Modeling the impacts of ocean warming and acidification on marine fish and ecosystems in the Barents Sea

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Stefan Königstein
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(*Dr. rer. nat.*)

artec
Sustainability
Research Center

Universität Bremen

Prüfungsausschuss (thesis advisory committee)

Gutachter 1:

Prof. Dr. Hans-Otto Pörtner

Alfred–Wegener–Institut Helmholtz–Zentrum für Polar– und Meeresforschung, Bremerhaven / Fachbereich 2, Universität Bremen

Gutachter 2:

PD. Dr. Hauke Reuter

Leibniz–Zentrum für Marine Tropenforschung (ZMT), Bremen

Prüfer 1:

Prof. Dr. Matthias Wolff

Leibniz–Zentrum für Marine Tropenforschung (ZMT), Bremen / Fachbereich 2, Universität Bremen

Prüfer 2:

Prof. Dr. Stefan Gößling–Reisemann

Fachbereich 4, Fachgebiet Resiliente Energiesysteme, Universität Bremen

The dissertation was defended on May 22, 2017 at the University of Bremen.

Title picture: Watercolor painting found in a Youth Hostel in Stamsund (unknown artist), illustrating the cultural and socio–economic significance of Atlantic cod (*skrei*) for the Lofoten Islands and Northern Norway

GEFÖRDERT VOM

BIOACID
Biological Impacts of Ocean ACIDification

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und Forschung

Contents

**Papers have separate page numbering*

Zusammenfassung: Modellierende Analyse von Ozeanerwärmung und -versauerung und der Auswirkungen auf marine Ökosysteme und Ökosystemdienstleistungen

Produktivität und Dynamik der marinen Ökosysteme sind bekannterweise vom Klima beeinflusst. Zunehmend werden Auswirkungen des fortschreitenden globalen Klimawandels beobachtet, und für den weiteren Verlauf des 21. Jahrhunderts wird eine Intensivierung dieser Veränderungen in vielen Ozeanregionen erwartet. Unter kontinuierlich hohen anthropogenen Treibhausgasemissionen werden Ozeanerwärmung, Ozeanversauerung und Sauerstoffmangel zunehmend die marinen Ökosysteme verändern. Während diese Umweltfaktoren direkt organismische Prozesse in marinen Lebewesen beeinflussen, spielen auch indirekte Effekte durch biotische Wechselwirkungen eine entscheidende Rolle. Die menschlichen Gesellschaften sind in vieler Hinsicht abhängig von den Ozeanen und haben nur begrenzte Anpassungsmöglichkeiten an die zu erwartenden Veränderungen in den genutzten Ökosystemleistungen.

Ein integriertes Verständnis der marinen Systeme und deren menschlicher Nutzung ist daher notwendig, um die kommenden Veränderungen zu verstehen. Dies wird zunehmend von neueren ökosystembasierten und integrierten Managementansätzen verfolgt. Die Mechanismen und Unsicherheiten der künftigen Auswirkungen des Klimawandels und die Wechselwirkungen mit dem zunehmenden anthropogenen Druck auf marine Systeme müssen verstanden und eingebunden werden. Ökologische Modelle sind wichtige Werkzeuge, um diese Integration von Daten und Prozessen zu ermöglichen, da sie experimentelle Daten und Beobachtungen in Kontext setzen können und es uns ermöglichen, über einfache Extrapolationen zukünftiger Zustände und Erfahrungen hinauszugehen und ein Verständnis für die zukünftigen Veränderungen der marinen Ökosysteme zu schaffen. Während eine Vielzahl von Modellierungsansätzen zur Beantwortung spezifischer ökologischer Fragen zur Verfügung steht, gibt es erst sehr wenige Beispiele für eine erfolgreiche quantitative Integration über verschiedene Hierarchieebenen und unterschiedliche Arten von Daten und Wissen.

Die vorliegende Arbeit beschäftigt sich mit einer Fallstudie aus der Barentssee, einem Randmeer des Arktischen Ozeans, das zu den Meeresregionen gehört, in denen die frühesten Auswirkungen von Ozeanerwärmung und –versauerung bereits beobachtet bzw. erwartet werden. Diese Region bietet die Möglichkeit für eine integrative Betrachtung der Auswirkungen dieser Treiber auf marine Ökosysteme und die Bereitstellung von Ökosystemleistungen.

Die Arbeit wurde auf einer gründlichen allgemeinen Analyse der verfügbaren Ansätze zur Modellierung der Auswirkungen des Klimawandels auf marine Fischpopulationen aufgebaut (Paper 1). Diese wertet die Fähigkeiten der bestehenden Modellierungsansätze im Lichte der bisherigen

Anwendungen und jüngsten experimentellen Ergebnisse und Beobachtungen aus, und identifiziert Prozesse, die besser integriert werden müssen.

Auf der Grundlage der Beteiligung von gesellschaftlichen Akteuren, durch persönliche Interviews und zwei Workshops in Norwegen, wurde ein ökologisches Modell zur Untersuchung der spezifischen Fragen in der Barentssee-Region entworfen (Paper 2). Dadurch konnten die Interessen und das Erfahrungswissen der Akteure in die Modellstruktur integriert und potenzielle Anpassungsoptionen für die Nutzergruppen identifiziert werden.

Als eine spezifische wissenschaftliche Frage von hoher Wichtigkeit und Ungewissheit wurden die möglichen Auswirkungen der Ozeanversauerung auf die Nachwuchsrekrutierung der Fischbestände identifiziert. Zur Untersuchung dieses Aspekts wurde ein Modell entwickelt, das die experimentell quantifizierten Effekte unterschiedlicher Temperaturen und pH-Werte auf Eier und Larven des Atlantischen Kabeljaus einbindet (Paper 3), und einen neuartigen Ansatz zur Integration empirischer Daten in Projektionen der Bestandsrekrutierung von Meeresfischen darstellt.

Schließlich wurde ein integratives Nahrungsnetzmodell der Barentssee entwickelt, das auf der in der Arbeit mit den Akteuren entwickelten Struktur und einem prozessbasierten wissenschaftlichen Verständnis basiert. Das Modell wurde mit empirischen Daten und Schätzungen von organismischen Prozessraten parametrisiert, um die bekannten dynamischen Schwankungen im Nahrungsnetz der Barentssee zu simulieren, und potenzielle Verschiebungen unter Ozeanerwärmung und Versauerung zu erforschen (Paper 4).

In der anschließenden Diskussion werden die Artikel zusammengefasst und ihre Beziehung zueinander verdeutlicht, und die Implikationen für Nutzergruppen und mögliche gesellschaftliche Anpassungsoptionen werden hervorgehoben. Auswirkungen auf die Fischerei sowie kulturelle Ökosystemleistungen in den Bereichen Bildung und Erholung, damit verbundene mögliche Anpassungsoptionen für Akteursgruppen, und Interaktionen mit anderen Nutzungsarten und erwarteten Veränderungen unter Klimawandel werden charakterisiert. Die eingeschränkten Anpassungsmöglichkeiten einiger Nutzergruppen deuten darauf hin, dass diese Akteure in ökosystembasierten Governanceprozessen in der Region stärker berücksichtigt werden sollten.

Die vorliegende Studie veranschaulicht damit die Möglichkeiten, Experimente, Beobachtungen und das Wissen von gesellschaftlichen Akteuren in eine integrative Bewertung der Klimawandelauswirkungen auf die Meeresökosysteme einzubinden. Auf der Grundlage der prozessbasierten Modellierung und der Beteiligung der Akteure kann das Verständnis der Klimawandelauswirkungen in den marinen Ökosystemen verbessert werden. Von großer Bedeutung sind verbesserte interdisziplinäre Zusammenarbeit und Kommunikation, um eine Gesamt-Systemperspektive voranzubringen, in verschiedene Beschreibungsskalen und Wissensarten verbunden werden – eine Aufgabe, zu der zielgerichtet gestaltete ökologische Modelle wesentlich beitragen können.

Summary

Marine ecosystems are known to be climate–dependent, and impacts from progressing global climate change are increasingly observed and anticipated to intensify in the course of the 21st century. Under continuously high anthropogenic greenhouse gas emissions, drivers such as ocean warming, ocean acidification, and deoxygenation will increasingly affect marine ecosystems and the provision of marine ecosystem services to human societies. Environmental drivers affect organismal processes directly, but also have indirect effects through biotic interactions. Human societies are dependent on the ecosystem services provided by the oceans, and have limited adaptive capacities to changes in ecosystem service provision.

An integrated evaluation of marine–human systems is thus necessary to understand coming changes, and is increasingly pursued by recent ecosystem–based and integrated assessment and management approaches. The uncertainty of future climate change impacts and the interactions with the increasing anthropogenic pressures on marine systems need to be addressed. Ecological models are important tools to provide this integration of data and processes, as they can put experimental and observational data into context, and enable us to move beyond simple extrapolations of future states and experiences, creating an understanding of the changes in marine ecosystems anticipated in the future. While a wide variety of modeling approaches is available to answer specific ecological questions, a quantitative integration over different hierarchical levels, and different types of data and knowledge, is rarely achieved.

