

Original Article

Predicting ecosystem responses to changes in fisheries catch, temperature, and primary productivity with a dynamic Bayesian network model

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The recent adoption of Bayesian networks (BNs) in ecology provides an opportunity to make advances because complex interactions can be recovered from field data and then used to predict the environmental response to changes in climate and biodiversity. In this study, we use a dynamic BN model with a hidden variable and spatial autocorrelation to explore the future of different fish and zooplankton species, given alternate scenarios, and across spatial scales within the North Sea. For most fish species, we were able to predict a trend of increase or decline in response to change in fisheries catch; however, this varied across the different areas, outlining the importance of trophic interactions and the spatial relationship between neighbouring areas. We were able to predict trends in zooplankton biomass in response to temperature change, with the spatial patterns of these effects varying by species. In contrast, there was high variability in terms of response to productivity changes and consequently knock-on effects on higher level trophic species. Finally, we were able to provide a new data-driven modelling approach that accounts for multispecies associations and interactions and their changes over space and time, which might be beneficial to give strategic advice on potential response of the system to pressure.

Keywords: Bayesian network, fisheries catch, species dynamics, temperature and productivity scenarios.

Introduction

The North Sea is a dynamic system, heavily modified by humans and climate. Thus, there is an increasing demand for tools with which to explore alternative hypotheses about ecosystem response to change in pressures (Mackinson and Daskalov, 2007). In this study, we present an approach to explore how species and trophic groups respond to change in human and climate pressures and understand potential trade-offs between such ecosystem components, given a set of alternate scenarios.

The North Sea has been exploited for centuries by the surrounding countries and the state of its environment has been altered greatly by human activities (Jennings and Kaiser, 1998). Fishing pressure can change the structure of marine populations and

consequently influence the nature of their responses to climate (Planque *et al.*, 2010). However, in late 1990s the EU began a fleet reduction scheme and most recently, the EU Common Fisheries Policy introduced significant changes to how fisheries are to be managed, including a landings obligation and management plans that take account of biological and technical interactions (EC, 2013). The ecosystem-based approach to fisheries management acknowledges that fisheries are part of the environment and cannot be managed in isolation (Cury *et al.*, 2005) and requires recognition of the ecosystem dynamics and structure.

One way to understand ecosystem dynamics is to incorporate multispecies information and interactions with both physical and biological components that would reduce uncertainty in

predicting the species response to change in fisheries and climate. The biological characteristics of any species stock are dependent upon and shaped over time by its interactions with other species and the rest of the ecosystem (Mackinson and Daskalov, 2007). As such, by using multispecies ecosystem models, the species effects can be quantified across space and over time, under different fisheries exploitation and climate scenarios.

Many studies using different techniques have been undertaken to utilize environmental information and provide advice to meet management needs and understand future environmental states (Lewy and Vinther, 2004; Mackinson and Daskalov, 2007; Ulrich *et al.*, 2011; Lynam and Mackinson, 2015). Although, such models incorporate a large percentage of the higher trophic groups, they lack important extrinsic drivers, such as climate variation (e.g. Ecopath with Ecosim in Mackinson and Daskalov, 2007), which is fundamental for interpreting community dynamics. In addition, for such models to be valuable, they would also need to reflect the link between an input that can be managed (fisheries catch) and the response (e.g. change in species biomass), and therefore require an anthropogenic involvement (García-Carreras *et al.*, 2015). Our modelling approach of utilizing multiple associations between species and their environment presents a more comprehensive route to projecting future ecosystem change allowing empirical data to be combined with some existing knowledge to build scenarios that describe possible alternative futures.

Predicting species response to ecosystem changes is challenging because of the variability in observations and uncertainty in potential associations. However, machine learning techniques have been proposed to be an appropriate approach with desired properties to address uncertainty in prediction (Uusitalo, 2007). In particular, probabilistic methods such as Bayesian Networks (BNs) provide estimates of the uncertainty associated with predictions, as demonstrated by Fernandes *et al.* (2010). With the recent adoption of BNs in predictive ecology, few assumptions can be made about the data and complex, spatially varying interactions can be recovered from collected field data, as demonstrated by Trifonova *et al.* (2015). Such probabilistic models allow predictions to be made across very different platforms and organisms (Smith *et al.*, 2006) through the use of a network structure and inference that allow us to ask “what if” type questions of the data. For example, one could ask, what is the probability of seeing a change in the biomass of cod, given that we have observed a change in the probability distribution of catch and/or herring biomass?

Originally, BNs were introduced in the context of bioinformatics research but there has been significant progress in their application to environmental problems (Chen and Pollino, 2012; Uusitalo *et al.*, 2012; Hamilton *et al.*, 2015), to manage fisheries resources (Lee and Rieman, 1997) and for other uses (Olson *et al.*, 1990). As applied in ecology, BNs represent probabilistic dependencies among species and ecosystem factors that influence the variables’ likelihood in an intuitive, graphic form (Jensen, 2001), therefore different expertise can have a quantitative indication of the range of possible scenarios consistent with the data to give strategic advice on potential ecosystem response. The visual nature of BNs can help to communicate modelling results and they allow a variety of perspectives of natural and anthropogenic effects to be represented (Levontin *et al.*, 2011).

In this study, we are interested in the characteristics of BNs to demonstrate the effects of change in human and environmental pressures on the forward projections of variables of interest. A

dynamic BN model was applied to investigate the consequences of fisheries catch, temperature and primary productivity scenarios on different fish and zooplankton species. Through the developed scenarios, we explore the specific trends of species in response to change in pressures and examine potential trade-offs between the species of interest but also with other trophic groups of species. The approach we are using is a modified version of the model in Trifonova *et al.* (2015), which uses the functional network approach to predict the dynamics of species groups, accounting for trophic associations and interactions with external stressors and unmeasured hidden effects at spatial and temporal scale. Now, we extend this approach to model individual fish and zooplankton species data further into the future by developing a set of scenarios, accounting for their spatially differentiated biotic and abiotic associations, which are important because species interactions can increase or reduce future changes at different scales, influencing the emergence of winners and losers (Barange *et al.*, 2014). Hence, we aim at predicting species year-to-year variations and understanding their dynamics, which is essential to give strategic advice on potential response of the system to pressure.

