ORIGINAL ARTICLE

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 multi-species 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

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\begin{vmatrix} x_{1_T} \\ x_{2_T} \\ x_{3_T} \\ x_{4_T} \\ x_{5_T} \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_{51} & 0 & c_{55} \end{vmatrix} \times \begin{vmatrix} x_{1_{T-1}} \\ x_{2_{T-1}} \\ x_{3_{T-1}} \\ x_{4_{T-1}} \\ x_{5_{T-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_{1_{T-1}} \\ z_{2_{T-1}} \\ z_{3_{T-1}} \\ z_{4_{T-1}} \end{vmatrix} + \begin{vmatrix} \delta_{1_T} \\ \delta_{2_T} \\ \delta_{3_T} \\ \delta_{4_T} \\ \delta_{5_T} \end{vmatrix}. \quad (2)
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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:

$$ x_t = a + bx_{T-1} + cz_{T-1} + \delta T \quad (1) $$

More specifically for our case:

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 (δ) 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
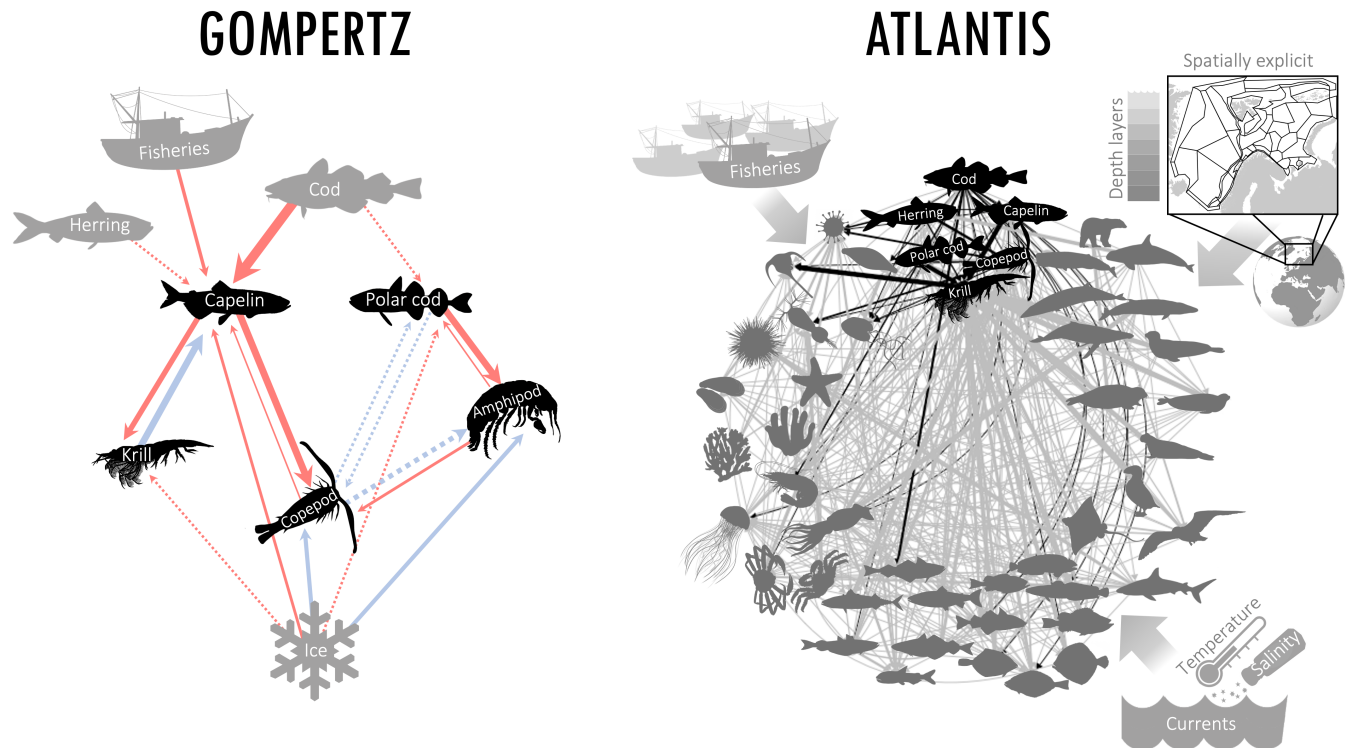
GOMPERTZ

