R.A., Thiele, J.C., Ayllón, D., 2020. The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. JASSS 23, 7. https://doi.org/10.18564/jasss.4259

Hansen, C., Drinkwater, K.F., Jähkel, A., Fulton, E.A., Gorton, R., Skern-Mauritzen, M., 2019a. Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. PloS one 14, e0210419. https://doi.org/10.1371/journal.pone.0210419

Hansen, C., Nash, R.D.M., Drinkwater, K.F., Hjøllo, S.S., 2019b. Management Scenarios Under Climate Change – A Study of the Nordic and Barents Seas. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00668

Hansen, C., Samuelsen, A., 2009. Influence of horizontal model grid resolution on the simulated primary production in an embedded primary production model in the Norwegian Sea. Journal of Marine Systems 75, 236–244. https://doi.org/10.1016/j.jmarsys.2008.10.004

Hansen, C., Skern-Mauritzen, M., van der Meeren, G., Jähkel, A., Drinkwater, K., 2016. Set-up of the Nordic and Barents Seas (NoBa) Atlantis model. https://doi.org/10.13140/RG.2.1.3339.9929

Heneghan, R.F., Galbraith, E., Blanchard, J.L., Harrison, C., Barrier, N., Bulman, C., Cheung, W., Coll, M., Eddy, T.D., Erauskin-Extramiana, M., Everett, J.D., Fernandes-Salvador, J.A., Gascuel, D., Guiet, J., Maury, O., Palacios-Abrantes, J., Petrik, C.M., du Pontavice, H., Richardson, A.J., Steenbeek, J., Tai, T.C., Volkholz, J., Woodworth-Jefcoats, P.A., Tittensor, D.P., 2021. Disentangling diverse responses to climate change among global marine ecosystem models. Progress in Oceanography 198, 102659. https://doi.org/10.1016/j.pocean.2021.102659

Henson, S.A., Beaulieu, C., Ilyina, T., John, J.G., Long, M., Séférian, R., Tjiputra, J., Sarmiento, J.L., 2017. Rapid emergence of climate change in environmental drivers of marine ecosystems. Nat Commun 8, 14682. https://doi.org/10.1038/ncomms14682

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., De Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., de Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., Thépaut, J.-N., 2020. The ERA5 global reanalysis. Quarterly Journal of the Royal Meteorological Society 146, 1999–2049. https://doi.org/10.1002/qj.3803

Höffle, H., Solemdal, P., Korsbrekke, K., Johannessen, M., Bakkeplass, K., Kjesbu, O.S., 2014. Variability of northeast Arctic cod (Gadus morhua) distribution on the main spawning grounds in relation to biophysical factors. ICES Journal of Marine Science 71, 1317–1331. https://doi.org/10.1093/icesjms/fsu126

Hordoir, R., Skagseth, Ø., Ingvaldsen, R.B., Sandø, A.B., Löptien, U., Dietze, H., Gierisch, A.M.U., Assmann, K.M., Lundesgaard, Ø., Lind, S., 2022. Changes in Arctic Stratification and Mixed Layer Depth Cycle: A Modeling Analysis. Journal of Geophysical Research: Oceans 127, 2021JC017270. https://doi.org/10.1029/2021JC017270

ICES, 2021. Arctic Fisheries Working Group (AFWG). ICES Scientific Reports. 3:58, 817 pp. https://doi.org/10.17895/ices.pub.8196

ICES, 2020. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 2:82, 1019 pp. https://doi.org/10.17895/ices.pub.7475

IPCC, 2022. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Kearney, K.A., Alexander, M., Aydin, K., Cheng, W., Hermann, A.J., Hervieux, G., Ortiz, I., 2021. Seasonal Predictability of Sea Ice and Bottom Temperature Across the Eastern Bering Sea Shelf. Journal of Geophysical Research: Oceans 126, e2021JC017545. https://doi.org/10.1029/2021JC017545

Kirtman, B.P., Bitz, C., Bryan, F., Collins, W., Dennis, J., Hearn, N., Kinter, J.L., Loft, R., Rousset, C., Siqueira, L., Stan, C., Tomas, R., Vertenstein, M., 2012. Impact of ocean model resolution on CCSM climate simulations. Clim Dyn 39, 1303–1328. https://doi.org/10.1007/s00382-012-1500-3

Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D.M., Skjæraasen, J.E., 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. PNAS 111, 3478–3483. https://doi.org/10.1073/pnas.1316342111

Kjesbu, O.S., Sundby, S., Sandø, A.B., Alix, M., Hjøllo, S.S., Tiedemann, M., Skern-Mauritzen, M., Junge, C., Fossheim, M., Thorsen Broms, C., Søvik, G., Zimmermann, F., Nedreaas, K., Eriksen, E., Höffle, H., Hjelset, A.M., Kvamme, C., Reecht, Y., Knutsen, H., Aglen, A., Albert, O.T., Berg, E., Bogstad, B., Durif, C., Halvorsen, K.T., Høines, Å., Hvingel, C., Johannesen, E., Johnsen, E., Moland, E., Skuggedal Myksvoll, M., Nøttestad, L., Olsen, E., Skaret, G., Skjæraasen, J.E., Slotte, A., Staby, A., Stenevik, E.K., Stiansen, J.E., Stiasny, M., Sundet, J.H., Vikebø, F., Huse, G., 2021. Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic. Fish and Fisheries 23, 601–615. https://doi.org/10.1111/faf.12635

Kovacs, K.M., Lydersen, C., 2008. Climate Change Impacts on Seals and Whales in the North Atlantic Arctic and Adjacent Shelf Seas. Science Progress 91, 117–150. https://doi.org/10.3184/003685008X324010

Kraft, B., Rivera, A.M., Mozfar, B., Skern, R., Dahle, G., Sundby, S., Thorsen, A., Asplin, L., Wehde, H., 2021. Assessment of Fish Spawning in the North Sea; Final Project Report of KINO-2, 2017–2021. Havforskningsinstituttet nr 2021-17.