Methods

We used a modelling approach that integrates the functional network approach (combination of known topological features of food webs with quantitative variation in species interactions with their environment and surrounding stressors) with a dynamic BN model. We first modify the model to make future projections of species (and trophic groups). Then, we use the model in combination with alternate scenarios of fisheries catch, temperature and productivity to explore species (and trophic groups) trends in response to change in pressures.

Data

The analyses are based on the database of the International Bottom Trawl Survey (IBTS, <https://datras.ices.dk>) for Quarter 1 (January to March), maintained by the International Council for the Exploration of the Sea (ICES) and conducted within ICES areas between 51 and 62° latitude (Figure 1, only areas 1–7 were considered in the study here due to limited quality and consistency of the data on the remaining spatial areas). In the study, catch per unit effort data were extracted for the years: 1983–2015 and converted to biomass (kg/h), using length–weight relationships and summing by species and year (www.fishbase.org). Next, individual fish species were aggregated by summing up the data into the relevant trophic group: pelagics (*P*), small piscivorous (*SP*), and large piscivorous and top predators (*LP*). (FishBase was used as a guidance point). The following fish species were separated as specific variables of interest: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), European plaice (*Pleuronectes platessa*), sole (*Solea solea*), saithe (*Pollachius virens*), and whiting (*Merlangius merlangus*). The species were chosen due to their high commercial importance and contribution to total landings (<http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>). We also used biomass data for zooplankton species and data for sea surface temperature (*temperature*), net primary production (*Net PP*) and fisheries catch. See the **Supplementary Materials**, section 1.1 for a detailed description of these variables and their sources. The data were standardized (sample mean removed from each observation, which is then divided by the *standard deviation*) prior to

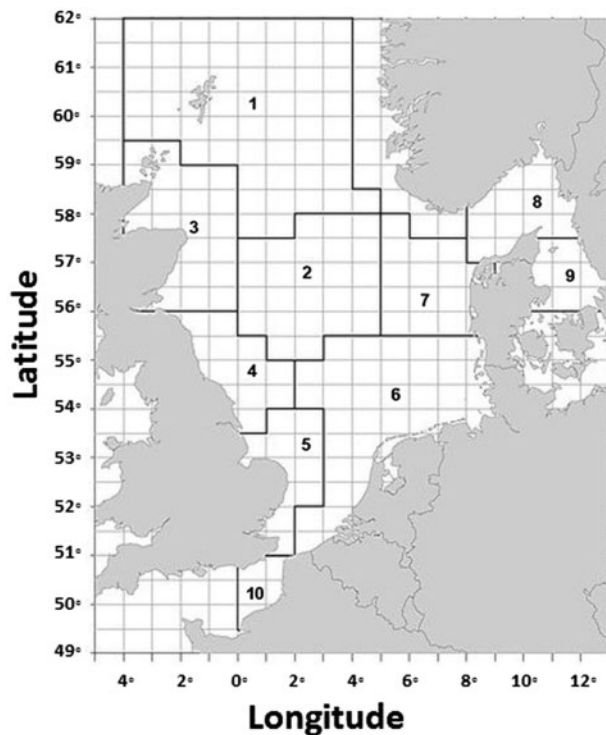


Figure 1. ICES statistical rectangles within the North Sea (areas 1–7 were used in this study). Source: ICES, Manual for the International Bottom Trawl Surveys.

conducting the modelling experiments but when visualizing the results, we reversed the standardization of the modelled values.

Bayesian networks

Formally, a BN describes the joint distribution (a way of assigning probabilities to every possible outcome over a set of variables, $X_1 \dots X_N$) by exploiting conditional independence relationships, represented by a directed acyclic graph (DAG) (Friedman *et al.*, 1999). The conditional probability distribution associated with each variable X encodes the probability of observing its values given the values of its parents, and can be described by a continuous or a discrete distribution. The DAG consists of nodes (or variables) and edges (or links) between the variables. “Parent” nodes are those from which arrows originate and “child” nodes are those to which arrows are pointing. Edges between nodes represent dependence relationships. Here, the observed variable nodes in the network are Gaussian nodes, so we assume continuous distribution with mean μ and covariance Σ . Each node in the DAG is characterized by a state which can change depending on the state of other nodes and information about those states propagated through the DAG. By using this kind of inference, one can change the state or introduce new data or evidence (change a state or confront the DAG with new data) into the network, apply inference and inspect the posterior distribution (which represents the distributions of the variables given in the observed evidence). Given a graphical structure, BNs naturally perform prediction using inference. Modelling time series is achieved by using an extension of the BN known as the Dynamic Bayesian Network (DBN), where nodes represent variables at particular time slices, Figure 2a (Friedman *et al.*, 1999). The

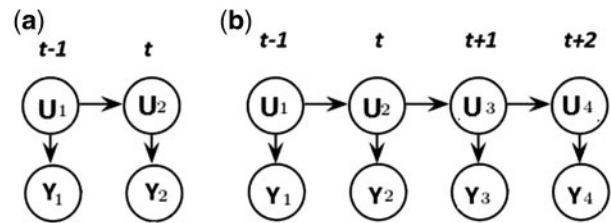


Figure 2. (a) A two slice DBN (b) the same model unrolled for $T = 4$ slices.

semantics of a DBN can be defined by “unrolling” the two-slice DBN into T time slices (Figure 2b). The parameters for slices $t = t, t+1, \dots$ do not change over time, i.e. the model is time invariant which allows unbounded amount of data to be modelled with a finite number of parameters (Murphy, 2002). In the study, DBNs allow us to integrate heterogeneous data at different scales and make robust predictions of the temporal species dynamics under modelled scenario interactions with external stressors. DBNs can model the dynamics of a dataset through the use of a latent or hidden variable (HV). This latent variable is used to model unobserved variables and missing data and can infer some underlying state of the series when applied through an autoregressive link that can capture relationships of a higher order (Murphy, 2001). Specifically, the HV was chosen to most easily reflect complex interdependencies between and among species and their environment that might represent something external to the community, which is not purely constrained within the model structure.