ATLANTIS

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 overconfidence 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 contraining 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.
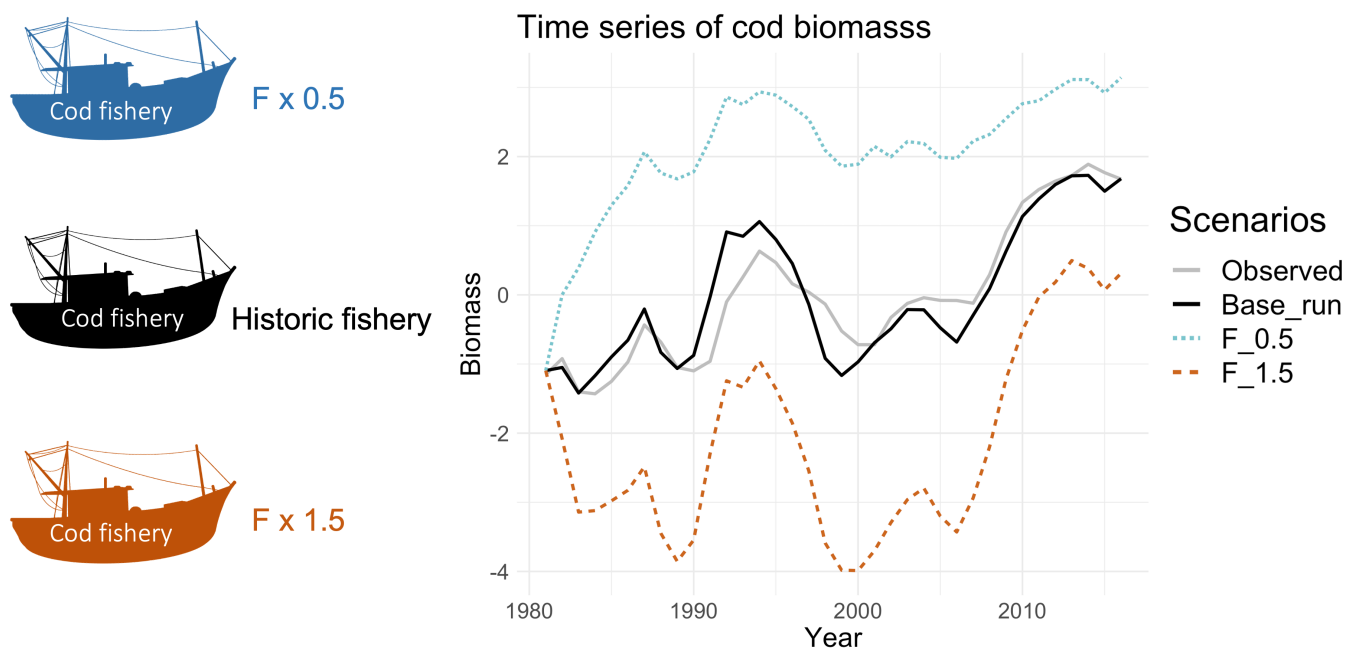

FIGURE 2 Biomass of NEA cod in both models normalised to zero mean and unit standard deviation. Black line shows simulated biomass from Atlantis used as the base case in both models, while the grey line shows observed biomass used in the original Gompertz model. Dotted lines show scenarios from Atlantis 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