Langangen, Ø., Färber, L., Stige, L.C., Diekert, F.K., Barth, J.M.I., Matschiner, M., Berg, P.R., Star, B., Stenseth, N.Chr., Jentoft, S., Durant, J.M., 2019. Ticket to spawn: Combining economic and genetic data to evaluate the effect of climate and demographic structure on spawning distribution in Atlantic cod. Global Change Biology 25, 134–143. https://doi.org/10.1111/gcb.14474

Langehaug, H.R., Sandø, A.B., Årthun, M., Ilıcak, M., 2019. Variability along the Atlantic water pathway in the forced Norwegian Earth System Model. Clim Dyn 52, 1211–1230. https://doi.org/10.1007/s00382-018-4184-5

Lee, Y.J., Matrai, P.A., Friedrichs, M.A.M., Saba, V.S., Aumont, O., Babin, M., Buitenhuis, E.T., Chevallier, M., de Mora, L., Dessert, M., Dunne, J.P., Ellingsen, I.H., Feldman, D., Frouin, R., Gehlen, M., Gorgues, T., Ilyina, T., Jin, M., John, J.G., Lawrence, J., Manizza, M., Menkes, C.E., Perruche, C., Le Fouest, V., Popova, E.E., Romanou, A., Samuelsen, A., Schwinger, J., Séférian, R., Stock, C.A., Tjiputra, J., Tremblay, L.B., Ueyoshi, K., Vichi, M., Yool, A., Zhang, J., 2016. Net primary productivity estimates and environmental variables in the Arctic Ocean: An assessment of coupled physical-biogeochemical models. Journal of Geophysical Research: Oceans 121, 8635–8669. https://doi.org/10.1002/2016JC011993

Lindstrøm, U., Smout, S., Howell, D., Bogstad, B., 2009. Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. Deep Sea Research Part II: Topical Studies in Oceanography, The Proceedings of the ECONORTH Symposium on Ecosystem Dynamics in the Norwegian Sea and Barents Sea 56, 2068–2079. https://doi.org/10.1016/j.dsr2.2008.11.017

Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., Eddy, T.D., Cheung, W.W.L., Galbraith, E.D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J.L., Bopp, L., Büchner, M., Bulman, C.M., Carozza, D.A., Christensen, V., Coll, M., Dunne, J.P., Fulton, E.A., Jennings, S., Jones, M.C., Mackinson, S., Maury, O., Niiranen, S., Oliveros-Ramos, R., Roy, T., Fernandes, J.A., Schewe, J., Shin, Y.-J., Silva, T.A.M., Steenbeek, J., Stock, C.A., Verley, P., Volkholz, J., Walker, N.D., Worm, B., 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. Proceedings of the National Academy of Sciences 116, 12907–12912. https://doi.org/10.1073/pnas.1900194116

Melsom, A., Lien, V.S., Budgell, W.P., 2009. Using the Regional Ocean Modeling System (ROMS) to improve the ocean circulation from a GCM 20th century simulation. Ocean Dynamics 59, 969–981. https://doi.org/10.1007/s10236-009-0222-5

Mitchell, I., Daunt, F., Frederiksen, M., Wade, K., 2020. Impacts of climate change on seabirds, relevant to the coastal and marine environment around the UK. Marine Climate Change Impacts Partnership, Lowestoft, pp. 382–399.

Mohr, S.H., Wang, J., Ellem, G., Ward, J., Giurco, D., 2015. Projection of world fossil fuels by country. Fuel 141, 120–135. https://doi.org/10.1016/j.fuel.2014.10.030

Murray, A.G., Parslow, J.S., 1997. Port Phillip Bay integrated model: final report. CSIRO Environmental Projects Office 44, 201. https://doi.org/10.4225/08/585d683f7b126

Nilsen, I., Hansen, C., Kaplan, I., Holmes, E., Langangen, Ø., 2022. Exploring the role of Northeast Atlantic cod in the Barents Sea food web using a multi-model approach. Fish and Fisheries 1–16. https://doi.org/10.1111/faf.12671

Olsen, E., Hansen, C., Nilsen, I., Perryman, H., Vikebø, F., 2019. Ecological Effects and Ecosystem Shifts Caused by Mass Mortality Events on Early Life Stages of Fish. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00669

O'Neill, B.C., Tebaldi, C., van Vuuren, D.P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J.-F., Lowe, J., Meehl, G.A., Moss, R., Riahi, K., Sanderson, B.M., 2016. The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. Geoscientific Model Development 9, 3461–3482. https://doi.org/10.5194/gmd-9-3461-2016

Pauly, D., Watson, R., 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. Philos Trans R Soc Lond B Biol Sci 360, 415–423. https://doi.org/10.1098/rstb.2004.1597

Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P.E., Nascimento, M.C., Blanchet, M.-A., Ellingsen, I.H., Jørgensen, L.L., Blanchet, H., 2021. Overexploitation, Recovery, and Warming of the Barents Sea Ecosystem During 1950–2013. Frontiers in Marine Science 8.