Model description

Here, the modelling approach is a modified version of the hidden spatial dynamic Bayesian network model developed in Trifonova *et al.* (2015) (we will refer to the model as HSDBN). The model structure represents a potential “end-to-end” ecosystem model of each area’s trophic dynamics by incorporating data driven interactions with some expertise knowledge (known topological features of food webs) on the zooplankton dynamics. This model is an extension of the published model in terms of predicting species data further into the future and modelling individual fish species dynamics under different effects from biotic and abiotic scenarios. In addition to modelling individual fish species, we also model the aggregated species groups: P , SP , and LP to account for the trophic effect in predicting future changes. We incorporate only one HV and instead of a second HV , as originally in Trifonova *et al.* (2015), we incorporate the observed zooplankton biomass for the North Sea. In addition to the three spatial nodes: P sp., SP sp., and LP sp., we add an additional spatial node (the average biomass of the relevant fish species from the spatial neighbourhood (the three or four nearest neighbours) of the current area) as a parent node to the fish species variable, to account for the effect of spatial autocorrelation. In this way, we build the notion that one area’s dynamics is likely to affect another into the model and analysis. The observed variables in the model include *total catch*, a *single fish species catch*, *temperature*, *Net PP*, *total zooplankton biomass*, a *single fish species* and three aggregated trophic species groups: P , SP , and LP and the equivalent spatial nodes from above. This totals 13 observed variables per area. The HSDBN structure varies but the general form is presented in Figure 3a, with example for one of the areas in Figure 3b. Hence,

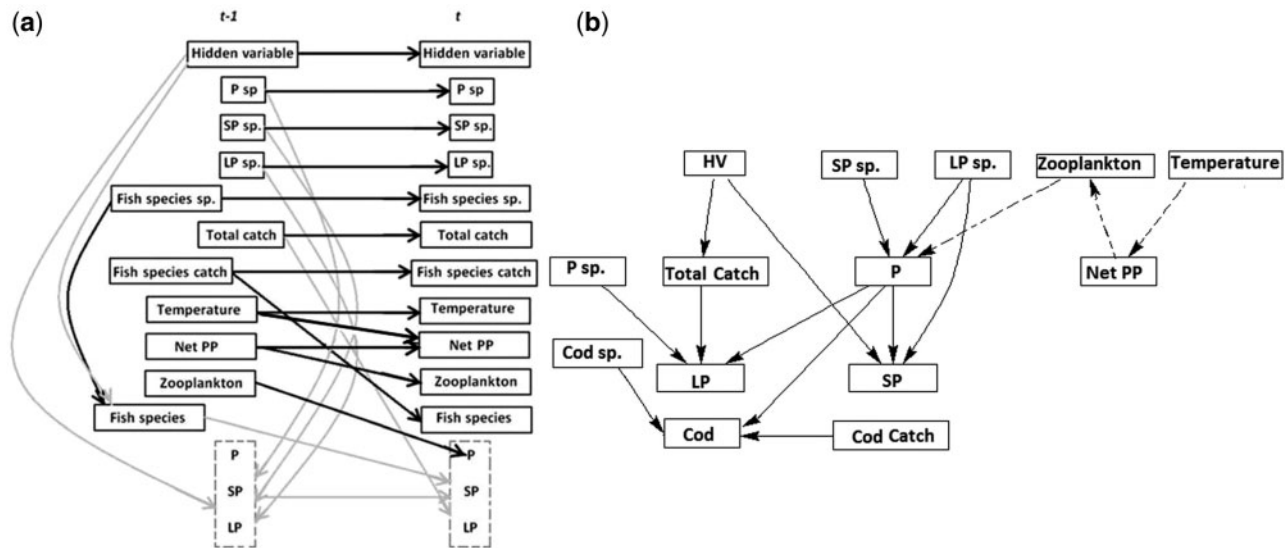


Figure 3. General structural form of the HSDBN model (a). Solid line represents fixed edges across areas. The spatial nodes (*P sp.*, *SP sp.*, *LP sp.*, *Fish species sp.*), *HV*, *catch* and *temperature* are individually linked to either *P*, *SP*, or *LP* (represented by the dotted surrounding), depending on the spatial area (grey line). Connectivity between *P*, *SP*, and *LP* and with the *fish species* also differs spatially. Network structure for area 4 (b) that models the dynamics of cod. The edges shown by a dotted line are defined by expert knowledge.

we can explore multiple species associations and model their future dynamics with interactions from external stressors and under specific scenario conditions. Using a recognized model structure, we can compare the modelled scenario outputs across spatial and temporal scales, accounting for the spatial heterogeneity and ecological complexity.