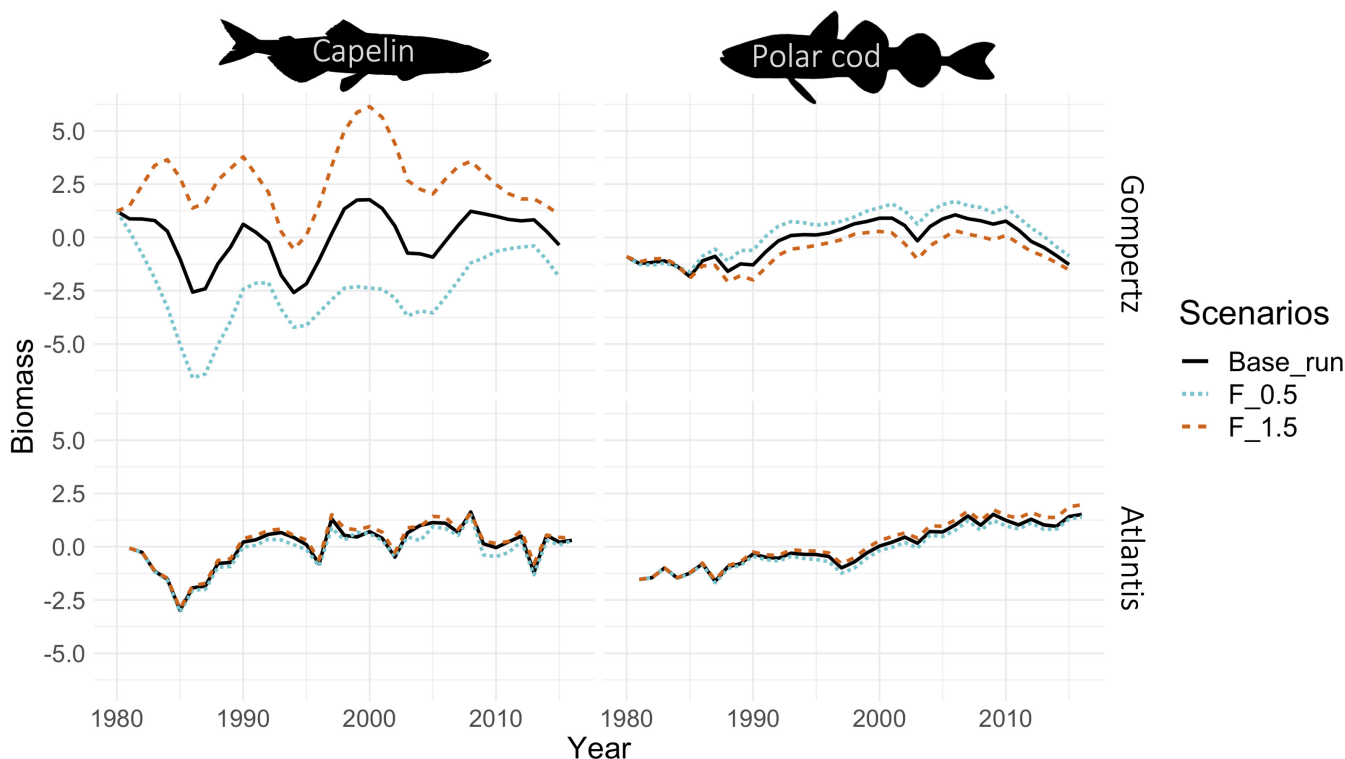| Scenario	Description	Mean F ± sd
Base_run	Historic NEA cod fishery	0.32 ± 0.12
F_0.5	Historic NEA cod fishery multiplied by 0.5	0.16 ± 0.06
F_1.5	Historic NEA cod fishery multiplied by 1.5	0.47 ± 0.18

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.
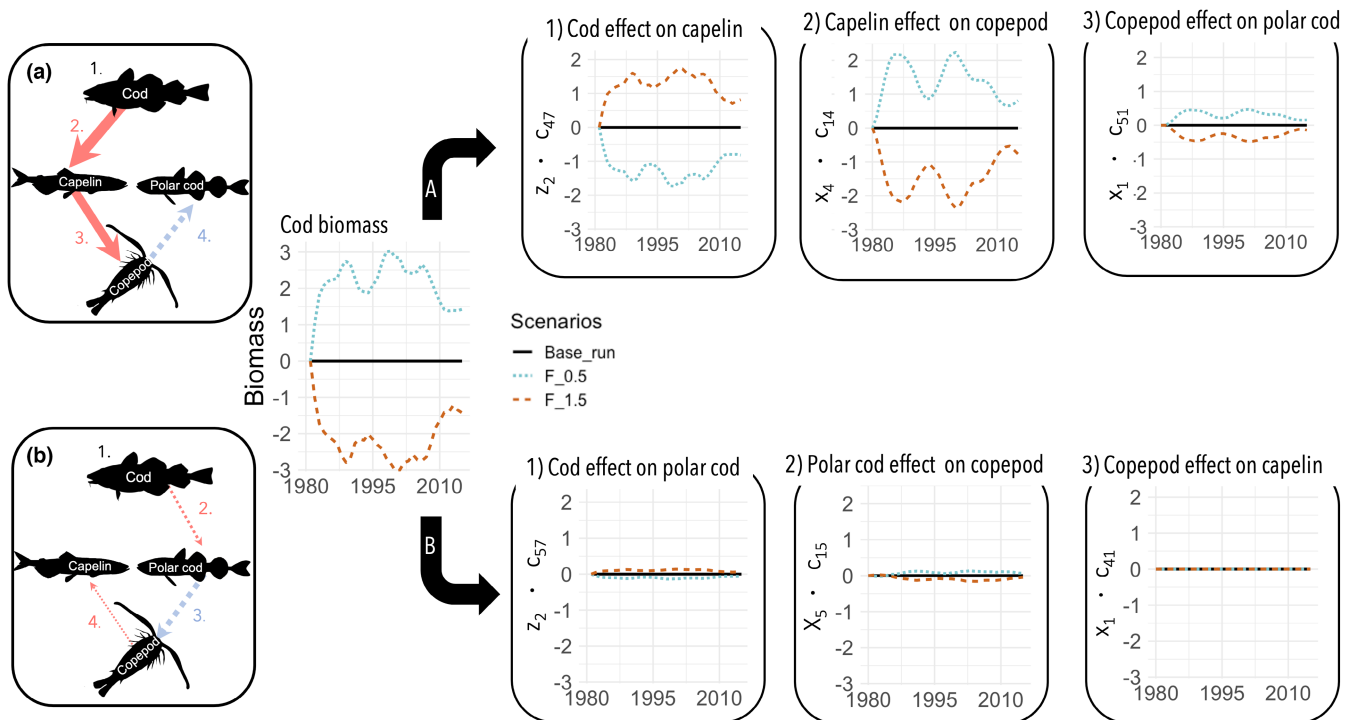