Plagányi, É.E., 2007. Models for an Ecosystem Approach to Fisheries. FAO Fisheries Technical Paper. 108p. https://doi.org/10.25607/OBP-392

Planque, B., Favreau, A., Husson, B., Mousing, E.A., Hansen, C., Broms, C., Lindstrøm, U., Sivel, E., 2022. Quantification of trophic interactions in the Norwegian Sea pelagic food-web over multiple decades. ICES Journal of Marine Science 79, 1815–1830. https://doi.org/10.1093/icesjms/fsac111

Planque, B., Lindstrøm, U., Subbey, S., 2014. Non-Deterministic Modelling of Food-Web Dynamics. PLOS ONE 9, e108243. https://doi.org/10.1371/journal.pone.0108243

Righton, D.A., Andersen, K.H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., Hinrichsen, H.-H., Bendall, V., Neuenfeldt, S., Wright, P., Jonsson, P., Huse, G., Kooij, J. van der, Mosegaard, H., Hüssy, K., Metcalfe, J., 2010. Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima. Marine Ecology Progress Series 420, 1–13. https://doi.org/10.3354/meps08889

RStudio Team, 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA [WWW Document]. URL http://www.rstudio.com/ (accessed 5.1.18).

Sandø, A.B., Johansen, G.O., Aglen, A., Stiansen, J.E., Renner, A.H.H., 2020. Climate Change and New Potential Spawning Sites for Northeast Arctic cod. Frontiers in Marine Science 7.

Sandø, A.B., Melsom, A., Budgell, W.P., 2014. Downscaling IPCC control run and future scenario with focus on the Barents Sea. Ocean Dynamics 64, 927–949. https://doi.org/10.1007/s10236-014-0731-8

Seland, Ø., Bentsen, M., Olivié, D., Toniazzo, T., Gjermundsen, A., Graff, L.S., Debernard, J.B., Gupta, A.K., He, Y.-C., Kirkevåg, A., Schwinger, J., Tjiputra, J., Aas, K.S., Bethke, I., Fan, Y., Griesfeller, J., Grini, A., Guo, C., Ilicak, M., Karset, I.H.H., Landgren, O., Liakka, J., Moseid, K.O., Nummelin, A., Spensberger, C., Tang, H., Zhang, Z., Heinze, C., Iversen, T., Schulz, M., 2020. Overview of the Norwegian Earth System Model (NorESM2) and key climate response of CMIP6 DECK, historical, and scenario simulations. Geoscientific Model Development 13, 6165–6200. https://doi.org/10.5194/gmd-13-6165-2020

Skogen, M.D., Hjøllo, S.S., Sandø, A.B., Tjiputra, J., 2018. Future ecosystem changes in the Northeast Atlantic: a comparison between a global and a regional model system. ICES J Mar Sci 75, 2355–2369. https://doi.org/10.1093/icesjms/fsy088

Small, R.J., Curchitser, E., Hedstrom, K., Kauffman, B., Large, W.G., 2015. The Benguela Upwelling System: Quantifying the Sensitivity to Resolution and Coastal Wind Representation in a Global Climate Model. Journal of Climate 28, 9409–9432. https://doi.org/10.1175/JCLI-D-15-0192.1

Smedsrud, L.H., Esau, I., Ingvaldsen, R.B., Eldevik, T., Haugan, P.M., Li, C., Lien, V.S., Olsen, A., Omar, A.M., Otterå, O.H., Risebrobakken, B., Sandø, A.B., Semenov, V.A., Sorokina, S.A., 2013. The Role of the Barents Sea in the Arctic Climate System. Reviews of Geophysics 51, 415–449. https://doi.org/10.1002/rog.20017

Steinacher, M., Joos, F., Frölicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S.C., Gehlen, M., Lindsay, K., Moore, J.K., Schneider, B., Segschneider, J., 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences 7, 979–1005. https://doi.org/10.5194/bg-7-979-2010

Stige, L.C., Eriksen, E., Dalpadado, P., Ono, K., 2019. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsz063

Tittensor, D.P., Novaglio, C., Harrison, C.S., Heneghan, R.F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G.L., Büchner, M., Cheung, W.W.L., Christensen, V., Coll, M., Dunne, J.P., Eddy, T.D., Everett, J.D., Fernandes-Salvador, J.A., Fulton, E.A., Galbraith, E.D., Gascuel, D., Guiet, J., John, J.G., Link, J.S., Lotze, H.K., Maury, O., Ortega-Cisneros, K., Palacios-Abrantes, J., Petrik, C.M., du Pontavice, H., Rault, J., Richardson, A.J., Shannon, L., Shin, Y.-J., Steenbeek, J., Stock, C.A., Blanchard, J.L., 2021. Next-generation ensemble projections reveal higher climate risks for marine ecosystems. Nat. Clim. Chang. 11, 973–981. https://doi.org/10.1038/s41558-021-01173-9

Tjiputra, J.F., Polzin, D., Winguth, A.M.E., 2007. Assimilation of seasonal chlorophyll and nutrient data into an adjoint three-dimensional ocean carbon cycle model: Sensitivity analysis and ecosystem parameter optimization. Global Biogeochemical Cycles 21. https://doi.org/10.1029/2006GB002745

Tjiputra, J.F., Roelandt, C., Bentsen, M., Lawrence, D.M., Lorentzen, T., Schwinger, J., Seland, Ø., Heinze, C., 2013. Evaluation of the carbon cycle components in the Norwegian Earth System Model (NorESM). Geoscientific Model Development 6, 301–325. https://doi.org/10.5194/gmd-6-301-2013

Tjiputra, J.F., Schwinger, J., Bentsen, M., Morée, A.L., Gao, S., Bethke, I., Heinze, C., Goris, N., Gupta, A., He, Y.-C., Olivié, D., Seland, Ø., Schulz, M., 2020. Ocean biogeochemistry in the Norwegian Earth System Model version 2 (NorESM2). Geoscientific Model Development 13, 2393–2431. https://doi.org/10.5194/gmd-13-2393-2020

Vancoppenolle, M., Bopp, L., Madec, G., Dunne, J., Ilyina, T., Halloran, P.R., Steiner, N., 2013. Future arctic ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent mechanisms. Global Biogeochemical Cycles 27, 605–619. https://doi.org/10.1002/gbc.20055

Wang, J., Feng, L., Tang, X., Bentley, Y., Höök, M., 2017. The implications of fossil fuel supply constraints on climate change projections: A supply-side analysis. Futures 86, 58–72. https://doi.org/10.1016/j.futures.2016.04.007

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Data availability statement

The data that support the findings of this study are available on request from the corresponding author.