Experiments

The experiments involved prediction of survey data under scenarios of fisheries catch, temperature and Net PP. The network architecture varied with the areas but the method of prediction was universal. Given the probability distribution over $\mathbf{X}[t]$ where $\mathbf{X} = X_1 \dots X_n$ are the n variables observed along time t , to predict the biomass of each species and/or trophic group, we inferred the biomass at time $t + 1 \dots t + 5$ by using the observed evidence (or available data) from $t - 1$ and t . The choice of 2020 as the horizon for this study was chosen to limit uncertainty and, more importantly, to reflect the need for short-term predictions in fish stock management. We used an exact inference method: the junction tree algorithm (Murphy, 1998). The *HV* is specified as a discrete node which is parameterized using the Expectation Maximization algorithm in a maximum likelihood sense and assumes a discrete distribution. Non-parametric bootstrap [re-sampling with replacement from the training set, (Friedman *et al.*, 1999)] was applied 250 times for each modelling scenario to obtain statistical validation in the predictions for each area (number of iterations was found to be optimum through experimentation). First, we predict the survey data for each area using historical observations, we refer to this model output as *Historical*. Then, we use different fixed year levels from each individual fish species catch data to design our fisheries catch scenarios. We use scenarios at varying levels of fisheries catch: *low*, *medium*, and *high* (these to be referred from now on as scenarios of *L.FC.*, *M.FC.*, and *H.FC.*, respectively). We choose from the fisheries catch data 3 years equivalent to these levels and keep each level fixed from the

chosen “scenario” year until the year 2015. We keep the other measured variables unchanged. For example, in order to model the dynamics of cod in area 4 in response to change in fisheries catch, we chose from the cod catch data the year 1995 to represent the year from which the scenario of *M.FC.* starts. Figure 4a illustrates the data input assuming this scenario and the generated output. Note, that the data input for testing the *M.FC.* model, prior to the chosen scenario year, includes all of the observed variables (and one unmeasured *HV*) up to 1995 and after 1995–2015, the input is only the fixed values of the total fisheries catch and cod catch (5×10^4 tonnes live weight) (Figure 4b). In this way, we rule out the simple idea that observed values after the “scenario” year are causing the results to stabilize.

We perform this for each individual fish species and across each area, according to the originally published model structure. For example, in area 4 catch is a direct parent to *LP*, so in this area, we would investigate fisheries catch scenarios for individual *LP* fish species such as cod (Figure 3b). At the same time, we predict other fish species which are represented by the trophic species groups (*P*, *SP*, and *LP*). Essentially, each area is characterized by a sub-model, driven by the spatial dynamics of the species of interest (there could be more than one sub-model for an area) that accounts for any specific biotic and abiotic interactions between that species and other variables. In this way, we can keep the historically driven interactions between variables and examine their modelled trends under potential changes in stressors such as fisheries catch. Hence, we can examine how different ecosystem components respond to varying levels of fisheries catch, accounting for the heterogeneous nature of the modelled variables and driving factors within each area and their changes over time.

- (i) Data input and output for Medium Fisheries Catch scenario for cod, area 4
- (ii) Fisheries Catch Level for Medium Fisheries Catch scenario for cod, area 4

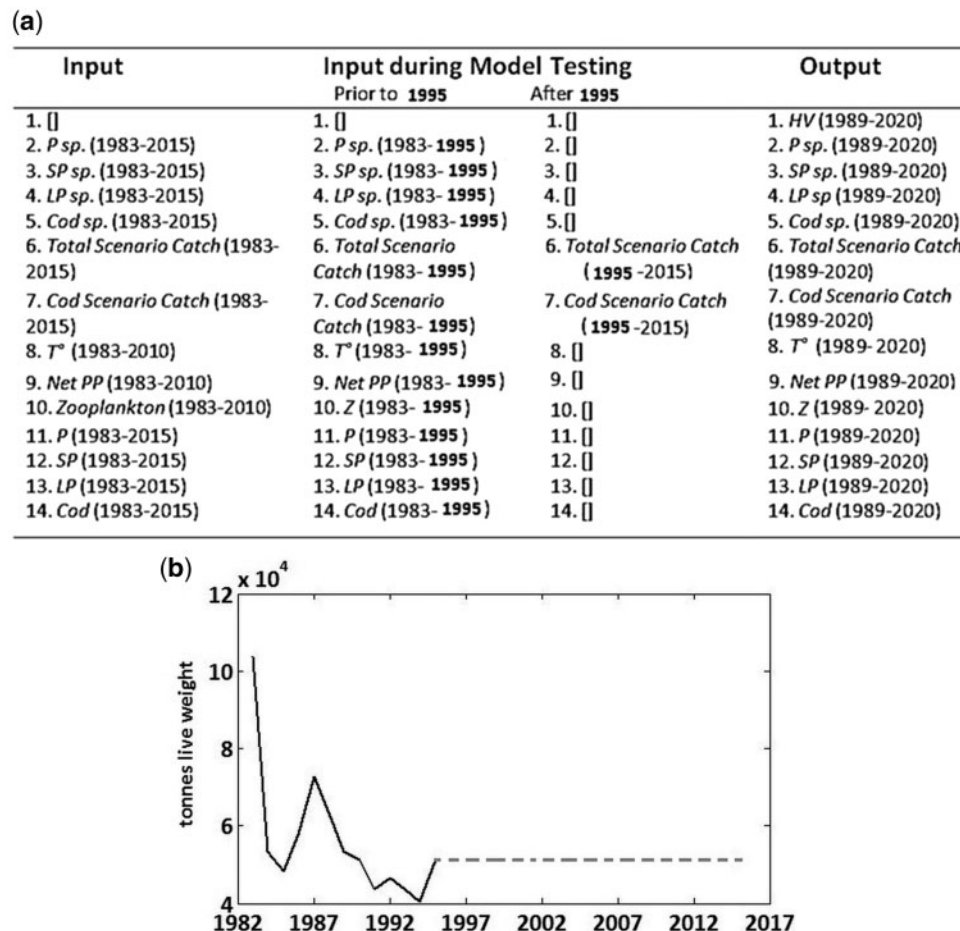


Figure 4. An example matrix from a Medium Fisheries Catch scenario model with initial input used in model definition, the input during model testing and the generated output (a). The time window for each variable is shown in brackets. Note, the time window for the output starts from 1989. “[]” represents variables for which no evidence is introduced and which are predicted. *Z* stands for zooplankton. The observed cod catch prior to the scenario year of 1995 (solid line) and fixed catch level for the Medium Fisheries Catch scenario (dashed line) is shown in (b).

