Ecological Modelling 360 (2017) 94–107

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Investigating the potential impacts of ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic food-web model

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ARTICLE INFO

Article history:
Received 25 November 2016
Received in revised form 30 June 2017
Accepted 7 July 2017
Available online 15 July 2017

Keywords:
Barents Sea
Norwegian Sea
Ocean warming
Ecopath with Ecosim

ABSTRACT

Climate change in the Norwegian and Barents (NorBar) Seas is expected to generate major alterations to the marine food-web and its associated uses. However, our current capacity to quantify the potential ecological impact of physical change is hindered by a lack of fundamental knowledge regarding the forces and trophic interactions which have driven historic ecosystem dynamics. Here we used a historic (1950) food web model (Ecopath with Ecosim, EwE) of the NorBar Seas fitted to time series between 1950 and 2014 to simulate ecosystem response to changes in ocean temperature over the next 85 years to 2100 under a range of temperature scenarios including a large scale climate variability indices (Atlantic Multidecadal Oscillation, AMO). Fishing, top-down/bottom-up trophic interactions, a primary production anomaly and annual ocean temperature were all found to be important drivers of modelled ecosystem dynamics in the NorBar Seas from 1950 to 2014. Under projected temperature scenarios, the biomass of pelagic species, such as mackerel and blue whiting, increased with rising ocean temperature, whereas the biomass of boreal species, such as redfish, prawns and capelin, decreased. Whilst within favourable temperature conditions, cod biomass is predicted to decrease under the warmest scenarios due to the reduced availability of preferred prey and the increased pressure of pelagic predation upon juvenile cod. The model produced by this study provides a useful baseline approximation of the 1950–2014 NorBar ecosystem, from which future research can propagate, and offers valuable insight into the systems potential response to changing ocean temperature. Such quantitative advancements are fundamental to achieve sustainable development in rapidly changing marine ecosystems.

1. Introduction

The Arctic has been labelled the most rapidly changing environment on the planet, warming at two to three times the global rate (IPCC, 2014; Polyakov et al., 2010). Changes in sea ice, water temperature, light penetration, nutrient cycling, pollution and ocean acidification act collectively upon the Arctic ecosystem (Dalpadado et al., 2012), generating major, yet unknown, changes to the structure, stability and efficiency of Arctic food-webs (Kedra et al., 2015). Given the rate of change, the severity of this knowledge gap is particularly worrying as it threatens our ability to adapt marine management and policy to achieve sustainable ecological and socio-economic development in the Arctic.

The Barents Sea and the Norwegian Sea represent two ecoregions subject to physical change within the Arctic. Rather than through direct warming, it is the increased northern penetration and residence time of warm, saline Atlantic waters which drives warming in the Norwegian and Barents (NorBar) Seas (Polyakov et al., 2005; Wassmann et al., 2011). As well as being hydrographically linked, the multitude of ontogenetic and seasonal migrations undertaken by biota between the Norwegian and Barents Seas (Yaragina and Dolgov, 2009) make them hard to disentangle from a fisheries management (ICES, 2015) and food-web perspective (Dommasnes et al., 2001), with the direct and indirect consequences of overfishing historically transcending ecoregion boundaries (Hamre, 1994).

Arctic species in the NorBar Seas, especially those which are ice-dependent, are predicted to be the most adversely impacted by rising temperatures (Kedra et al., 2015). Boreal species, such as Atlantic cod (*Gadus morhua*), have started to migrate north with rising temperatures (Drinkwater, 2009, 2011), whilst the distri-

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http://dx.doi.org/10.1016/j.ecolmodel.2017.07.002

butions of pelagic species, such as blue whiting (*Micromesistius poutassou*) (Hátún et al., 2009) and mackerel (*Scomber scombrus*) (Astthorsson et al., 2012), are expanding north and east, benefiting from warmer waters and the increased primary production associated with reduced seasonal ice cover (Loeng et al., 2005). The impact of these changes on the NorBar food-web are difficult to quantify with our current knowledge. To credibly forecast the potential impact of ocean warming on the NorBar food-web our focus must therefore be to increase our relatively limited quantitative understanding of the ecosystem.

The development of new and existing food-web models provides a means to evaluate the ecosystem-level consequences of ocean warming. A popular tool for exploring food-web dynamics is Ecopath with Ecosim (EwE). Within Ecopath the user constructs a mass-balanced snapshot of their ecosystem (Christensen et al., 1992), which is then used as a baseline to forward-project time-dynamic simulations in Ecosim (Christensen et al., 2014). To date, few Ecosim models employ the use of time series data for model calibration (Heymans et al., 2014) and even fewer include ocean temperature as an environmental driving force. Instead, existing EwE models of the NorBar Seas have focused on the impacts of fishing (Dommasnes et al., 2001) and the interactions between fisheries and marine mammals (Blanchard et al., 2002) using mass-balanced, uncalibrated ecosystem snapshots. However, recent studies have shown that, incorporating temperature as a driver in a food-web model can increase that model's capacity to reproduce observed trends and project the potential impact of ocean warming (Serpetti et al., under review).