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Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Supplementary materials for:

Trivial gain of downscaling in future projections of higher trophic levels in the Nordic and Barents Seas

Downscaling NorESM2 with Nemo-NAA10km

The two paragraphs below describe how NorESM2 was downscaled with Nemo-NAA10km. More detailed information can be found in Hordoir et al. (2022).

Design of Atmospheric Forcing – NorESM2 to Nemo-NAA10km

Nemo-NAA10km uses a bulk formulation for its connection with the atmosphere following Large and Yeager (2009). The wind velocity fields are extracted from the NorESM simulations at an altitude of 10m. Air temperature and specific humidity are also extracted at an altitude of 2m from the NorESM simulations. The long wave and short-wave radiation fields are provided by NorESM, so are solid and liquid precipitation fields, as well as the sea level pressure. A random check on surface ocean stresses for Nemo-NAA10km and NorESM shows that the fields are almost similar. The bulk formulation uses a relative wind speed when computing ocean surface stresses following the ocean-atmosphere coupling performed in NorESM, which differs from the reference Nemo-NAA10km reference simulation made in hindcast mode (Hordoir et al., 2022) that uses an absolute wind speed following the re-analysis used in hindcast mode for which the atmosphere sees a static ocean.

Design of Oceanic Forcing – NorESM2 to Nemo-NAA10km

Nemo-NAA10km has two open boundary conditions for which the forcing is extracted from NorESM for temperature and salinity only. Using the sea level data from NorESM proved to give non-realistic results. The structure of the Atlantic temperature and salinity stratification simulated by NorESM can not be used directly, as the mixed layer depth at this boundary in NorESM is much greater than that simulated by Nemo-NAA10km in hindcast mode, and produces an un-realistic AMOC of 60 Sv. Therefore we chose to use the temperature and salinity trend from the NorESM mixed layer interpolated on the open boundary condition of Nemo-NAA10km, and apply it to the climatological mixed layer used for some part of the simulation done in Hordoir et al. (2022).

As in the hindcast simulation of Hordoir et al. (2022), tidal forcing is applied as a forcing through the open boundary conditions, as well as through a tidal potential. As in Hordoir et al. (2022), the runoff field is considered as climatological (i.e., seasonal variability but no inter-annual variability). The simulations starts in 1950 with the same initial fields used in Hordoir et al. (2022).

Model description of the NoBa Atlantis model

A model description of the NoBa Atlantis model which follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models, as updated by Grimm et al. (2020) can be found in the below.

Purpose and pattern

The purpose of this modelling exercise was to reproduce historical patterns in biomass in order to explore the effects of the resolution of the physical forcing on ecosystem projections. We evaluate the model by its ability to reproduce patterns such as historical catches, total stock biomass, and spawning stock biomass. This required tuning of the commercial species by altering the parameter files to fit the new physical forcing provided by NEMO. All commercial species were tuned and compared to data taken from the ICES annual assessment reports (ICES, 2021, 2020) and non-commercial species were monitored.

Entities, state variables and scales

The model combines oceanography, population dynamics, spatial distributions, nutrient cycling, fisheries, and species interactions in a spatially explicit domain. The model components are modelled as individual species (e.g., mackerel, Northeast Atlantic cod) or aggregated into functional groups (e.g., small pelagic fish, large demersal fish) for species of similar life history and ecological characteristics. Most vertebrate species are age-structured while invertebrates are gathered into biomass pools. The model tracks the flow of nutrients through the trophic levels using nitrogen as the currency, giving the weights of all components as mg nitrogen (mg N).

Process overview and scheduling

The major processes on growth, diet, consumption, mortality, and recruitment are as described in (Audzijonyte et al., 2017). In this version, parameters regarding mortality, recruitment and distribution were altered to take into account new physical forcing. See table S1 for more details regarding which parameters that were tuned.

Design concepts

Emergence

Species distribution and population development emerges from the changes in physical forcing. These changes may also impact the predator-prey relationships between species and can therefore lead to alterations in the ecosystem structure.

Fitness

Fitness can be measured in biomass, catches, numbers and distribution of the species

Objectives

The objective measure used by the model is to investigate the effect of using a high- and a low-resolution physical forcing, given the already coarse resolution grid of the model.

Sensing

Species are assumed to sense the change in temperature and will therefore change its distribution if the temperature is outside the species temperature range.

Interactions

Species-interactions through diet matrix and overlap in time and space.

Stochasticity

Atlantis is a deterministic model, and there is no stochasticity in the processes included.

Collectives

The model contains functional groups where species with similar life history traits are gathered into one group. This was done due to practical reasons and lack of data.

Observations

Growth rates, total stock biomass, spawning biomass, catches, predator-prey relationships, distributions

Initialization

The model was initiated with biomass levels corresponding to those observed in the early 1980s. Details on these and their parameters can be found in Hansen et al. (2016). For these simulations, parameters regarding reproduction, mortality and distribution were altered (see section on Entities, state variables and scales, and table S1). The fisheries mortalities were extended to include harvest rates until 2020, and age-dependent fisheries were implemented for all commercial vertebrates.

Input

Details on the input files can be found in (Hansen et al., 2016, 2019a). New and updated fisheries were implemented from 1980-2020, and an age specific mortality was included to ensure that the fisheries only catch above certain age classes. The fishing mortalities and age specific mortality were estimated based on ICES annual assessment reports (ICES, 2021, 2020). The mean fishing mortalities (F) and standard deviations (sd) are given below.