We generate a 10% increase temperature scenario (*T.I.*) and Net PP scenarios: 30% increase and 30% decline (referred from now on as: *Net.I.* and *Net.D.*) to understand the effects of temperature on primary production and its potential knock-on effects on different zooplankton species and trophic species higher up the food chain. We did consider a scenario of temperature decline but we only present the results following a potential increase in temperature. We used 1990 as the “divergent year”, which is the year to start the scenario changes from by manipulating the temperature or Net PP data to either increase or decline but keeping the rest of the observed data unchanged, e.g. if the average sea surface temperature for 1990 is 9°C, then for 1991 it would be 9.9°C. For these two types of scenarios, the number of observed variables in the experimental set-up is 12 (*total catch*, *temperature*, *Net PP*, *Calanus finmarchicus*, *Calanus helgolandicus*, *small copepods*, *P sp.*, *SP sp.*, *LP sp.*, *P*, *SP*, and *LP*).

Results

In the following, we describe the outputs from the modelled fisheries catch, temperature and Net PP scenarios by examining future trends of individual fish and zooplankton species at spatial and temporal scales. We explain the results from the scenarios by

examining if the predictions of the ecosystem components were to increase or decline. Our results demonstrate some variability in the future trends of different species, which we explain through the use of “what if” type descriptions of the model structures in response to predicted changes in the other variables.

Fisheries catch scenarios

Cod

First, looking at the *Historical* output, the model managed to capture the cod variations throughout time and predicted some increase in near future years which were then followed by some decline (Figure 5c).

Second, looking at the scenario outputs, as we would expect, the scenario of *High Fisheries Catch* (*H.F.C.*) resulted in the lowest modelled cod survey data in areas 4 (Figure 5d) and 6 (thus, addressing in detail only area 4 but look at Figure 3a and b in the [Supplementary Materials](#) for area 6). We notice a sudden decline in early 1990s (as a result from the high scenario catch level), but then the modelled values were characterized by some fluctuating trend, that was higher than the observed data. This does not mean that if cod could continue to be fished at the highest

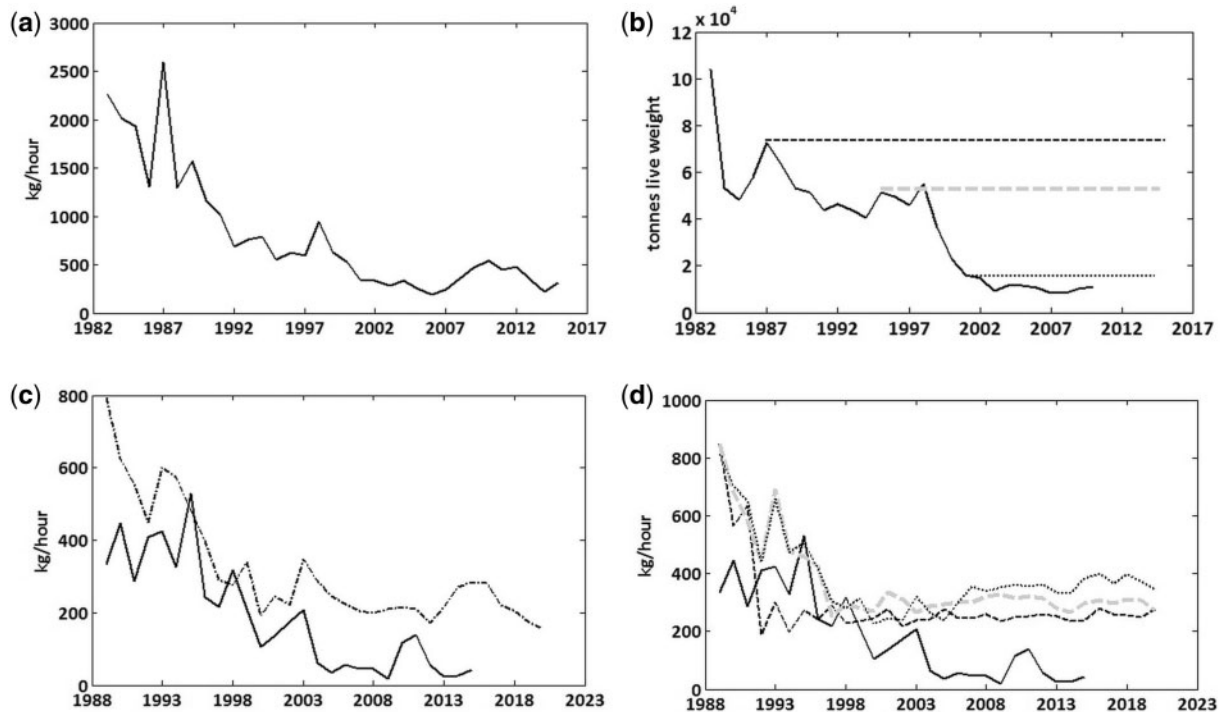


Figure 5. Recorded spatial cod data is shown in (a). The observed cod catch (live weight in tonnes) with the three fixed year levels of fisheries catch scenarios for the time window 1983–2015 is shown in (b). Recorded survey cod data (solid line) with the generated output by the *Historical* model (dotted line) for the time window 1989–2020 for area 4 is shown in (c). Recorded survey cod (solid line) with the modelled cod is shown in (d) under fisheries catch scenarios of high (black dashed line), medium (grey dashed line) and low (black dotted line) levels for the time window 1989–2020.