The presented thesis revolves around a case study from the Barents Sea, which is among the marine regions with the earliest impacts of ocean acidification and warming expected and already observed, providing an integrative view of the impacts of these drivers on marine ecosystems and the provision of ecosystem services in the focus region.

The work was built upon a thorough general analysis of available modeling approaches for modeling climate change impacts on marine fish populations (Paper 1). This analysis assessed capacities of the existing modeling approaches and recent applications, and revealed processes which need to be incorporated better in the light of recent experimental and observational results.

A modeling framework to address the specific questions in the Barents Sea region was developed based on participation of stakeholders gained during personal interviews and two workshops (Paper 2). This served to incorporate their concerns and knowledge into the model structure and identify potential adaptation options for the stakeholder groups.

To address one specific scientific question of high importance and uncertainty, the anticipated impacts on fish stock recruitment, an early life stage model was developed which incorporates the experimentally quantified effects of ocean acidification and warming on Atlantic cod eggs and

larvae (Paper 3). This model offers a new approach to integrating empirical data on environmental and food-web drivers into recruitment projections of marine fish.

Finally, an integrative food–web model based on the structure developed in the stakeholder work and on current process–based understanding was parameterized with empirical data and estimates of organismal rates, to simulate the dynamic fluctuations in the Barents Sea food web and explore potential shifts in composition and dynamics under ocean warming and ocean acidification (Paper 4).

In the thesis discussion, the papers are summarized and put into context, and the implications for the user groups in the region and possible societal adaptation options to the projected changes are highlighted. Impacts on fisheries, cultural and recreational ecosystem services, associated adaptation options for stakeholder groups, and interactions with other uses of the ocean system and expected changes under climate change are delineated. To advance ecosystem–based governance in the area, the limitations in adaptation options of some user groups point to the need to better consider these groups in decisions and regulations concerning fisheries and marine areas.

The Barents Sea study thus exemplifies the possibilities to integrate experiments, observations and stakeholder input into integrative assessments of marine ecosystems under climate change. Based on the insights gained from process–based modelling and stakeholder participation, it is described how understanding and projections of climate change impacts on marine–human systems can be advanced, pointing out the importance of improved interdisciplinary cooperation and communication and an integrative perspective to link across scales and subsystems – tasks to which purposefully designed models can contribute substantially.

Articles included in this dissertation and author contributions

1. **Modeling climate change impacts on marine fish populations: Process-based integration of ocean warming, acidification and other environmental drivers.** Stefan Koenigstein, Felix C. Mark, Stefan Gößling-Reisemann, Hauke Reuter, Hans-Otto Pörtner (2016). *Fish and Fisheries* 17, 4.

   SK conceived and wrote the major part of the manuscript (90–95%). FM contributed text to the section 'From drivers to processes‘, which formed the basis of the ‚organism‘ subsection and was incorporated into the ‚population' and ‚community' subsections. HR guided the general conceptualization of the paper. All authors, as well as three international colleagues and three anonymous reviewers, contributed comments and suggestions to the first and/or revised draft.

* In this published version of the dissertation, the original published version of the article has been replaced by the self-archived version (accepted manuscript) due to copyright reasons *

2. **Stakeholder-Informed Ecosystem Modeling of Ocean Warming and Acidification Impacts in the Barents Sea Region**. Stefan Koenigstein, Matthias Ruth, and Stefan Gößling-Reisemann (2016). *Frontiers in Marine Science* 3, 93.

   SK conceived and drafted the manuscript. SGR and MR contributed comments, additions and corrections to the manuscript and reviewed the final version.

3. **Forecasting future recruitment success for Atlantic cod in the warming and acidifying Barents Sea**. Stefan Koenigstein, Flemming T. Dahlke, Martina H. Stiasny, Daniela Storch, Catriona Clemmesen & Hans-Otto Pörtner. (2017; submitted to *Global Change Biology*)

   SK conceived and drafted the manuscript. CC, DS, MS and FD contributed experimental data and descriptions of the experimental treatments, integrated into the supplement of the paper ('Experimental setups'). HOP, SGR and HR provided suggestions during the development of the model. All authors provided comments and suggestions on the final manuscript.

4. **Impacts of ocean warming and acidification on marine food web dynamics in the Barents Sea**. Stefan Koenigstein et al. (manuscript draft)

   SK conceived and drafted the manuscript. Hans-Otto Pörtner provided comments and suggestions on the draft. The model development and evaluation was supervised and supported with suggestions by Stefan Gößling-Reisemann.

Supplement: Stefan Koenigstein & Stefan Goessling-Reisemann (2014): Ocean acidification and warming in the Norwegian and Barents Seas: impacts on marine ecosystems and human uses. Stakeholder consultation report.

This report summarizes the statements of the stakeholders from interviews and the first workshop, and background information about the project, aimed at stakeholders and the general public. It was published open–access on the European science platform Zenodo.
http://dx.doi.org/10.5281/zenodo.8317

SK conceived and wrote the report. SGR contributed suggestions and corrections.

Related work

Within the project work in the project BIOACID phases 2 and 3, two stakeholder workshops were conducted which, together with the interview series, formed the basis for the stakeholder work (Paper 2). The first workshop was held in Bergen on October 17th, 2013. The second workshop was conducted in Tromsø on June 11th and 12th, 2015.

The topic of sustainable use of marine systems and ecosystem services by societal groups has been developed into a the concept for a classroom game which has been selected as one of the winners within the competition "Hochschulwettbewerb Wissenschaftsjahr 2016/17 Meere und Ozeane: Zeigt Eure Forschung!“. The concept "Die Ozean GmbH - Das Spiel um die Meere“ is funded with EUR 10.000,- by BMBF for the period 09/2016–08/2017. http://www.hochschulwettbewerb.net/ozean-gmbh/

Related publications

Other related publications in the preparation period of this dissertation (not part of this dissertation):

Reuter, H. & Koenigstein, S. (2017). Computermodelle als Werkzeuge der Meeresbiologen. In *Faszination Meeresforschung*, 2. Auflage. Eds. G. Hempel, K. Bischof and W. Hagen. Springer Berlin/Heidelberg.

Koenigstein, S. & Gößling-Reisemann, S. (2014). Ocean acidification and warming in the Norwegian and Barents Seas: impacts on marine ecosystems and human uses. Stakeholder consultation report. University of Bremen, artec Sustainability Research Center doi:10.5281/zenodo.8317.

Cohen-Rengifo, M., Crafton, R.E., Hassenrück, C., Jankowska, E., Koenigstein, S., Sandersfeld, T., Schmid, M.S., Schmidt, M., Simpson, R., & Sheward, R.M. (2013). Marine Ecosystems and Climate Change. In A. Dummermuth, & K. Grosfeld (Eds.), Climate change in the marine realm: an international summer school in the framework of the European Campus of Excellence. Reports on polar and marine research, 662. Alfred Wegener Institute for Polar and Marine Research, Bremerhaven.

THESIS INTRODUCTION

Climate change impacts on marine organisms and ecosystems

The biological dynamics and productivity of marine ecosystems is driven by environmental conditions. Under progressing global climate change, changes in ecological dynamics of marine systems have been observed in recent decades, and are expected to further progress in the course of the 21st century. Under continuously high anthropogenic greenhouse gas emissions, drivers such as ocean warming, ocean acidification (decreasing pH values), and deoxygenation (insufficient oxygen levels) are anticipated to affect marine organisms, drive changes in marine ecosystem structure and dynamics, and affect the provision of marine ecosystem services to human societies (Hoegh-Guldberg et al. 2014; Pörtner et al. 2014; Gattuso et al. 2015). Ocean warming is already observed to lead to poleward shifts in the spatial distribution of marine organisms, causing local changes in the composition of marine ecological communities, with regional extinctions of organisms by exceeding the thermal tolerance limits (Poloczanska et al. 2013). Ocean acidification, the decrease in water pH via increasing solution of atmospheric CO_2, is anticipated to impact different planktonic organism groups in marine ecosystems (Kroeker et al. 2013), and potentially affect survival and performance of early life stages of economically important fish stocks under future ocean pH values (Cooley et al. 2009; Denman et al. 2011). Yet, considerable uncertainty compounds the analysis of ecosystem-level effects of multiple climate change drivers, and their interactions with anthropogenic impacts (Gattuso et al. 2015; Riebesell & Gattuso 2015).