	Blue whiting	*Capelin*	*Greenland halibut*	*Haddock*	*Mackerel*	*Cod*	*Beaked redfish*	*Golden redfish*	*Saithe*	*Herring*
F	0.28	0.40	0.03	0.30	0.98	0.40	0.05	0.22	0.33	0.13
sd	0.08	0.68	0.01	0.10	0.22	0.11	0.04	0.09	0.13	0.09

Submodels

Atlantis has several available modules related to management and economics. However, in this case only the harvest module was applied.

Tables

Prior to the study the biomasses and catches of all commercial species were tuned to fit the historical values. The tuning was conducted for species where the biomass was much higher or lower than observations. This was primarily done by tweaking the parameters in the biol-file related to recruitment, mortality, or growth rate. Parameters that governed the density dependent movement and depth restrictions were also updated to ensure that the species were distributed correctly. Table S1 describes in detail which parameters that were altered.

Table S1. *Detailed overview of which parameters that were altered to ensure that the species corresponded to observed values. The name of the parameter in the model and a short description is included as well as which changes that were done to which species.*

Parameter	Description	Species	Value before	Value after
BHalpha_XX	Parameter that governs the recruitment	Mackerel Haddock Redfish Other redfish	9.55 x10^{9} 0.01 x10^{8} 3.25 x10^{11} 0.75 x10^{9}	2.50 x10^{10} 0.07 x10^{8} 3.25 x10^{8} 0.05 x10^{8}
mQ	Parameter that governs the mortality of juvenile and adults	Cod Greenland halibut Other redfish	1.75 x10^{-10} 9.48 x10^{-10} 1.09 x10^{-10} 4.20 x10^{-09} 9.05 x10^{-11} 1.05 x10^{-10}	1.75 x10^{-10} 1.48 x10^{-10} 1.09 x10^{-11} 4.20 x10^{-10} 9.05 x10^{-12} 0.25 x10^{-11}
maxtodepth	Parameter that restricts the total allowed depth that the species can be in.	Cod Haddock Saithe Greenland halibut Redfish Skates and rays	4000 4000 4000 4000 4000 4000	600 1000 500 2200 1500 2000
ddepend	Parameter that governs the movement	Sharks Arctic seabirds	2 2	0 0
mum	Parameter that specifies the maximum growth rate	Dinoflagellates	0.55	0.95
max_move_temp	Parameter that limits the maximum tolerated temperature	Mackerel Blue whiting Redfish Haddock Arctic seabirds	6.0 1.0 4.0 2.0 -0.5	0.0 -1.9 -0.5 -0.5 -1.9
min_move_temp	Parameter that limits the minimum tolerated temperature	Capelin Redfish Polar cod	6.0 30.0 2.0	9.0 10.0 10.0
max_spawn_temp	Parameter that limits the maximum temperature for spawning	Polar cod Haddock	21.0 6.0	10.0 10.0
min_spawn_temp	Parameter that limits the minimum temperature for spawning	Snow crab Capelin Mackerel Blue whiting Greenland halibut Polar cod Haddock Arctic seabirds	1.0 2.0 9.0 7.0 0.0 0.0 4.0 4.0	-1.9 -1.9 2.0 0.0 -1.9 -1.9 -0.5 -1.9

Table S2. *List of species and functional groups in the NoBa model, including corresponding abbreviations and species the group is parameterized as separated in guilds.*

Category	Species	Abb.	Species included
Whale	Killer whale	KWH	
	Fin whale	FWH	
	Minke whale	MWH	
	Sperm whale	SWH	
	Humpback whale	HWH	
Other mammals	Polar bear	POB	
	Harp seal	HAS	
	Hooded seal	HOS	
	Ringed seal	RIS	
	Bearded seal	BES	
Seabird	Arctic seabirds	SBA	
	Boreal seabirds	SBB	
Shark	Sharks, other	SHO	Picked dogfish, Porbeagle, Tope shark
	Skates and rays	SSK	Arctic skate, starry ray, sailray, longnosed skate, thornback ray, round skate, spinytail skate
Demersal fish	Demersal fish, large	DEL	Monkfish, Atlantic halibut, Atlantic wolffish, northern and spotted wolffish
	Demersal fish, other	DEO	Ling, Tusk
	Flatfish, other	FLA	European plaice, common dab, winter flounder
	Greenland halibut	GRH	
	Haddock	HAD	
	Long rough dab	LRD	
	Northeast Arctic cod	NCO	
	Polar cod	PCO	
	Redfish	RED	Beaked redfish
	Redfish, other	REO	Golden redfish
Pelagic fish	Blue whiting	BWH	
	Capelin	CAP	
	Mackerel	MAC	
	Norwegian Spring Spawning herring	SSH	
	Pelagic fish, large	PEL	Atlantic salmon
	Pelagic fish, small	PES	Lumpfish, Norway pout
	Saithe	SAI	
Mesopelagic	Mesopelagic fish	MES	Silvery lightfish, glacier lantern fish
	Cephalopods	CEP	*Gonatus fabricii*
Benthos	Benthic filter feeders	BFF	Selected molluscs, barnacles, moss animals, anemones
	Corals	COR	*Lophelia pertusa*
	Sponges	SPO	*Geodia baretti*
	Prawn	PWN	*Pandalus borealis*
	Red king crab	KCR	
	Snow crab	SCR	
	Detritivore benthos	BD	Selected annelids, echinoderms
	Predatory benthos	BC	Echinoderms, sea urchins, annelids and anemones
Zooplankton	Gelatinous zooplankton	ZG	*Aurelia aurita, Cyanea capillata*
	Large zooplankton	ZL	*Thysanoessa inermis*
	Medium zooplankton	ZM	Parameterized as *Calanus finmarchicus*
	Small zooplankton	ZS	Small copepods, oncaea, pseudocalanus
Phytoplankton	Dinoflagellates	DF	
	Large phytoplankton	PL	Diatoms
	Small phytoplankton	PS	Flagellates
Bacteria	Benthic bacteria	BB	
	Pelagic bacteria	PB	
	Carrion	DC	
	Labile detritus	DL	
	Refractory detritus	DR	