recorded level the stock would still be ok but more likely when the cod survey values and spatial biomass in neighbouring areas (Figure 5a) are low and catch is high (Figure 5b), another species might increase and a year later that would cause the cod to increase. For example, in this area, cod is influenced by the dynamics of species group *P* (Figure 3b), which were predicted to be relatively stable with an increasing trend in the near future, partly explaining the modelled cod results here. Under the scenario of *Medium Fisheries Catch* (*M.FC.*), the modelled survey data seemed to be genuinely stable throughout time that was higher than the scenario of *H.FC.* However, we notice that these two scenarios seem to converge in the near future, highlighting the similarity in species response to contrasting levels of fisheries catch, thus still having the need to identify a potential “optimum” level of fisheries catch. The scenario of *Low Fisheries Catch* (*L.FC.*) resulted in the highest modelled cod survey data, highlighting the importance of fisheries catch on this species dynamics and identifying a potential “optimum” level of fisheries exploitation comparing to the medium and high levels from above.

- (a) Cod spatial data, area 4
- (b) Cod catch, area 4
- (c) Cod survey data and *Historical* output, area 4
- (d) Cod survey data and modelled scenario cod, area 4

Whiting

The *Historical* model managed to reflect on the declining trend of whiting throughout time and predicted some rising trends in the

near future which were then followed by some decline (Figure 6c).

We found the opposite of what we were expecting from the fisheries catch scenarios for whiting in area 3: a scenario of *L.FC.* produced whiting predictions that were characterized with the lowest trend throughout time (Figure 6d). The surrounding predictions of the whiting spatial node were also characterized by a declining trend, which in combination with the medium to high catch from *M.FC.* and *H.FC.* and relatively low values of the *P* species group (network shown in Figure 6a) might allow for another species to increase (e.g. larger predator), which in turn would cause the projected whiting values here. We also note that the predicted trends from the *M.FC.* and *H.FC.* scenarios were relatively similar. Interestingly, the *hidden variable* (*HV*) captured some of the expected “correct” characteristics: the scenario of *L.FC.* projected a strongly increasing trend of the *HV*, that was much higher than the *HV* from the *Historical* model. The *HV* is linked to the *LP* species group (which includes cod), so it is capturing changes in the variance of their survey data, due to species associations and interactions (*LP* is influenced by *SP* and *P sp.*) and consequent trade-offs between species, that were not easily detected by the model predictions alone. Thus, still having the need to identify a potential “optimum” level of fisheries catch to account for the effect of trade-offs between species.

- (i) Area 3
- (ii) Whiting catch, area 3
- (iii) Whiting survey data and *Historical* output, area 3

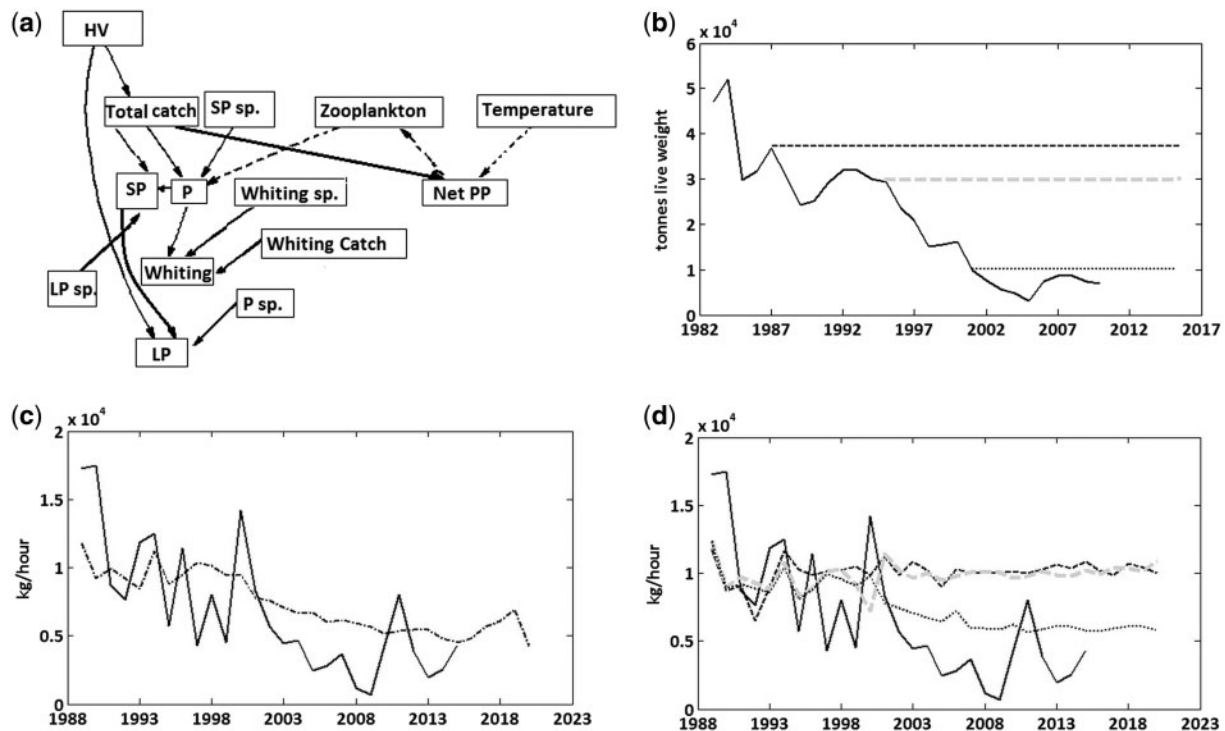


Figure 6. The model structure for area 3 is shown (a). The dotted edges are defined by the expert. The observed whiting catch (live weight in tonnes) with the three fixed year levels of fisheries catch scenarios for the time window 1983–2015 is shown in (b). Recorded whiting survey (solid line) data with the generated output by the *Historical* model (dotted line) for the time window 1989–2020 for area 3 is shown in (c). Recorded survey (solid line) with the modelled whiting data under fisheries catch scenarios of high (black dashed line), medium (grey dashed line), and low (black dotted line) levels for the time window 1989–2020 is shown in (d).