A fundamental problem with predicting climate impacts on marine systems is that it is unclear to what extent future drivers can be extrapolated from empirically observed changes in ecosystems, as marine systems may be exposed to combinations of drivers that have not yet been observed, and thus extrapolations to unprecedented conditions are necessary (Jennings & Brander 2010). Direct environmental effects on marine organisms are modulated by species interactions in the food web, lead to indirect effects on other species, and changing dynamics of ecological communities (Kordas et al. 2011). Thus, investigation of climate change effects on marine ecosystems has to integrate the organism, population, and community levels (Doney et al. 2012; Sydeman et al. 2015). Ecological community structure and dynamics are primary determinants of the resilience of marine ecosystems to environmental perturbations (Frank et al. 2006; Hunsicker et al. 2011). Direct impacts on one element of the food web can trigger cascading effects, and lead to regime shifts and food web restructuring under climate change (Mangel & Levin 2005). Anthropogenic impacts, such as the extraction of biomass by fisheries, interact with and exacerbate the pressure by climate change on marine ecosystems (Brander 2012). It is thus necessary to explicitly integrate additive and synergistic effects of climate change drivers, building upon an understanding of potentially affected biological processes (Rijnsdorp et al. 2009; Pörtner & Peck 2010), including biotic interactions and feedbacks, combining different types of models, and integrating among different hierarchical levels (Blackford 2010; Metcalfe et al. 2012).

When changes in multiple environmental drivers exceed organismal capacities, e.g. for aerobic metabolism and acid-base regulation, lower growth and performance rates, and above a critical threshold, death ensues (Pörtner & Farrell 2008). As in situ data on the effects of different driver combinations on organism performance is often difficult to obtain, experimental data and physiological knowledge can help to quantify the combined critical thresholds of temperature, oxygen, pH and other environmental drivers on organismal tolerance and performance, providing a mechanistic link from the physical environment to feedbacks in species, community and ecosystem processes (Monaco & Helmuth 2011). This facilitates the extrapolation to future species survival under combinations of environmental drivers that have not yet been observed, development of early-warning signs for changes in marine ecosystems with socio-economic consequences, integration of experimental and observational data and details on potential bottlenecks in life-histories of species, thus providing important additional information for their sustainable management (Brander 2010; Pörtner & Peck 2010; Metcalfe et al. 2012).

Although climate change is global, regionally divergent changes in physical drivers will act on the oceans, and the responses and resilience will vary among oceanic regions, as the productivity and biodiversity of marine ecosystems is driven by the physical conditions and climatic patterns (Hoegh-Guldberg et al. 2014). Atmospheric drivers, ocean currents and sea–bottoms that shape the habitat for marine organisms differ among ocean regions and ecological provinces, leading to typical characteristics in terms of ecosystem structure and functioning (Longhurst 2007). A regional focus thus offers improved possibilities for studying marine system behavior and resilience, and enables comparison among systems (Salihoglu et al. 2013).

Consequences for human societies – ecological models as tools for improving understanding and management

The oceans are of primary socio-economic and cultural importance for human societies around the globe, providing a range of ecosystem services, such as food provision from fisheries and aquaculture, carbon uptake and climate regulation, bioremediation, nutrient cycling, or recreation and cultural services (Beaumont et al. 2007). Thus, a wide range of human uses and activities will be affected by climate change impacts on marine systems, while the most important ecosystem services used and the impacts exhibited by human societies differ among regions. For instance, coastal upwelling regions display the highest fisheries productivity, while coral reefs provide nursery habitat for fish, high biodiversity and opportunities for tourism (Allison & Bassett 2015).

Climate change and the associated ecological changes are thus a major challenge for the governance of marine systems (Perry et al. 2010; Charles 2012). However, economic and nutritional dependence on marine resources, and thus vulnerability towards climate change effects, differs strongly among countries (Allison et al. 2009). While societies have a range of options to adapt to changes in marine systems, these depend on economic, social and cultural conditions (Perry et al. 2011; Haynie & Pfeiffer 2012).

At the same time, climate change impacts on marine systems under human use have to be seen in the frame of anthropogenic impacts, such as the extraction of biomass by fisheries, as these can exacerbate the pressure by climate change on the ecosystem (Brander 2012). As a result of the growing recognition of the multi-faceted interactions of marine ecosystems with societal uses, increased efforts are undertaken worldwide to establish ecosystem–based management approaches of the ocean and its resources (Browman & Stergiou 2005; Katsanevakis et al. 2011; Long et al. 2015). A current lack of structural and dynamic understanding of marine systems, especially with regard to non–linear behavior, e.g. tipping points, regime shifts and multiple equilibria, is among the foremost challenges for science–based governance and societal adaptation (Perry et al. 2011; Rice et al. 2014). These can also arise from interactions with human exploitation. For instance, slow societal adaptation to fast environmental changes can lead to overuse and collapse of living marine resources, as has happened e.g. to the Gulf of Maine cod and the Norwegian herring stock (Hannesson & Herrick 2006; Pershing et al. 2015).

For the assessment and management of marine ecosystems and their use by societies, ecological simulation models are important tools (Plaganyi 2007; Espinoza-Tenorio et al. 2012). Yet, to model the impacts of climate change and ocean acidification, which affect a wide range of organisms and organismal processes, as well as their trophic interactions and interactions with anthropogenic drivers such as overfishing and pollution, is a complex task that requires the development of advanced models, integrating effects on different processes in various organisms, and incorporating experimental results (Blackford 2010; Le Quesne & Pinnegar 2012). The reliability and utility of the present, highly simplified models, e.g. classical fisheries models, stationary species distribution models and statistical correlations, for these extrapolations under a future climate has thus increasingly been called into question (Brander et al. 2013; Rose & Allen 2013; Woodin et al. 2013).

Recent approaches have extended the integration of biological processes and their sensitivities into the established models, e.g. incorporating organismal sensitivities and biotic interactions into species distribution models (Cheung et al. 2011; Fernandes et al., 2013), and habitat suitability and oceanographic drivers into food web models (Christensen et al. 2014; de Mutsert et al., 2016). On the other hand, a range of complex 'end-to-end’ models, which aim to incorporate processes on all levels of description from physical drivers to marine ecosystems and human uses, have been in development for the last approx. 15 years (Travers et al. 2007; Fulton 2010; Rose et al. 2010; Moloney et al. 2011). These highly complex models demand large–scale research efforts, and at the present stage still suffer from problems with parameterization, calibration, validation and assessment of uncertainty, which restricts their application in management and policy advice (Rose 2012; Voinov & Shugart 2013; Evans et al. 2015).

For increasing whole–system understanding and deriving management advice based on environmental dynamics, purposefully simplified models of intermediate complexity provide a promising alternative (Allen & Fulton 2010; Hannah et al. 2010; Plaganyi et al. 2012), as they can incorporate management–relevant system indicators (e.g. keystone species, biodiversity indices, energy flux parameters) and be used to identify possible regime shifts and tipping points under changing environmental drivers (Plaganyi et al. 2014). In any case, the variety of different aspects to be considered in these models require them to be based on interdisciplinary research efforts (Griffith & Fulton 2014).

A regional case study in the fast–changing Barents Sea

Arctic regions are a hotspot of climate change and ocean acidification (Denman et al. 2011; Hoegh-Guldberg et al. 2014). Marine ecosystems in arctic and subarctic areas are being affected by warming of waters and decreasing sea ice extent (Darnis et al. 2012). Under ocean warming and diminishing sea ice, Arctic food webs are progressively changing towards boreal communities, with pronounced changes in subarctic fish stocks and impacts on fisheries expected (Hollowed & Sundby 2014; Kortsch et al. 2015). Ocean acidification is anticipated to additionally affect the productivity of lower trophic levels and some fish stocks, and thus alter food web structure and energy transfer in Arctic regions (AMAP 2013).

The Barents Sea is a subarctic shelf sea with high biological productivity, a habitat for several important pelagic and demersal fish stocks, such as Atlantic cod, herring and capelin (Wassmann et al. 2006; Loeng & Drinkwater 2007; Olsen et al. 2010). The Barents Sea has experienced substantial warming in the last decades and is projected to experience further warming in the course of this century, leading to shifts in ecosystem functioning and community composition, spatial distribution, productivity and biomass of fish stocks, and thus, socio-economic impacts on human societies in the region (Stenevik & Sundby 2007; Johannesen et al. 2012; Fossheim et al. 2015). The Barents Sea thus represents an ideal study region for the impact of climate variability and change on marine living resources (Michalsen et al. 2013; Haug et al. 2017).

Fisheries represent the second most important economic sector after the offshore oil industry in Norway, and are managed on a national level based on scientific advice and on agreements with the

European Union, Russia and other nations (Gullestad et al. 2014; Jentoft & Mikalsen 2014). Norway is actively pursuing the establishment of the ecosystem–based management approach, and the potential impacts of climate change, ocean acidification, and concurrent changes in anthropogenic drivers on marine ecosystems expected in the course of this century are of a high interest for long–term adaptive planning. This has been manifested in ecosystem–based management plans for the Barents Sea and Lofoten area and other marine areas (Hoel et al. 2009; Harsem & Hoel 2012; Hoel & Olsen 2012) and a sustainability approach to management of marine fisheries (Gullestad et al. 2014; Sainsbury et al. 2014). Estimates of socio–economic impacts of ocean acidification in Norway are highly uncertain and hampered by the incomplete understanding of affected ecological processes (Armstrong et al. 2012, Haug et al. 2017). An improved understanding of climate change and ocean acidification impacts would thus be highly valuable for governance mechanisms for marine areas and resources in Norway.