Table S3. *List of the change in the center of gravity of the distribution for the commercial species. The change is given in km and the direction of the change for the various parameter settings. Red numbers mark the simulation where the greatest change was observed.*

Species	Season	Ref	Ice	Temp	Temp_ice	Dir
Saithe	Fall	71.4	70.3	70.8	71.3	NW
Saithe	Summer	70.7	69.6	70.0	70.4	NW
Saithe	Spring	70.3	69.1	69.5	69.9	NW
Golden redfish	Spring	30.4	32.3	31.8	30.7	NE
Herring	Spring	30.3	34.4	40.0	46.9	NE
Saithe	Winter	26.7	26.3	26.5	26.7	SW
Green. halibut	Fall	22.9	23.1	18.1	18.2	NE
Green. halibut	Summer	22.8	22.9	18.0	18.2	NE
Green. halibut	Spring	22.7	22.8	17.9	18.1	NE
Herring	Winter	22.1	24.1	30.6	34.0	NE
Herring	Fall	20.6	23.1	29.2	32.2	NE
Green. halibut	Winter	20.5	20.7	15.6	15.8	NE
Herring	Summer	19.8	22.0	25.7	30.3	NE
Cod	Spring	>10km	>10km	24.5	24.1	NW
Cod	Winter	>10km	>10km	10.5	10.4	NW

Figures

The figure below shows the result of the tuning of the species with most species close to observed values. Please note that the biomasses of cod and beaked redfish are a bit off because the total stock biomass is not reported for those species, only the biomass of adult individuals. However, since the catches matched well with observations for these species, we decided to allow the simulated biomass to be a bit higher to account for the juvenile part of the stock.

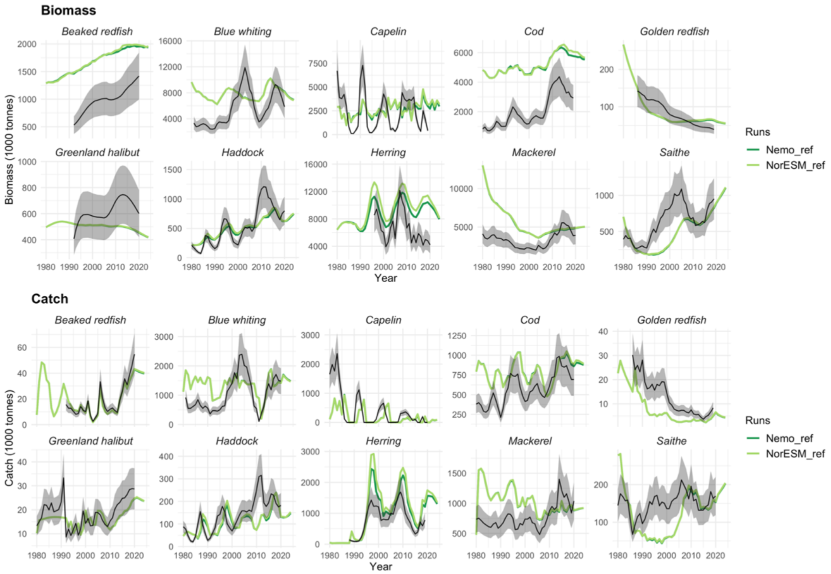


Figure S1. *Simulated biomass from NoBa compared to observations for commercial species. Green line represents the simulated biomass while the black line represents observations. Shaded area shows the 30 % uncertainty.*

The two figures below show the change in temperature and salinity in NorESM compared to Nemo. The difference is given in °C and psu for the early- (year 2005-2020) and late period (year 2085-2100) for all layers in the water column. The plots were made to get an overview of where the greatest differences were.

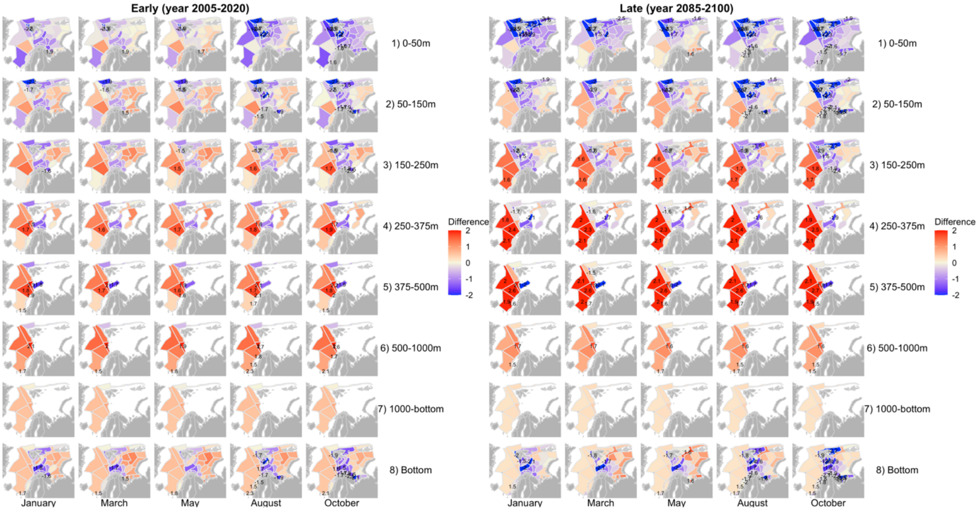


Figure S2. Temperature difference in NorESM compared to Nemo in the early and late period in the different depth layers down in the water column. Differences greater than ± 1.5 °C were labeled. The figure shows how the temperature in NorESM was colder in the upper parts of the water column especially in the Barents Sea, and warmer in the deeper layers in the Norwegian Sea. These differences seemed to slightly increase in the late period compared to the early.