(iv) Whiting survey data and modelled whiting, area 3

To summarize, for most species we were able to predict trends that were modelled to either increase or decrease in response to change in fisheries catch but this varied across areas, thus highlighting the spatial heterogeneity in terms of species-specific response to ecosystem change, the spatial relationship between neighbouring areas and trophic interactions. Finally, we need to mention that the aggregated species group biomass might include species not directly targeted by fisheries, which could potentially influence the scenario interpretations, however the fact that we accounted for “what if” type descriptions of all ecosystem components in the network model, should help us in the interpretation of our results.

Temperature and Net PP scenarios

We are now looking at the potential influence of temperature on the future projections of productivity and consequently how the productivity will influence the future trends of different zooplankton species. We have chosen to present results only for areas 1, 3, and 6 due to the contrasting nature of the physical and biochemical characteristics of these areas.

For area 1 (and area 3), the scenario of *T.I.* resulted in an increasing trend of *Net PP* throughout time that was also higher than the *Historical* model. However, the *T.I.* scenario projected some *Net PP* decline in the near future that was characterized by a converging trend with the projections of the *Historical* model, possibly indicating a drop in productivity. Conversely, for area 6,

the scenario of *T.I.* projected a trend of lower *Net PP* values than the *Historical* model, potentially due to larger temperature changes in southern areas. Similarly to areas 1 and 3, there was a drop in productivity projected from 2017 onwards.

Following a scenario of temperature increase, a lower trend (compared with the *Historical* model) throughout time was projected for *C. finmarchicus*, whilst the opposite was found for *C. helgolandicus*. In some areas, it was also the scenario of *Net PP* decline that led to higher values of both zooplankton species, as a consequence of temperature influence on productivity. However, at the same time, a distinct drop was found in the projected values of the *C. finmarchicus* species in the near future, highlighting that potential trade-offs will also emerge between lower trophic level species. Look at the [Supplementary Material](#) (2.2 Temperature and Net PP Scenarios) for a more detailed description of the zooplankton results in terms of the different spatial areas and the modelled predictions ([Supplementary Figure S7](#)).

We were able to detect a knock-on effect on the future dynamics of the *P* species group survey data, following changes in temperature and productivity. For some of the areas, it was the scenario of *Net PP* decline that led to an increase in the trends of the herring and *P* species group survey data. Look at the [Supplementary Materials](#), section 2.2 for a more detailed description of these results in terms of the different spatial areas and modelled predictions ([Supplementary Figure S8](#)).

To summarize, we found the modelled future zooplankton trends to be species-specific but there seems to be consistency in terms of their response to temperature change across the different areas, whilst more variability was found relating to productivity

changes. In addition, we were able to confirm the potential influence from productivity and to some extent temperature (depending on the area) changes to species, higher up the food chain.

Discussion

In this study, we explored the trends of ecosystem change in response to anthropogenic and environmental scenarios by modifying a dynamic data-driven functional network model, accounting for spatial heterogeneity and unmeasured spatial effects. It is important to note that we did not attempt to indicate levels of plausibility between these scenarios but rather explore the predictive results of species response to fisheries and environmental change. Our results highlighted that reducing fisheries catch will not necessarily lead to recovery of all commercially important fish species because fish consume one another, thus the total catch of one species will consequently affect that of others through knock-on effects in the food web. Overall, we found some spatial variability in terms of species response to different fisheries catch and productivity scenarios, highlighting the influence from factors such as trophic associations, spatial connectivity between areas and species interactions with their environment, that could potentially contribute towards the better understanding of ecological stability and resilience in a changing environment. However, at the same time, we found some universal species trends to changes in catch and temperature that could provide some strategic advice on potential response of the system to such pressures. Controlling for the level of fisheries exploitation but also considering trophic interactions and spatial values are of high significance in terms of short-term management. Our results allow dynamic assessment of choices, which should be able to provide strategic advice on potential system response to pressure. In terms of management objectives and expectations, we support the idea that for a given area, reorganization of the management strategies will be required to ensure that the right species are targeted and harvested sustainably (Simpson *et al.*, 2011). Management strategies must also take into account the local population dynamics and processes in a wider sense in order to maximize biodiversity and survival. Fisheries management measures will contribute to improvements in the biodiversity of the fish community, but food web interactions will mediate changes.

In the scenarios modelled here, some trade-offs between species emerged in terms of how they would respond to different levels of fisheries catch. Specifically, the potential recovery that we found for cod in the near future (and variance explained by the HV) could explain the modelled results for whiting because cod feeds on juvenile whiting (Mackinson *et al.*, 2009). Similar results were found by Lewy and Vinther (2004) and Lynam and Mackinson (2015), suggesting a more dominant role of the cod in the food web after recovering from exploitation. The potential recovery trend that we found for cod could be due to strict management regulations placed since the Millennium (Horwood *et al.*, 2006), which if continued, will hopefully give the stock a chance to rebuild completely in some areas where the cod was formerly abundant (Engelhard *et al.*, 2014).