Aims of the thesis

Derived from the state of the science and rationale described in the introduction, the aims of this dissertation were to

- Identify the potential and limitations of the presently available approaches for modeling climate change and ocean acidification impacts on marine fish and ecosystems
- Model the impacts of the drivers warming and acidification on Atlantic cod in the Barents Sea, incorporating experimental data and the current knowledge about relevant physiological and ecological processes
- Determine the expected impacts of potential changes in the ecosystem on the provision of marine ecosystem services and the significance for societal groups in the Barents Sea region
- Thus, identifying research directions for an improved integrated understanding of climate change and ocean acidification impacts on marine ecosystems and marine–human systems

Paper 1: Modeling climate change impacts on marine fish populations: Process-based integration of ocean warming, acidification and other environmental drivers

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Modelling climate change impacts on marine fish populations: Process-based integration of ocean warming, acidification, and other environmental drivers

Stefan Koenigstein[1,2], Felix C. Mark[2], Stefan Gößling-Reisemann[1,3], Hauke Reuter[4,5], Hans-Otto Pörtner[2,5]

[1] Sustainability Research Center (artec), University of Bremen; [2] Integrative Ecophysiology section, Alfred Wegener Institute (AWI) Helmholtz Centre for Polar and Marine Research; [3] Department of Resilient Energy Systems, University of Bremen; [4] Dept. of Theoretical Ecology and Modelling, Leibniz Center for Tropical Marine Ecology; [5] Faculty of Biology and Chemistry, University of Bremen

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Correspondence:
Stefan Koenigstein, University of Bremen, artec Sustainability Research Center, Enrique-Schmidt-Str. 7, D-28359 Bremen, Germany. E-mail: koenigstein@uni-bremen.de

Abstract

Global climate change affects marine fish through drivers such as warming, acidification and oxygen depletion, causing changes in marine ecosystems and socio-economic impacts. Experimental and observational results inform about anticipated effects of different drivers, but linking between these results and ecosystem level changes requires quantitative integration of physiological and ecological processes into models to advance research and inform management.

We give an overview of important physiological and ecological processes affected by environmental drivers. We then provide a review of available modelling approaches for marine fish, analysing their capacities for process-based integration of environmental drivers. Building on this, we propose approaches to advance important research questions.

Examples of integration of environmental drivers exist for each model class. Recent extensions of modelling frameworks have a greater potential for including detailed mechanisms to advance model projections. Experimental results on energy allocation, behaviour and physiological limitations will advance the understanding of organism-level trade-offs and thresholds in

response to multiple drivers. More explicit representation of life cycles and biological traits can improve description of population dynamics and adaptation, and data on food web topology and feeding interactions help detail the conditions for possible regime shifts. Identification of relevant processes will benefit the coupling of different models to investigate spatial-temporal changes in stock productivity and responses of social-ecological systems.

Thus, a more process-informed foundation for models will promote the integration of experimental and observational results and increase the potential for model-based extrapolations into a future under changing environmental conditions.

Key words: ecosystem modelling, environmental drivers, climate change, ocean acidification, fish ecophysiology, process understanding

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Introduction

The productivity of marine fish stocks is influenced by a multitude of environmental factors. In the near future, many stocks will be increasingly affected by climate change including global ocean warming, ocean acidification, oxygen loss and other long-term and more regional environmental changes such as salinity, nutrient redistribution or eutrophication and pollution (Roessig et al., 2005, Cochrane et al., 2009, Hollowed et al., 2013, Pörtner et al., 2014). Environmental drivers affect marine ecosystems, marine organisms and fish stocks through direct impacts on individual physiology and life history, and/or indirectly via changes in primary productivity or ecological (mainly food web) interactions, spatial configuration of habitats, or planktonic larval transport (Doney et al., 2012, Metcalfe et al., 2012).

Responses to these environmental drivers, e.g. through changes in productivity and spatial distribution will co-determine the future development of fish stocks and fisheries (Perry et al., 2005, Lehodey et al., 2006). For instance, periodic changes between anchovy and sardine regimes in the North Pacific can be explained by different optimum growth temperatures (Takasuka et al., 2007, Lindegren and Checkley, 2013), and warming temperatures have contributed to recently high stock levels in Barents Sea cod (Ottersen et al., 2006, Kjesbu et al., 2014). In tropical and upwelling areas, and due to the general warming trend, low oxygen availability can set physiological limits to fish stocks (Ekau et al., 2010, Stramma et al., 2010). Across marine ecosystems, ocean acidification has emerged as an additional threat for marine fish populations e.g. through impacts on larval behaviour and associated mortality as seen in coral reef fish (Munday et al., 2010).

Climate change impacts different hierarchical levels of biological organization, from individual physiology and population level changes to community and ecosystem shifts (Le Quesne and Pinnegar, 2012). Many of the direct effects on organisms can only be observed and investigated at the cellular or individual level, and to assess their overall stock effects, they have to be scaled up to population and community level, thus integrating processes on the different levels (Rijnsdorp et al., 2009, Pörtner and Peck, 2010). Physiological processes link the physical environment to individual-level responses and thus help to gain principal mechanism-based understanding of climate change impacts on populations and ecosystems (Pörtner and Farrell, 2008, Denny and Helmuth, 2009, Chown et al., 2010).

To anticipate climate change effects in marine ecosystems, ecological simulation models allow for the inclusion of processes on different hierarchical levels of biological organization, and an analysis of their mutual feedbacks. Models may integrate the impacts of multiple drivers on fish from the physiological to the community and ecosystem levels, and to analyse stock dynamics under different scenarios of environmental change. To improve model projections and test hypotheses about environmental determinants for fish stocks, it is necessary to investigate mechanisms underlying stock dynamics and distribution (Hollowed et al., 2009, Hare, 2014). As empirical or statistical descriptions are based on the observed range of the combined underlying factors, historical data and identified patterns for fish stocks may fail to resolve uncertainties of projections if the underlying processes, e.g. life history, energetics, and recruitment patterns, change and causalities are not understood (Mangel and Levin, 2005).

A more mechanistic formulation of models could be based on the explicit consideration of physiological and ecological processes that determine observed phenomena (Baskett, 2012, Metcalfe et al., 2012). This could increase the projection capacities of models under new combinations of environmental drivers (Jørgensen et al., 2012, Russell et al., 2012). These models could make better use of results from advanced experiments on multiple drivers (Denman et al., 2011, Dupont and Pörtner, 2013) and be tested with observations on stock dynamics in already changing environments, facilitating development of early-warning signs for productivity changes in fish stocks (Brander, 2010). In the light of recently increased efforts to establish ecosystem-based fisheries management approaches and the growing importance of societal climate adaptation, an integration of knowledge about ecological and physiological processes seems necessary more than ever before (Cury et al., 2008, Miller et al., 2010, Persson et al., 2014).

Although models for use in climate change projections and ecosystem-based fisheries management have been reviewed for general strengths and weaknesses (Keyl and Wolff, 2007, Plagányi, 2007, Stock et al., 2011, Hollowed et al., 2012) and some approaches for better integration of physiological data and mechanistic concepts have been proposed (Metcalfe et al., 2012, Persson et al., 2014), a systematic inspection of possible directions for advancement is currently lacking. An up-to-date and comprehensive review of modelling approaches for marine fish and options for direct integration of environmental effects therefore seems timely and may facilitate better interdisciplinary exchange and well-coordinated progress in this fast-developing field.

In this article, we will provide an overview of potentially relevant physiological and ecological processes to understand climate change impacts on fish stocks (section two). We then review available modelling approaches and present examples for marine fish species, analysing them for their potential and limitations to incorporate environmental impacts on the identified processes (section three). In the closing section, we exemplify the challenges and potential for the advancement of models by addressing five key questions in regard to climate change impacts on marine fish, in the context of changes in their ecosystems and in human resource uses.

From drivers to processes: Physiological and ecological processes affected by environmental drivers

Physiological processes act from the cellular to the organism level, and can be used to explain direct effects of environmental drivers and individual tolerance towards changes. They affect and are affected by higher levels of biological organization, such as the population or community and ecosystem interactions, where ecological processes can serve to extrapolate the impacts of climate change, ocean acidification and other drivers (Pörtner and Peck, 2010, Monaco and Helmuth, 2011, Gaylord et al., 2015). As a framework for structuring our analysis of modelling approaches, we will consider physiological and ecological key processes, organized by the level of biological organization on which they act primarily (Fig. 1). This is intended to help the reader identify potentially relevant processes as the basis for choosing an appropriate model.