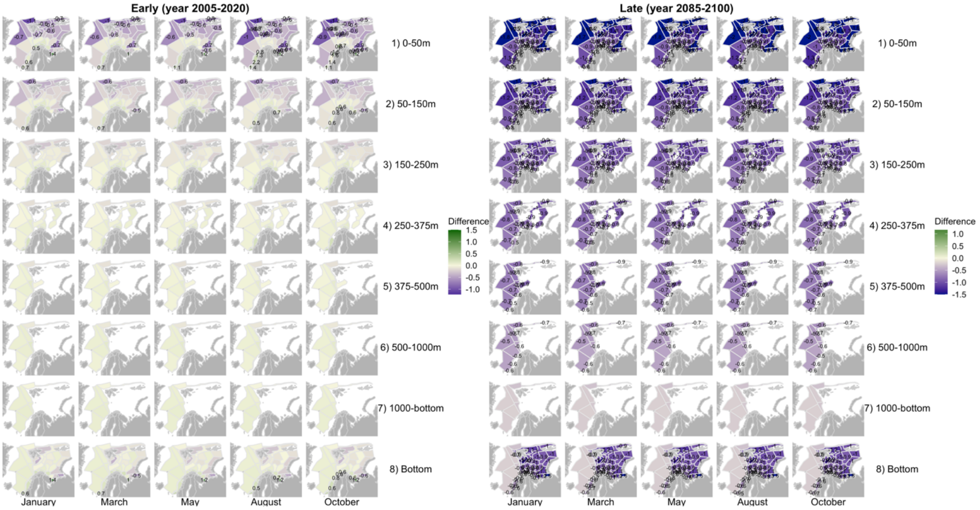


Figure S3. Salinity difference in NorESM compared to Nemo in the early and late period in the different depth layers down in the water column. Differences greater than ± 0.5 psu were labeled. The figure shows how the salinity in NorESM was lower in the upper layers in the early period, and decreased in all layers in the late period.

Figure S4 compares the monthly sea ice cover for the early- and late periods in Nemo and NorESM. The ice-covered area was calculated by summarizing areas of polygons with ice concentration > 30 %. Nemo projected more ice in the spring (February-May), while NorESM projected more during the rest of the year, especially in the late summer (July-September). In the late period NorESM projected more ice than Nemo in all months except April and December.

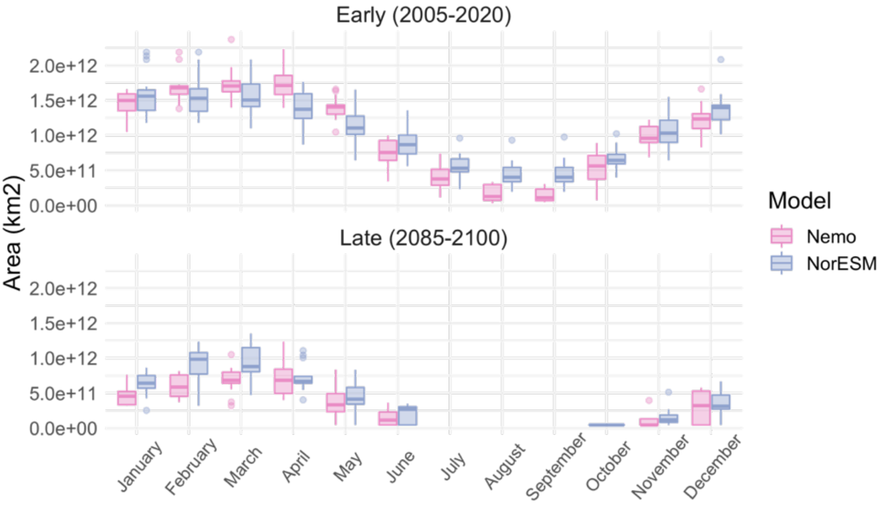
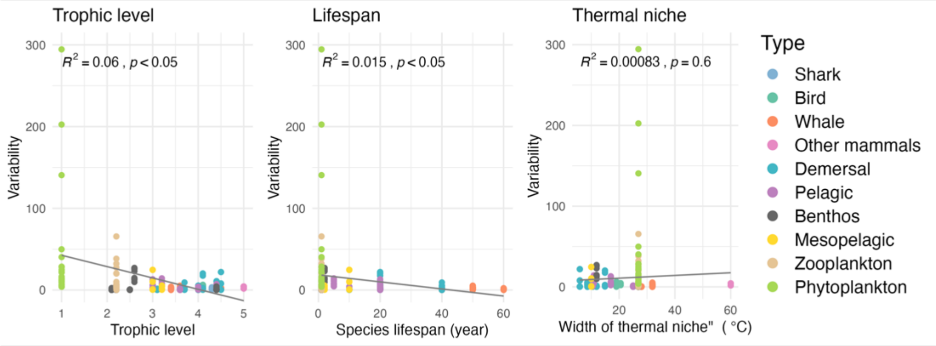


Figure S4. Monthly averaged of area covered by sea ice from Nemo and NorESM for the early (year 2005-2020) and late (year 2085-2100) period. The areas covered by ice was considered when the concentration is > 30 %.