One of the differences between our model and others is the incorporation of a HV, adopted to capture unmeasured spatial effects and changes in species variance that are not purely constrained within the model structure. For some of the areas, the HV was characterized by a decline and showed high sensitivity in terms of catch variation, outlining that such areas seem to exhibit a range of discontinuous disturbance exacerbated by spatial

differences in recruitment and survival. Conversely, for some of the other areas, the learned HVs were projected to increase, following some of the scenarios, which are reflective of the underlying biomass changes, relating to potential knock-on effects, as it was found for area 3. Specifically, our results of modelling whiting in response to different fisheries levels and consequent rising trophic interactions and sensitivities that were captured by the HV, suggest that for effective management, reorganization of the fishing strategies in the mixed-fisheries context will be required to ensure that the right species are targeted and harvested sustainably (Simpson *et al.*, 2011). These results highlight that the use of a HV when modelling species response to change is potentially useful in providing insights on the spatially specific dynamics and patterns in terms of ecological stability and resilience that can contribute towards the general advice on potential response of the system to pressure.

Overall, our results showed there were spatial differences in terms of “optimum” level of fisheries catch, suggesting spatial variability regarding community stability and the potential higher influence of trophic interactions in some areas or spatial connectivity in others, compared with fisheries exploitation. For example, we found some similarity in the modelled whiting predictions from the medium and high fisheries scenarios for area 3, which might be due to similarity in the level of fisheries catch but also due to the fact that trophic interactions are potentially more important for controlling the whiting dynamics compared with fisheries, as discussed in Trifonova *et al.* (2015) for this area. This suggests that stocks cannot be managed in isolation from each other (Cury *et al.*, 2005). Thus, highlighting the need to use multi-species models accounting for spatial connectivity. Multispecies models have been proved useful in terms of providing long-term information on stock recovery and most importantly, have been used to evaluate precautionary reference points for fishery management (Pinnegar *et al.*, 2008). In doing so, multispecies and ecosystem models are anticipated as being helpful to guide strategic management decisions (Mackinson and Daskalov, 2007). As such, multispecies stock assessments and simulation models (e.g. SMS, 4M, Gadget, multispecies IBMs) are becoming more refined (Plagányi, 2007).

Although, we analyse the different scenarios in respect to the species of interest in the relevant area, we do acknowledge that one area's dynamics likely affect another by introducing the spatial nodes into the model structure. In this way, we also increase the confidence in the robustness of the approach and contribute to increased knowledge of model behaviour. One main issue encountered is the uncertainty in future trends, which is obviously inherent to any model linking external factors to species interactions. These linkages are of major importance for mixed-fisheries management (Ulrich *et al.*, 2011). However, the fact that we were able to recover genuine trends of species dynamics throughout space and time in Trifonova *et al.*, (2015) and that we were able to identify similarity in our results here with other modelled species predictions (Lewy and Vinther, 2004; Vinther *et al.*, 2004; Lynam and Mackinson, 2015) contributes to strengthening the confidence that our approach can provide some strategic advice on modelling species response to change.

Here, the modelling framework was built to handle complex systems such as the North Sea, so consequently we assume there is a degree of complexity when modelling fisheries. The assumptions are based on key processes within the environment accounting for influence from external factors such as fisheries catch.

One aspect of the underlying processes that could be further investigated includes fishermen behaviour or effort information to estimate catch potentials for distinct fleets. An example of one model that incorporates this is the *Fcube* (Fleet and Fisheries Forecast) model. However, for the *Fcube* to be established at a regional scale requires substantial analysis and due to its short-term applicability, is often used as a routine advice model at the same level as a single-stock assessment model (Ulrich *et al.*, 2011). Another example of a model that uses information on technical interactions alongside biological information from stock assessments is the MTAC developed by Vinther *et al.* (2004). However, the MTAC did not prove to be robust and flexible enough for mixed-fisheries and there were also problems with data availability (Ulrich *et al.*, 2011).

The HSDBN model represents a flexible framework of medium complexity between single-stock assessments and multi-species models such as Ecopath (Mackinson and Daskalov, 2007). By extending our model to use scenarios rather than optimization and adding additional parameters compared with more traditional approaches, we extract simple proxies that are indicative at the regional scale but also work at the level of the broad picture. A similar dynamic framework for the North Sea, accounting for multiple-species interactions, was developed by Lynam *et al.* (unpublished) (presented at PICES Symposium on “Effects of climate change on the world’s oceans”, March 2015), using a threshold-Generalized Additive Model. The approach is data-demanding and it includes external factors but does not include a spatial component. In our model, we account for the complexity of the spatio-temporal distribution by allowing a framework that accounts for the heterogeneous nature of the driving factors within each area (unique model structure for each area) and their changes over time. Explicit spatiality is a key parameter in our model which does add some complexity to the model structure and it is data-demanding but accounting for additional sources of variation seems to remove spurious interactions and reveal the genuine complexity of such diverse and exploited ecosystems such as the North Sea. Although, we allow for some variability, the model has proven its high flexibility enabling latent effects and testing alternative hypotheses about species and their dynamics to reduce scientific uncertainty.

Finally, in the modelled scenarios here, we found that some species appear more robust to changes in fisheries exploitation, compared with others; however, changes in temperature and productivity might be more important in terms of the species long-term sustainability. It was interesting to see that our results of modelling a drop in future productivity coincides with other work that could be related to the overall future productivity conditions expected in the North Sea (Blanchard *et al.*, 2012).

Increase in temperature leads to an increase in lower trophic level species and consequently their predators, which we found true for some areas, whilst in others, the effect of temperature on fish was less evident due to interactions with productivity, which could be acting more strongly than the effect of fishing (Blanchard *et al.*, 2010). For example in area 3, the influence of productivity is likely to mask the effects from fisheries, or cause a mixture of responses due to multiple causal mechanisms and stressors on the ecosystem (Halpern *et al.*, 2008). Such results confirm that species response to any future changes in temperature will be determined by their spatial habitat because temperature variations consequently lead to spatial variability in

productivity, potentially causing further forcing on higher level trophic species and mixture of responses at spatial scales.

Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

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