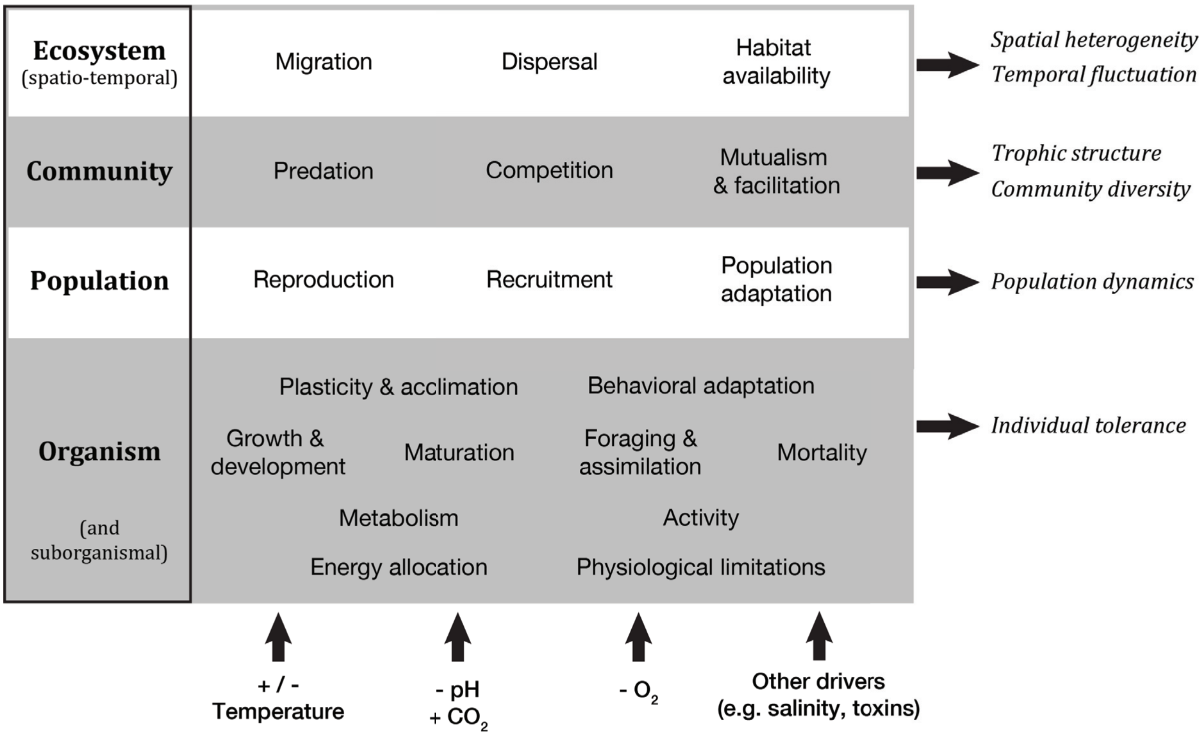

Figure 1: Overview over physiological and ecological processes, as a framework to assess potential effects of environmental drivers on fish stocks. Processes are separated among different levels of biological hierarchy, from organism and suborganismal (cell and tissue or organ) processes to population, community, and spatio-temporal ecosystem processes. Environmental drivers such as warming, acidification, hypoxia and others (bottom) act directly on organisms and indirectly affect processes on higher levels, shaping the characteristics resulting at each level of description (right). Higher-level processes are aggregate descriptions of processes on lower levels, and this framework is proposed to represent an easily observable and quantifiable description, but alternative descriptions are possible (e.g., recruitment can be described as the product of growth, foraging and mortality of early life stages, and evolution is the product of individual plasticity, acclimation and adaptations, and population adaptation). For details on processes and effects, see section two.

Organism level processes, and suborganismal processes interacting on the individual level

Environmental drivers can affect a range of processes at the organismal level, and individual tolerance of fish is co-defined by suborganismal (i.e. tissue and cellular) level capacities and processes (cf. Fig. 1). Basic organism processes such as routine activity, growth and reproduction are sustained only in a limited range of temperatures, indicating thermal specialization. Through its effects on metabolic processes in ectothermic animals, temperature modifies development and growth rates. Elevated temperatures entail increased metabolic rates and energy turnover (Clarke and Johnston, 1999). However, when a critical temperature is reached, aerobic physiological performance fails to increase further or is even reduced, due to limited oxygen availability and capacities of respiratory, ventilatory, and cardiovascular systems. Sustained performance relies on aerobically produced metabolic energy, thus oxygen availability sets general limits to fish metabolism and growth (Pauly, 2010). Organismal capacities vary between behavioural types and habitat adaptations, e.g. active pelagic swimmers *vs.* benthic ambush predators, eurythermal *vs.* stenothermal habitats (Pörtner et al., 2004). Individual fish behaviour thus has consequences for population, community and ecosystem processes, and behavioural adaptation may also buffer impacts of environmental drivers on individuals and populations (Mittelbach et al., 2014).

Limitations to an animal's performance and tolerance to unfavourable environmental conditions will eventually become visible at the whole animal level, but are co-defined at the cellular level. While temperature may be the most important factor in setting these limits (Pörtner and Peck, 2010), further environmental factors such as ocean acidification or hypoxia (low O_2 levels) can modify aerobic capacity and temperature limits (Pörtner, 2010, 2012). Hypoxia has for instance been shown to reduce food uptake and limit metabolic and growth rates and development of early life stages in fish (Ekau et al., 2010). More recently, ocean acidification (declining oceanic pH and elevated CO_2 levels) has been identified as an additional driver, underscoring the necessity to integrate physiological responses and experimental results on interactions among drivers into models and projections (Fabry et al., 2008, Riebesell and Gattuso, 2015).

High seawater CO_2 levels increase CO_2 diffusion into the bloodstream of marine fish, which is generally compensated within hours to days by an active accumulation of bicarbonate (HCO_3^-) to maintain the extracellular pH required for efficient cellular functioning (e.g. Heisler, 1984, Brauner and Baker, 2009, Melzner et al., 2009b). The increased energy demand of compensatory metabolic processes such as acid-base regulation (Deigweiher et al., 2008, Melzner et al., 2009a) can entail shifts in the animal's energy budget, and lead to acclimatory responses in various physiological processes. Consequently, ocean acidification will act in addition to, or synergistically with, ocean warming, leading to decreased upper critical temperatures (Pörtner and Peck, 2010). Recent studies have demonstrated a considerable chronic impact of ocean acidification, e.g. on cellular metabolism (Strobel et al., 2012, Strobel et al., 2013), metabolic rate (Michaelidis et al., 2007, Enzor et al., 2013), respiratory performance (Couturier et al., 2013) and aerobic scope (Rummer et al., 2013).

Thus, consideration of the physiological processes involved in individual responses can serve to integrate the effects of multiple drivers (increasing temperature, acidification, hypoxia) and to assess the combined effect on the organism and the energetic cost of individual acclimation.

Population level processes: recruitment, reproduction, population adaptation

Processes at the population level, such as recruitment, determine the dynamics of fish stocks and can be strongly influenced by the physical environment (Rothschild et al., 1989, Myers, 1998, Ottersen et al., 2013, Szuwalski et al., 2014). Increasing temperatures lead to faster development of fish larval stages, earlier maturation at smaller sizes and reduced *per-capita* fecundity, affecting population productivity (Rijnsdorp et al., 2009, Baudron et al., 2014).

Embryos and larval stages do not yet express the fully developed capacities for acid-base regulation of juvenile and adult fish. Thus, additional stressors such as ocean acidification, hypoxia or pollution can lead to increased mortality and impaired growth performance (Franke and Clemmesen, 2011, Baumann et al., 2012, Frommel et al., 2012, Nikinmaa, 2013). Increased temperature and ocean acidification can also affect reproductive output and gamete survival, impacting reproduction of the population (Inaba et al., 2003, Frommel et al., 2010, Miller et al., 2015). Thus, egg and larval stages are potential bottlenecks in life history and in adaptation of fish to multiple environmental drivers (Melzner et al., 2009b, Rijnsdorp et al., 2009).

Whether adaptation of fish populations can keep pace with future changes in environmental conditions is an important open research question (Rijnsdorp et al., 2009). Population adaptation can happen within the range of phenotypic plasticity, e.g. through behavioural adaptation, developmental and trans-generational acclimation (Crozier and Hutchings, 2014), or by evolution of adaptive genetic divergence (Nielsen et al., 2009, Reusch, 2014). While genomic markers have been linked to ecological differentiation e.g. in Atlantic cod (Hemmer-Hansen et al., 2013), most available studies have found plastic responses, and studies reporting trans-generational plasticity under conditions of climate change are relatively scarce for large and long-lived fish species (Crozier and Hutchings, 2014, Munday, 2014). However, some laboratory and in situ experiments demonstrate that heritable effects can significantly enhance tolerance to environmental drivers and involve metabolic readjustments (Donelson and Munday, 2012, Miller et al., 2012, Shama et al., 2014). Effects of climate change at the population level may also act synergistically with impacts of human exploitation, as fishing pressure can lead to a reduction in size at maturation (Law, 2000, Jørgensen et al., 2007) and to a higher sensitivity towards environmental fluctuations in exploited stocks (Perry et al., 2010).

