

Spatio-temporal Bayesian network models with latent variables for revealing trophic dynamics and functional networks in fisheries ecology



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ABSTRACT

Ecosystems consist of complex dynamic interactions among species and the environment, the understanding of which has implications for predicting the environmental response to changes in climate and biodiversity. However, with the recent adoption of more explorative tools, like Bayesian networks, in predictive ecology, few assumptions can be made about the data and complex, spatially varying interactions can be recovered from collected field data. In this study, we compare Bayesian network modelling approaches accounting for latent effects to reveal species dynamics for 7 geographically and temporally varied areas within the North Sea. We also apply structure learning techniques to identify functional relationships such as prey–predator between trophic groups of species that vary across space and time. We examine if the use of a general hidden variable can reflect overall changes in the trophic dynamics of each spatial system and whether the inclusion of a specific hidden variable can model unmeasured group of species. The general hidden variable appears to capture changes in the variance of different groups of species biomass. Models that include both general and specific hidden variables resulted in identifying similarity with the underlying food web dynamics and modelling spatial unmeasured effect. We predict the biomass of the trophic groups and find that predictive accuracy varies with the models' features and across the different spatial areas thus proposing a model that allows for spatial autocorrelation and two hidden variables. Our proposed model was able to produce novel insights on this ecosystem's dynamics and ecological interactions mainly because we account for the heterogeneous nature of the driving factors within each area and their changes over time. Our findings demonstrate that accounting for additional sources of variation, by combining structure learning from data and experts' knowledge in the model architecture, has the potential for gaining deeper insights into the structure and stability of ecosystems. Finally, we were able to discover meaningful functional networks that were spatially and temporally differentiated with the particular mechanisms varying from trophic associations through interactions with climate and commercial fisheries.

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1. Introduction

1.1. Fisheries and ecoinformatics

In recent decades it has become clear that ecosystem structure and function can change over relatively short time scales (Scheffer et al., 2001). Changes in the marine environment are believed to be more

rapid in the 21st century causing both ecological and industrial implications (Fernandes et al., 2013). Therefore being able to predict the dynamics of the species and their environment at spatially and temporally resolved scales, is of growing importance for the protection of natural biodiversity and human resources which poses new challenges for analytical tools and computational statistics (Aderhold et al., 2012).

One way to understand ecosystem dynamics is examination of the functional relationships (such as prey–predator, Fig. 1) between species along with their interaction with stressors such as temperature change and fisheries exploitation in their potential habitat (space) and across time. In this way, learning functional relationships can provide a metric for assessing community structure and resilience in response to natural and anthropogenic influences (Gaston et al., 2000). If we can model the function of the interaction rather than the species itself, data can be used to confirm key functional relationships and to predict impacts of forces such as fishing and climate change.

Abbreviations: BN, Bayesian network; IBTS, International Bottom Trawl Survey; ICES, International Council for the Exploration of the Sea; CPUE, catch per unit effort; P, pelagics; SP, small piscivorous; LP, large piscivorous and top predators; Net PP, net primary production; DAG, directed acyclic graph; CPD, conditional probability distribution; CPT, conditional probability table; DBN, dynamic Bayesian network; HMM, hidden Markov model; ARHMM, autoregressive hidden Markov model; HV, hidden variable; EM, Expectation Maximization algorithm; SSE, sum of squared error.

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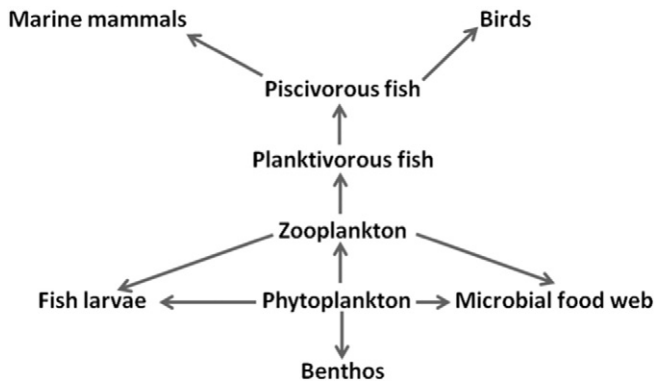


Fig. 1. A generalized marine food web showing the functional relationships between trophic levels where direction of links represents prey–predator interactions.

The North Sea is a diverse ecological system with complex climate–ocean interactions and exploited fisheries since 1900 (Smith, 1994). Significant warming trends are evident throughout but the most intense are documented in the southern and eastern North Sea (Simpson et al., 2011). Exploitation has led to significant reductions in the abundance of some target species and non-target species have been impacted because of incidental catch and subsequent discard (Gislason, 1994). Fishing pressure can change the structure of marine populations and consequently influence the nature of their responses to climate (Planque et al., 2010), which could have impacts on the value of commercial fisheries (Perry et al., 2005). Due to the high biological productivity and valuable fisheries resources of the North Sea, understanding the species dynamics and modelling their interactions with external stressors over space and time, is of primary interest in the present work.