FIGURE 4 Direct and indirect effects of NEA cod in the Gompertz model. The two pathways of how capelin and polar cod and affected are presented to the left with arrows showing the strength of the interaction (thickness) and whether the effect is positive (blue) or negative (red). Note that the arrows 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
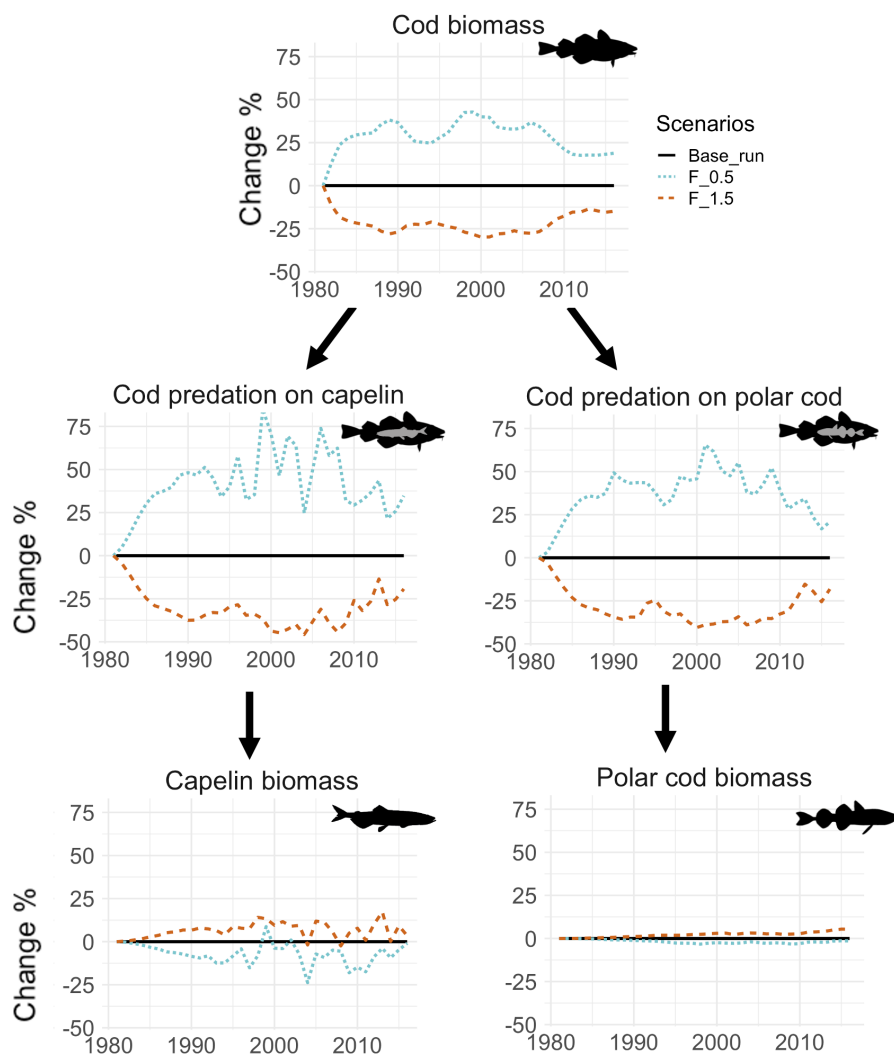
FIGURE 5 The effect of NEA cod on capelin and polar cod explained through changes in NEA cod predation in the Atlantis model. Black line shows the base line scenario and dotted lines show scenarios where the fishing mortality of NEA cod was reduced (blue dotted lines) or increased (orange dashed lines) 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