Community level processes: predation, competition, mutualism & facilitation

Direct environmental effects on fish are influenced by species interactions in the food web, and can lead to indirect effects on other species (e.g. Link et al., 2009, Engelhard et al., 2014, Bogstad et al., 2015). The response of a marine ecosystem to changes of one stock depends on the type of trophic control, i.e. bottom-up or top-down (Frank et al., 2006), and the characteristics of predator-prey interactions are a primary determinant of marine community resilience (Hunsicker et al., 2011). Cascading effects triggered by direct impacts on one element of the food web may be especially relevant in top-down controlled systems (Frank et al., 2006), can lead to regime or phase shifts, and therefore have to be considered when discussing effects of climate change (Mangel and Levin, 2005, Link et al., 2009).

Changes in prey biomass and composition can influence the energy uptake for fish due to different energy content or size of food particles (Beaugrand et al., 2003, Beaugrand and Kirby, 2010). Regional changes in zooplankton communities are correlated to rising water temperatures and may facilitate range shifts of fish stocks, which follow the occurrence of their preferred prey (Brander, 2010, Dalpadado et al., 2012). Calcifying zooplankton species, e.g. pteropods, may be vulnerable to ocean acidification and warming (Lischka and Riebesell, 2012). Non-calcifying zooplankton, such as copepods, have displayed a reduced overall energy content under warming and acidification (Hildebrandt et al., 2014), and may also be impacted indirectly through reduced food quality of phytoplankton (Rossoll et al., 2012).

Changes in trophic interactions and energy transfer will be modulated by individual animal feeding behaviour. Behaviour and sensory systems of fish can be influenced by elevated CO_2 levels putatively through interaction with neuronal receptors (Briffa et al., 2012, Nilsson et al., 2012, Hamilton et al., 2014). Effects have been shown to occur in all life stages in laboratory and field experiments mostly of tropical reef fish (but see Jutfelt et al., 2013, Jutfelt and Hedgarde, 2013) and include impaired olfactory, visual and hearing abilities (Simpson et al., 2011, Leduc et al., 2013, Chung et al., 2014), reduced capacities for learning, homing and decision-making (Devine et al., 2012, Ferrari et al., 2012), and reduced or delayed behavioural responses towards predators (Ferrari et al., 2011, Munday et al., 2013a, Nagelkerken et al., 2015).

In sharks, warming and acidification can impair growth and hunting behaviour (Pistevos et al., 2015).

Thus, changes in planktonic community composition and predator-prey interactions point at probable changes in food composition for fish and in marine community dynamics. Other interactions, such as mutualism, facilitation or parasitism, may also be affected by changed occurrences and sensitivities of species, and influence the response at the community level.

Spatial ecosystem level processes: migration, dispersal, habitat availability

The spatial heterogeneity of marine habitats influences the range of environmental conditions experienced by individuals, and interacts with population and community processes (Ciannelli et al., 2008). Changes in distribution ranges of marine fish species under climate change, are based on the spatial processes migration and dispersal, and on the availability of suitable habitat (Roessig et al., 2005). For instance, vertical foraging migrations or large-distance seasonal migrations can be linked to characteristic temperature corridors (e.g. Kitagawa et al., 2000, Stensholt, 2001). Spatial structure and distribution of stocks can be shaped by migratory behaviour and larval dispersal, as governed by oceanic currents and bottom topography (e.g. Rindorf and Lewy, 2006, Knutsen et al., 2007). Local impacts of climate change e.g. in spawning or nursery grounds can thus disrupt spatial life cycles via recruitment success (Petitgas et al., 2012, Llopiz et al., 2014). Spatial structure of fish stocks also influences the response to harvesting (Ciannelli et al., 2013).

Ocean warming may reduce dispersal distances and decrease population connectivity due to faster larval development, and can lead to shifts in seasonal spawning timing (O'Connor et al., 2007, Asch, 2015). Experimental and empirical data can elucidate these spatial-temporal organism-habitat connections. Processes such as migration and recruitment can in principle be described as a result of behavioural responses to the spatial environment, governed by physiological capabilities and limitations (cf. Fiksen et al., 2007). Observational and telemetry data can be used to inform about population movements (Metcalfe et al., 2012), and genomic methods can reveal fine-scale population structuring and local or regional adaptive differentiation in fish species (Nielsen et al., 2009).

From processes to models: Modelling approaches and their capacity for process-based integration of environmental drivers

In this section, the main types of models used to investigate marine fish are analysed for their capacity to incorporate the effects of environmental drivers on specific physiological and ecological processes. For clarity, we divide the models into seven categories: 1) single-species population dynamic models, 2) multi-species population dynamic models, 3) trophodynamic & mass-balanced models, 4) species distribution models (SDMs), 5) trait-based & size-spectrum models, 6) individual-based models (IBMs), and 7) bioenergetic models. These categories represent historical developments, but no definitive functional distinctions. Modelling approaches are under rapid development and continuously incorporating new possibilities, sometimes originating from other model classes. Finally, we describe approaches and issues for the coupling of models and coupled end-to-end models.

We aim to explain the underlying concepts, and review recent applications and extensions with regard to the incorporation of environmental drivers, to give a guideline in the choice of a suitable modelling approach. Furthermore, we present relevant freely available software packages, to encourage the reader to try out models and gain a better understanding of the underlying assumptions.

Single-species population dynamic models

Single-species population dynamic models descend from models used for traditional fisheries stock assessment (Ricker, 1954, Beverton and Holt, 1957). These models rely on catch and survey data to estimate fish stock size, and simulate stock dynamics based on estimated population-level parameters like biomass, growth rate, recruitment, fishing and natural mortality (Hilborn, 2012). Extensions have divided stocks into age and/or size classes that can possess varying mortalities and growth (Deriso et al., 1985, Fournier et al., 1990), and 'matrix population' models consider both factors e.g. by describing stages within age classes (Caswell, 2001).

Organism: Stock models with both size- and age-structure can integrate adjustments of size-dependent or age-dependent processes (e.g. growth, mortality, development as shift to the next stage) based on environmental effects. The effects of temperature have been incorporated by tuning the growth function, e.g. for climate-dependent variations in Atlantic cod stocks (Brander, 1995, Clark et al., 2003), and by adjusting natural mortality, e.g. in an age-structured model for Pacific saury (*Cololabis saira*, Scomberesocidae; Tian et al., 2004). Assumed effects of changes in temperature, salinity and hypoxia on growth, mortality and reproduction have been integrated in a matrix projection model for Atlantic croaker (*Micropogonias undulatus*, Sciaenidae; Diamond et al., 2013).

Population: Stock assessment models aggregate early life stages in an empirical stock-recruitment relationship (Needle, 2001), which determines critical characteristics of the produced stock dynamics (e.g. Cabral et al., 2013). Environmental drivers have been incorporated into recruitment functions (Hollowed et al., 2009), e.g. as temperature effects on North Sea and Baltic cod (Köster et al., 2001, Clark et al., 2003), on tropical rock lobster (*Panulirus ornatus*, Palinuridae; Plaganyi et al., 2011) and on Baltic sprat (*Sprattus sprattus*, Clupeidae; Voss et al., 2011). The influences of atmospheric oscillations and regional oceanographic regimes on recruitment have been incorporated e.g. for Atlantic cod (Brander and Mohn, 2004), Northern rock sole (*Lepidopsetta polyxystra*, Pleuronectidae;

Hollowed et al., 2009) and jackass morwong (*Nemadactylus macropterus*, Cheilodactylidae; Wayte, 2013).

Simpler, non stage-structured 'surplus production' models have investigated stock dynamics as driven by temperature regimes and climate oscillations (Rose, 2004, Holsman et al., 2012). Matrix projection models can incorporate more process detail, integrating reproduction and estimating recruitment from growth, maturation and cannibalism processes, as applied for Atlantic cod (Frøysa et al., 2002, Andrews et al., 2006) and Atlantic croaker (Diamond et al., 2013).

Community: Food web interactions are not explicitly incorporated in single-species assessment models (see 'multi-species population dynamic models'), but are indirectly considered through model fitting to stock observations. Stock models could take into account changes in community level processes via adjusting stock growth or an additional mortality parameter.

Spatial consideration: Movement of stocks has been integrated through grid cells connected by advection and diffusion e.g. for albacore (*Thunnus alalunga*, Scombridae; Fournier et al., 1998) and for Atlantic cod (Andrews et al., 2006). By modelling the dynamics of metapopulations with distinct sub-stocks, differences in population parameters and more detailed spatial processes such as migration, spatially disaggregated spawning, and larval diffusion can be incorporated (Goethel et al., 2011).