1.2. Functional network models

Interactions among species make it difficult to predict how ecological communities will respond to environmental degradation, yet to do so we must understand the functional networks that form the systems (Dunne et al., 2002). The functional network approach to understand community structure and resilience is an on-going approach combining known topological features of food webs with quantitative variation in species interactions with their environment and surrounding stressors to predict community stability. Recently, an approach has arisen in biology that is capable of inferring network structures, capturing nonlinear, dynamic and arbitrary combinatorial relationships: Bayesian networks (BNs) (Heckerman et al., 1995). BNs have been applied to reveal gene regulatory networks using gene microarray data (Friedman et al., 2000) and were shown to reveal known pathways of neural information networks from brain electrophysiology data (Smith et al., 2006). Such a flexible technique capable of identifying the complex relationships involved in bioinformatics potentially offers a valuable method in ecological studies (Milns et al., 2010). Therefore, our work aims to adapt this novel methodology to infer the network structure directly from the collected field data.

There has been significant progress in developing models using classical statistical techniques (Krivtsov, 2004) to understand the structure and stability of some ecological networks in a changing environment, however such methods often limit the underlying interactions from expanding beyond the current food web paradigm (Faisal et al., 2010). Our network approach of analysing multiple associations between groups of species and their environment presents a more comprehensive route to revealing interactions within the ecosystem (Aderhold et al., 2012) directly from the data, rather than taking an “existing” network structure and analysing it in terms of summary statistics. BNs are efficient in integrating variables presented at different scales (Wooldridge et al., 2005), allow empirical data to be combined with existing knowledge (Uusitalo, 2007), operate within a data poor

environment (Uusitalo, 2007) and integrate the uncertainty associated with species dynamics due to the action of multiple driving factors.

The objective of this paper is to model the species dynamics and their interactions with external stressors at geographically and temporally varied areas within the North Sea. We evaluate the potential usefulness of Bayesian inference for ecological data by examining the predictive capability of different dynamic BN architectures. We correct for spatial autocorrelation by introducing a *spatial node*—a parent node representing the spatial neighbourhood of a node. We also account for latent variable effects by introducing two hidden variables—one *general* to detect overall change in the species biomass and another *specific* to capture spatial unmeasured effects. We produce a novel approach of modelling ecosystem dynamics that accounts for the *heterogeneous* nature of the driving factors within *each spatial area* and their changes over *time*. We examine the models' accuracy in predicting biomass, in response to any changes in temperature and fisheries catch or given there is a change in another species group biomass and therefore aid towards the better understanding of North Sea trophic dynamics, which is influential for future management options and long-term viability of populations. We investigate not just functional relationships between groups of species but also their interactions with external stressors that vary across space and time in order to clarify what mechanisms are involved in shaping the functional ecological networks and derive insights on the community structure and resilience.

Methods in Section 2 describe the fisheries data and the use of BN modelling techniques applied to the data. Results in Section 3 demonstrate the predictive capability of all applied modelling approaches, outlining the performance of the proposed latent model with spatial autocorrelation, with analysis on the features of the hidden variables and species interaction networks identified by structure learning. Finally, the use of the techniques explored in this paper (namely, BNs, dynamic models with latent variables, spatial node) is discussed in Section 4 in terms of the wider fisheries literature.

2. Materials and methods

2.1. Data

The analyses are based on the database of the International Bottom Trawl Survey (IBTS) for Quarter 1 (January to March), maintained by the International Council for the Exploration of the Sea (ICES) and conducted within ICES areas between 51–62° latitude (Fig. 2, only areas 1 to 7 were considered in the study here due to limited quality and consistency of the data on the remaining spatial areas). These data are publically available from the ICES Database of Trawl Surveys (DATRAS; www.ices.dk). The IBTS is a scientific fishing survey that follows a standard protocol: at each station, a GOV trawl is towed at 3 to 4 knots for a predefined duration. All species caught in relatively low numbers are counted and measured, whilst for very large catches, subsamples are taken and the resulting data scaled to the total catch. The data are recorded as length–frequencies by tow for each species and converted to catch per unit effort (CPUE; numbers per length class per hour) using tow durations.

In the study, CPUE was extracted for the time window: 1983–2010 and converted to biomass (kg per hour), using length–weight relationships and summing up over the same species and within the same year (www.fishbase.org). Next, fish species were aggregated by summing up the biomass 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 nature of individual species summed into the trophic groups varied between the spatial areas but this was not of importance since they were always aggregated into the correct group. This was performed for each of the 7 areas and for each year in the time window. We also have available biomass data for different zooplankton species (source: ICES Working Group on Integrated Assessments of the North Sea—WGINOSE) but we decided to sum the

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