The aim of this study is to therefore advance the fundamental and quantified understanding needed to generate projections of the impacts of future change in the NorBar Seas. We provide a quantitative insight into the interactions and drivers which governed past ecosystem dynamics using an updated, time series-calibrated version of the Dommasnes et al. (2001) NorBar EwE model. Through the incorporation of functional responses, we explore the historic role of temperature and how, when coupled with trophic dynamics, the food-web may behave under a series of projected temperature scenarios.

2. Materials and methods

2.1. Study area

The study area covers International Council for the Exploration of the Sea (ICES) areas I (Barents Sea) and II (Norwegian Sea and a small portion of the Barents Sea) north to approximately 81°N, as previously defined by Dommasnes et al. (2001) and encapsulates a surface area of approximately 3,116,000 km^2 (ICES area I ≈ 1,006,100 km^2; ICES area II ≈ 2,109,900 km^2) (Fig. 1).

2.2. Construction of a 1950 mass balance ecopath model

The NorBar model was constructed using the EwE v.6.5.1 software package. EwE, established in 1984 by Polovina (1984) and subsequently updated (Christensen and Pauly, 1992; Walters et al., 1997), was primarily developed to overcome the fisheries management issues associated with modelling species in isolation (Pauly et al., 2000). EwE has three main components: Ecopath, Ecosim and Ecospace (http://www.ecopath.org/) (Christensen and Walters, 2004). Ecopath was used to create a static mass-balanced snapshot of the trophically linked resources in the NorBar food-web and their interactions in 1950 (Christensen, 2013) (Supplemental information A).

The trophic structure of the model represents the principle organisms in the NorBar food-web: an updated version of the EwE trophic structure proposed by Dommasnes et al. (2001) and includes important commercial species such as cod, herring (*Clupea harengus*), haddock (*Melanogrammus aeglefinus*) and capelin (*Mallotus villosus*) as well as primary producers such as phytoplankton and top predators such as mammals and seabirds. In addition to these commercially important species, other abundant fish species include Polar cod (*Boreogadus saida*), mesoplangic fish, mackerel and blue whiting. More information regarding the ecology and importance of functional groups can be found in the model descriptions of Dommasnes et al. (2001) and Blanchard et al. (2002). Where the Dommasnes model had 30 functional groups, the model constructed in this study has 34 functional groups. Dependent on the ecological or commercial importance of a species, their inclusion in the model is either as a single species group or aggregated into groups with other species that occupy a similar ecological niche (Supplemental Table B1). This models structure predominantly diverts from the Dommasnes structure in the lower trophic levels, where groups have been re-adjusted and a microbial loop has been added. These changes address the assessments of recent studies which stress the high importance of lower trophic organisms, warranting a more detailed representation of these groups in the model design (Dalpadado et al., 2012; Kvile et al., 2016; Slagstad et al., 2011).

As species often undergo ontogenetic shifts in diet and habitat during their lifetime, being able to model different stages of species enables a better understanding of the changes in the ecosystem. Unfortunately, not enough information is available for all species however data for commercially important species tend to be of greater quality and quantity, affording us the opportunity to create data based stanzas for these groups only. Cod, herring, haddock and capelin, were split into two life history stages (stanzas), juveniles (immature) and adults (mature). Splitting groups enables us to acknowledge the ontogenetic differences between adults and juveniles within the model structure. Adults are more important to the fisheries and are thus subject to higher catches and fishing mortalities whilst juveniles tend to experience higher natural mortality, have different consumption rates, diets and predation pressures. Splitting these groups to capture ontogenetic differences brings the model closer to reality by permitting the dynamics of juveniles and adults to directly influence each other (Christensen et al., 2004) (Supplemental Table B2).

2.2.1. Ecopath parameterisation

The Ecopath model was parameterised using data from fisheries surveys, stock assessments, literature, FishBase (Froese and Pauly, 2017) and existing ecosystem models. The development of this model relied heavily upon data from ICES which records collective catches and assessments dating back to 1950 (http://ices.dk/marine-data). The main parameters required by Ecopath to construct a mass-balanced ecosystem model are biomass (*B*), productivity/biomass (*P/B*), consumption/biomass (*Q/B*) and ecotrophic efficiency (*EE*). Biomass estimates for single species groups were preferentially taken from recent stock surveys. For groups with multiple species, their biomasses were summed and then divided by the model area. Fishing fleets were incorporated into the model to account for the fisheries catch and effort in the NorBar Seas. Fleets were generalised into the four predominantly used gear types: pelagic gear, demersal trawl, shrimp trawl and other gear (whalers and sealers) (Dommasnes et al., 2001).

Diets for trophic groups in 1950 were constructed based on a qualitative understanding of who eats whom in the NorBar Seas (Bogstad et al., 2000; Planque et al., 2014), taking quantitative reference from previous NorBar models (Blanchard et al., 2002; Dommasnes et al., 2001). There is no bulk stomach data available for the NorBar ecosystem in 1950, therefore the diet matrix was compiled using reference data from existing NorBar models and