Multi-species population dynamic models

Multi-species population dynamic models originate from the extension of single-species stock assessment models (Pope, 1979, Gislason, 1999, Lewy and Vinther, 2004). These models use diet data to couple several species via their feeding interactions, whereby the mortality rate of a stock is determined from its consumption by other species (Pope, 1991, Magnússon, 1995, Rose and Sable, 2009). Selection of the included species can be based on abundance, relevance from an economic or management perspective, or because of key interactions with the target species (Rindorf et al., 2013, Plaganyi et al., 2014b). Models include up to six species and often aim to evaluate interdependent fluctuations of fish stocks in response to environmental changes (e.g. Bogstad et al., 1997, Livingston, 2000).

Organism: Due to an underlying structure equivalent to single-species population dynamic models, multi-species models have essentially the same capacities and limitations for integrating organism-level processes. The explicit consideration of species interactions may allow a more realistic parameterization e.g. of natural mortality and growth (Hollowed, 2000).

Population: Restrictions apply as for single species stock models. However, multi-species models can include impacts of predation by other species on early life stages, as demonstrated e.g. for Atlantic cod and interacting species (Lewy and Vinther, 2004, Lindstrøm et al., 2009, Speirs et al., 2010). This would in principle allow for integration of food-web mediated environmental effects on recruitment success.

Community: Multi-species models incorporate predation and competition processes among the included species, with a moderate number of species assumed to be sufficient to describe regional food web dynamics (Rindorf et al., 2013). The predation process is formulated as a statistical 'functional response' between predator consumption and prey abundance (Holling type functions; Holling, 1959), where prey suitability is usually based on data from stomach content analysis (Magnússon, 1995). Environmental influence on the predation process has been incorporated by dynamically modelling stomach content and the impact of temperature on evacuation rates to represent metabolic activity, in a study with Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae) and its predators (Garrison et al., 2010).

Spatial consideration: Multi-species models can divide stock representations into several regional areas to include connecting processes such as seasonal migration patterns and larval dispersal, as realized for the Barents Sea (Tjelmeland and Bogstad, 1998, Lindstrøm et al., 2009).

Trophodynamic & mass-balance models

Trophodynamic or mass-balance models (also termed whole system or aggregate system models) build on the analysis of mass or energy flows in ecological networks (Polovina, 1984, Ulanowicz, 1985). Exchange of biomass as wet weight or energy equivalents is modelled among functional groups or 'compartments' (usually species or ecologically similar groups of species) in marine food webs. Available software packages include *Econetwrk* (Ulanowicz, 2004), which focuses on network analysis, *Ecotroph* (Gascuel and Pauly, 2009), which analyses biomass flow through trophic levels, and the multifunctional and widely utilised *Ecopath with Ecosim* package (EwE; Christensen and Walters, 2004).

Organism: Effects of temperature, acidification and hypoxia on physiological performance of organisms have been incorporated in Ecosim by forcing functional groups or by adjusting their aggregate production, consumption or mortality values (e.g. Ainsworth et al., 2011, Cornwall and Eddy, 2015). The spatial EwE extension *Ecospace* (Walters et al., 1999) permits specifying habitat quality based on various environmental factors, which then determines foraging capacity (Christensen et al., 2014a), and can divide life stages into smaller packages to approach 'individual-based' functionality (Walters et al., 2010).

Population: The ‚multi-stanza' feature in EwE facilitates the representation of life stages to describe recruitment (Christensen and Walters, 2004, Walters et al., 2010), but reproduction is not explicitly represented. As the underlying parameters are on functional group level, the analysis of plasticity and adaptation of populations is limited (Christensen and Walters, 2004).

Community: Energy flow over trophic levels can inform about general ecosystem characteristics and functioning (e.g. Link et al., 2008, Gascuel et al., 2011). The differentiation of represented compartments (species or functional groups) can be adjusted to optimize between food web resolution and data availability and reliability (Prato et al., 2014), informed by general ecological knowledge and sensitivity analyses (Link, 2010, Lassalle et al., 2014).

Predation is represented by a functional response depending on predator and prey biomasses (Christensen and Walters, 2004). In principle, vulnerability settings for each compartment provide an aggregate measure to integrate e.g. risk-sensitive foraging or predation behaviour (Ahrens et al., 2012). Via forcing functions, consumption and vulnerability parameters, or zooplankton groups and primary production can be adjusted to represent impacts of climate change on feeding interactions or food availability (e.g. Shannon et al., 2004, Field et al., 2006, Araújo and Bundy, 2012).

Spatial consideration: The *Ecospace* module of EwE can represent spatial-temporal distribution of biomass, including probability functions of movement (Walters et al., 2010). Habitat suitability, seasonal migrations and larval dispersal have been integrated e.g. for areas in the Mediterranean (Libralato and Solidoro, 2009, Fouzai et al., 2012). Two recently added features enable dynamic spatial-temporal environmental data input (Steenbeek et al., 2013a) and more detailed integration of variable habitat suitability factors (Christensen et al., 2014a).

Species Distribution Models (SDMs)

Species Distribution Models (SDMs, also termed niche-based models, climate envelope models, or predictive habitat distribution models) link observed geographical species distributions to environmental parameters, classically through regression analysis (Guisan and Zimmermann, 2000, Elith and Leathwick, 2009). Besides a wealth of applications in the terrestrial realm, SDMs are increasingly used for projecting future distributions of marine fish stocks from regional projections of environmental factors (Cheung et al., 2008, Cheung et al., 2009, Lenoir et al., 2010). Dedicated SDM software platforms enable the application and comparison of different algorithms (e.g. Thuiller et al., 2009).

Organism: Organism level effects of environmental drivers can readily be incorporated into SDMs as performance curves dependent on physical factors. To integrate multiple environmental variables, different suitability factors can be multiplied (e.g. Kaschner et al., 2006). Aerobic scope has been used to integrate effects of temperature, oxygen, pH and food energy into the population growth function for marine fish stocks (Cheung et al., 2011).

SDMs which aim to increase detail by including functional relationships between physical variables and species performance, e.g. thermodynamic energy transfer principles, have been termed mechanistic SDMs or mechanistic niche models (Dormann, 2007, Kearney and Porter, 2009). Under changing environmental conditions, increased care has to be taken in the choice of environmental variables, species-specific data, and applied algorithms to supply ecologically meaningful and robust projections (Araújo and Guisan, 2006, Heikkinen et al., 2006, Austin, 2007).

Population: A logistic population growth model incorporates temperature effects on population carrying capacity to model the global distribution of fish species (Cheung et al., 2008). As environmental correlations are usually based on the occurrence of adults, it is difficult to include ontogenetic shifts in environmental tolerance or preference in different life stages (Robinson et al., 2011), but more detailed, stage-structured representations of population processes have been achieved in terrestrial models (e.g. Fordham et al., 2013).

Community: The incorporation of community shifts under climate change represents a challenge for SDMs, as species interactions are only implicitly included in the empirically based response function. Depending on the scale of projections, changes in species interactions may significantly influence the performance of SDMs (Araújo and Rozenfeld, 2014). Mechanistic SDMs aim to exclude biotic interactions from the response function and consider them separately (Guisan and Thuiller, 2005) to take into account differential preferences of prey and predator for environmental factors (Robinson et al., 2011),

An SDM for the North Atlantic has been extended with community size-spectra to represent competition between species as a division of available food energy (Fernandes et al., 2013). For the Mediterranean Sea, a niche model has been coupled to a trophic network model to derive temperature-induced shifts in food webs (Albouy et al., 2014).

Spatial consideration: SDMs can provide high spatial resolution, but correlations are often limited by the availability of species occurrence data. Larval dispersal, adult migrations, habitat availability and regional primary production changes have been included into projections of worldwide distribution changes of marine fish (Cheung et al., 2009, Cheung et al., 2010). Seasonal migrations and other spatio-temporal processes governed by factors other than current environmental parameters (e.g. genetic) are more difficult to include (Robinson et al., 2011), but have been included e.g. in a habitat prediction model for southern Bluefin tuna (*Thunnus maccoyii*, Scombridae) under changing oceanographic conditions (Hartog et al., 2011).

Trait-based & size-spectrum models

Trait-based models constitute a relatively new approach, focusing on the description of individual characteristics and processes (traits), e.g. size, morphology or weight, which are defined to govern performance of organisms in a specific environment (Chown, 2012). These traits can be used together with metabolic scaling and predation rules to describe life histories and interactions (Brown et al., 2004, Andersen and Beyer, 2006) and to construct community size-spectrum models for fish (Benoit and Rochet, 2004, Pope et al., 2006). A multi-species size spectrum modelling package, is available with an example parameterized for the North Sea (Scott et al., 2014).