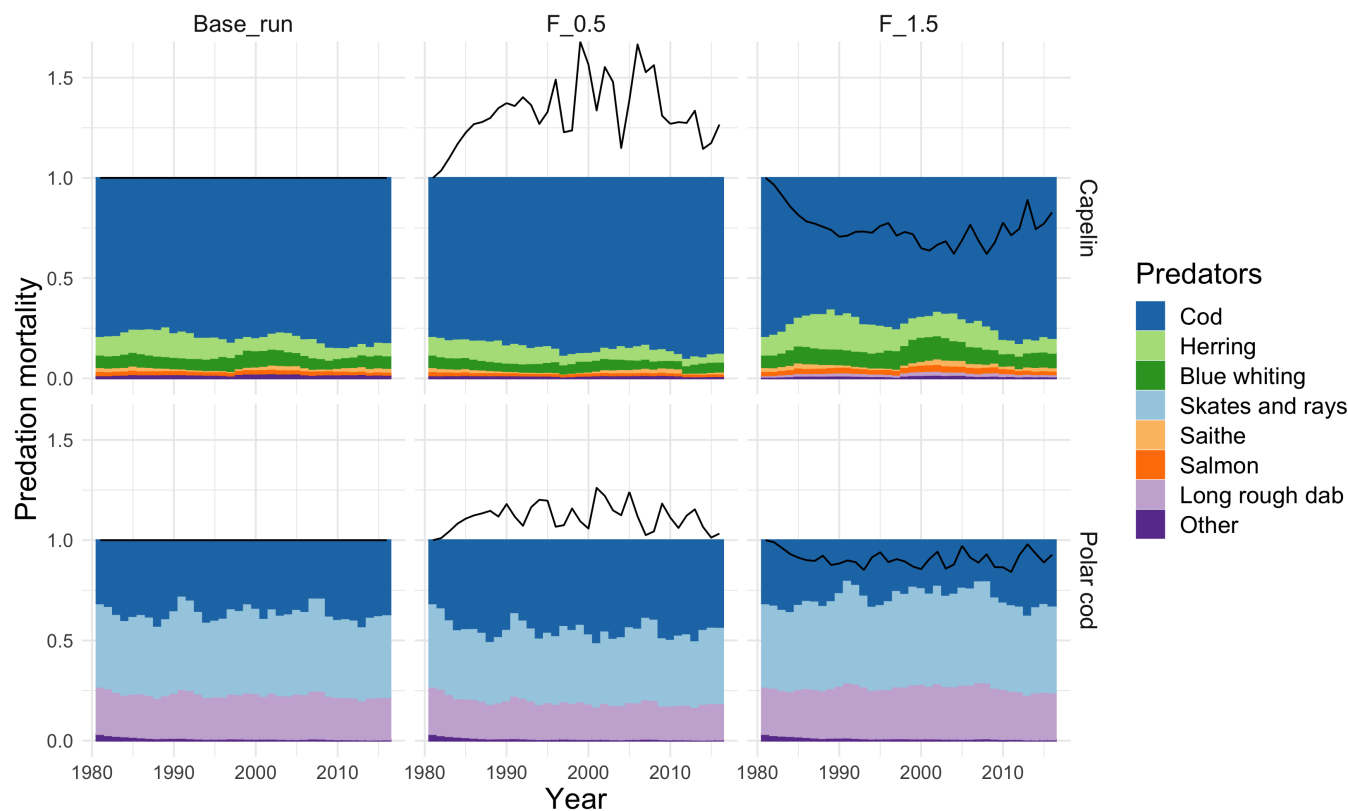
FIGURE 6 The portions of predation mortality for capelin and polar cod caused by various predators in Atlantis for the three scenarios. Black lines show how the total predation mortality varied between the scenarios

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.

For polar cod, the situation was somewhat different. The perturbations did not affect polar cod strongly in Atlantis, and in the

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.

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 multi-species 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.

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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