We also investigated which traits might influence stability of biomass to environmental change. Below we provide scatterplots as a quantitative analysis for the species variability with respect to physical forcing. The changes in biomass in NorESM compared to Nemo with the various parameter settings (_ref, _temp, _ice and _ice_t) from figure 4 were converted to absolute values as a measure of variability, and were plotted against trophic level, lifespan (a proxy for population growth rate or population productivity), temperature sensitivity (the width of the thermal niche) and core area (size of occupied habitat at model initialization for vertebrates). The r-squared value (R^2) which measures how well the regression model explains observed data (in this case how much of the variation can be attributed to trophic level, lifespan, thermal niche or core area) were included as well as the p-value to indicate significance ($p<0.05$).

a) All species



b) Vertebrate species

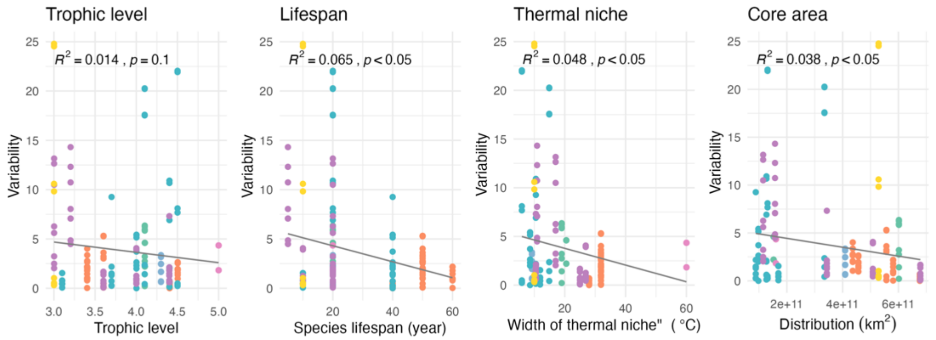


Figure S5. Correlation between variability and trophic level, lifespan (year), width of thermal niche (°C) and core area (km²). Results of all species were plotted with colors indicating which group they belong in and were separated into plots where either all species (a) or only vertebrates (b) were included. The r-squared value (R^2) which measures how well the regression model explains observed data (in this case how much of the variation can be attributed to trophic level, lifespan, thermal niche or core area) were included as well as the p-value to indicate significance ($p<0.05$). For vertebrates the thermal niche and core area were separated into juveniles and adults, as well as seasons.

We found that when including all species (a) as expected, there was a significant negative correlation between variability and trophic level and lifespan. However, this was not the case for the width of the thermal niche. The result related to the thermal niche could be due to the fact that our functional groups for plankton, invertebrates, and some non-commercial species are aggregates of species for which less is known about thermal tolerance, and therefore the width of the modelled temperature range is wider than for commercially important species receiving more attention in literature.

For vertebrates (b) the correlation between variability and trophic levels was insignificant, while as expected the correlation between stability and lifespan, thermal niche and core area were significant and negative. The r-squared values were quite low for all plots and showed that only 1.5-6.5 % of the variance in biomass could be attributed to the four traits we investigate here, which highlights the importance of additional traits and factors (such as predation, as well as food, nutrients, temperature, light availability etc.).

Using two sets of physical forcing and various temperature and ice sensitivity settings offered the opportunity to include uncertainty in the projections when studying the responses to climate changes. While the species in NoBa was grouped into categories and studied in figure 5, figure 6S explored the species within each category separately. The change in total biomass from the early period was plotted throughout the simulation for each species separately and the shaded area show the 95 % confidence interval based on all simulations.

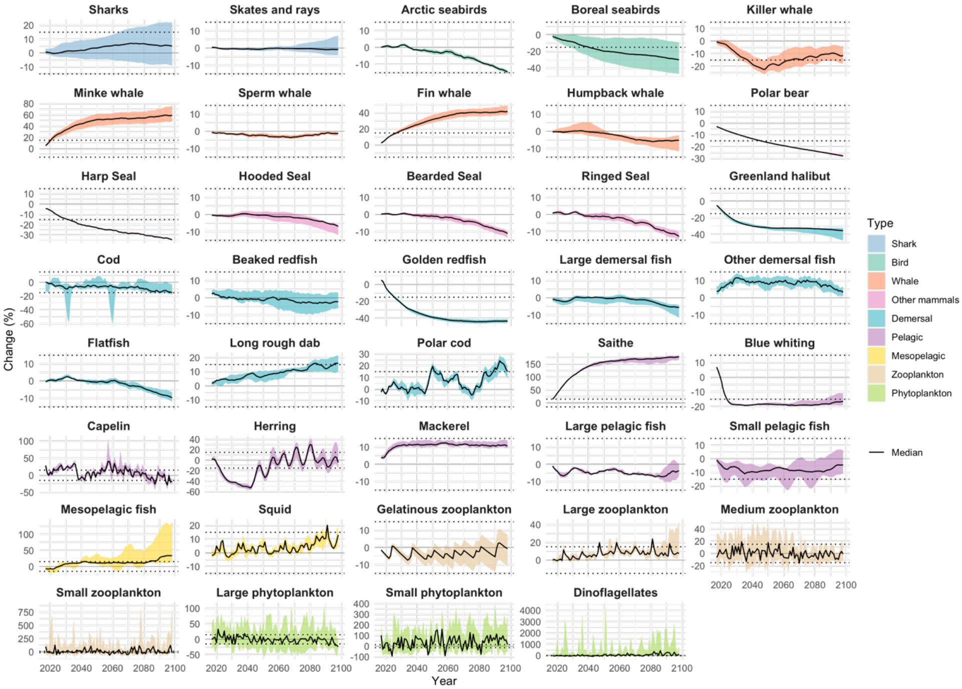


Figure S6. *Projected changes in biomass for various species. Black lines represent the median changes, while shaded area shows the 95 % confidence interval of all scenarios. Horizontal dotted lines depict changes greater than 15 %. Please note that the y-axis species differ between the species.*

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