Organism: Trait-based models can incorporate considerable detail on organism-level processes such as growth, foraging, reproduction and basal metabolism, modelling organismal trade-offs via energy allocation (Jørgensen and Fiksen, 2006). For Atlantic cod larvae, optimal vertical migration and life history strategies have been derived from responses to the environmental variables food, temperature and light (Kristiansen et al., 2009, Fiksen and Jorgensen, 2011). Recently, individual energy and oxygen budgets have been used to derive changes in growth, mortality and reproduction rates under ocean warming and project impacts on population characteristics and optimal behavioural and life history strategies (Holt and Jørgensen, 2014, Holt and Jørgensen, 2015).

Population: Trait-based models have high potential to describe processes shaping population dynamics, such as reproduction and recruitment, by basing them on individual life histories. These can be resolved for size, growth and maturation (e.g. Hartvig et al., 2011, Holt and Jørgensen, 2014). However, trait-based models usually include an empirical stock-recruitment relationship to determine recruitment and represent closure of life cycles (Jacobsen et al., 2014). Adaptation of fish populations to size-selective drivers (e.g. fisheries exploitation) can be quantified based on changes of individual growth, reproduction and mortality processes (Andersen and Brander, 2009). Eco-genetic or adaptive dynamics models investigate plasticity and evolutionary rates within populations (Dunlop et al., 2009).

Community: In size spectrum models, community interactions and food webs are usually constructed bottom-up, based on the realized interactions as governed by the integrated traits, e.g. 'size at maturation' (e.g. Jennings and Brander, 2010, Hartvig et al., 2011). Simple size spectrum models can investigate community shifts under temperature effects on growth (Pope et al., 2009). Behavioural, energy allocation and foraging processes can connect individual processes in more detail (Andersen and Beyer, 2013), and functional separation in interactions can be integrated by using coupled size spectra, as exemplified for pelagic predators and benthic detritivores (Blanchard et al., 2009).

Spatial consideration: Size spectrum models can use spatial input from oceanographic and biogeochemical models to incorporate e.g. temperature effects on feeding and mortality (Blanchard et al., 2012) and to simulate movement (Watson et al., 2014).

Individual-based models (IBMs)

Individual-based models (also termed agent-based models) are a bottom-up modelling approach, based on the simulation of individuals as separate entities. Their status is determined by internal state variables and changed by interactions with other individuals and the environment (e.g. foraging and predation), generating population and higher-level system properties (Huston et al., 1988, Judson, 1994, Grimm, 1999). Various IBM programming packages focus on agent-environment interactions (Railsback et al., 2006, Arunachalam et al., 2008). More specialized software tools model environmental impacts on the dispersal of planktonic fish larvae (Lett et al., 2008, e.g. Huebert and Peck, 2014).

Organism: IBMs for larval fish describe growth, development and mortality as dependent on environmental parameters (Hinckley et al., 1996, Hermann et al., 2001, Gallego et al., 2007). Behavioural rules can link environmental factors (e.g. light, temperature, oxygen) to metabolism, energy use, and predation risk (Fiksen et al., 2007). Energy allocation principles can be used to describe connections and trade-offs among internal processes in IBMs (Sibly et al., 2013). More detailed environmental and experimental data is needed for further advances in larval IBMs (Lett et al., 2010, Peck and Hufnagl, 2012).

Population: IBMs allow for consideration of inter-individual variation in fish responses and the resulting environmental selection (Van Winkle et al., 1993) and can thus be used to investigate population adaptation to changing environmental drivers (e.g. Anderson et al., 2013). While representing both detailed early life stages and closed life cycles of populations produces considerable model complexity and computational demands, IBMs can be used to integrate variation into more aggregate models (Rose et al., 2001).

IBMs have been used to investigate early life stage dynamics, connectivity between stocks and environmental impact on recruitment potential of marine fish (Mullon et al., 2002, Miller, 2007, Hinrichsen et al., 2011). Demographic changes under climate change have been investigated for Atlantic salmon (*Salmo salar*, Salmonidae; Piou and Prévost, 2012).

Community: IBMs are successful in detailing the predation of larval fish on zooplankton based on spatial co-occurrence, the environment and behavioural processes, e.g. investigating match-mismatch dynamics (Kristiansen et al., 2011). Thus, growth and mortality can be described as emergent properties of individual interactions, providing the predation functional response with ecological detail (Huse and Fiksen, 2010).

Changes in lower trophic levels can be integrated as ‘prey fields’ (aggregated prey densities in a defined space) into larval models (Hermann et al., 2001, Daewel et al., 2008). Size-governed predation processes have been resolved in a multi-species IBM for pelagic fish communities (OSMOSE; Shin and Cury, 2001, 2004; for this and other multi-species IBMs, see section on 'coupled and end-to-end models').

Spatial consideration: Biophysical IBMs can model impacts on larval dispersal, based on output from three-dimensional oceanographic models, as realized e.g. for larvae of walleye pollock (Theragra chalcogramma, Gadidae; Hermann et al., 2001), Southern African anchovy (Engraulis capensis, Engraulidae; Mullon et al., 2002), Atlantic cod (Vikebo et al., 2007, Heath et al., 2008) and Atlantic herring (Vikebo et al., 2010). A mechanism-based, not species-explicit model has been used to investigate climate change impacts on adult fish and mammal migrations (Anderson et al., 2013).

Bioenergetic models

Bioenergetic models simulate the internal energy budget of organisms by using rules for energy allocation. Metabolic processes such as feeding, respiration, growth and reproduction are linked to external parameters, e.g. food and temperature, to determine the organism’s performance (Brown et al., 2004, Hartman and Kitchell, 2008). Classic bioenergetic models have been applied to a variety of fish species (Hansen et al., 1993). In Dynamic Energy Budget (DEB) models (Kooijman, 2000, van der Meer, 2006), individuals are characterized by the state of different energy compartments such as structure, reserves and reproduction (Lika and Kooijman, 2011, Nisbet et al., 2012). Energy budget representations have also been integrated into other model types (see 'Organism' subsections of 'Trait-based & size-spectrum models', 'Individual-based models' and 'Coupled and end-to-end models' sections).

Organism: Energy budgets have been used to compare temperature-dependent organism performances and sensitivities among different fish species (van der Veer et al., 2001, Sousa et al., 2008, Freitas et al., 2010). While this provides the base for a mechanistic understanding of diverging organism performances under climate change, further research will be required to incorporate life history and behavioural detail, activity costs, and seasonal and ontogenetic variations in energy allocation (Beauchamp et al., 2007, Sibly et al., 2013) as well as the treatment of oxygen supply for metabolism (Pauly, 2010).

Population: Bioenergetic models have been scaled up to population level to determine parameters such as biomass, consumption and growth of fish stocks, based on changes in metabolic and feeding rates (Beauchamp et al., 2007, Perez-Rodriguez and Saborido-Rey, 2012). To include more detail on population level processes, DEBs have been integrated into matrix population models (e.g. Klanjscek et al., 2006) and energy allocation patterns adapted to the life-history of the organism (Nisbet et al., 2012).

Spawning dynamics resulting from temperature and food effects on energy budgets have been investigated for European anchovy (Pecquerie et al., 2009) and Atlantic Bluefin tuna (*Thunnus thynnus*, Scombridae; Chapman et al., 2011).The integration of energy budget models into IBMs allows more detailed upscaling of individual-level processes to population level (Hölker and Breckling, 2005, Sibly et al., 2013), and for DEB-IBM integration a software framework is available (Martin et al., 2011, Martin et al., 2013).

Community: Predator-prey interactions in bioenergetic IBMs determine energy transfer between individuals, and can therefore include changes in prey composition or energy content (Martin et al., 2011). Behavioural aspects of foraging are more difficult to include (Beauchamp et al., 2007). Dynamic Energy Budgets have been used to derive thermal ranges of fishes in the North Sea (Freitas et al., 2010), and can be integrated into size-spectra models to investigate community dynamics (Maury and Poggiale, 2013).

Spatial consideration: A DEB model has been coupled to biogeochemical and lower trophic level models to investigate the spatial distribution of North Atlantic flatfish species (Teal et al., 2012). To investigate detailed spatial processes, bioenergetic models have been integrated into size-structured models (e.g. Maury, 2010; see 'Coupled and end-to-end models'), and can be incorporated into individual-based and species distribution models, but data availability and the complexity of organismal plasticity and ontogenetic changes may limit their up-scaling to the ecosystem level (Freitas et al., 2010).

Coupled and end-to-end models

As each modelling approach has characteristic strengths and simplifications, coupling of different ecological models increases the potential for explicit process integration (cf. Reuter et al., 2010). A range of coupled models is available, and some consist of a complex array of submodels, connecting ecosystem levels and scientific disciplines (Moloney et al., 2011) to achieve an 'end-to-end' representation of climate change impacts, i.e. from physical oceanographic changes via nutrient dynamics and planktonic lower trophic levels, to fish stocks, other higher trophic levels and links to socio-economic dynamics (Travers et al., 2007, Fulton, 2010, Rose et al., 2010). To link across these levels, models can profit from detailing processes, e.g. related to energy allocation, feeding and behaviour (Nisbet et al., 2000, Brown et al., 2004, Kearney et al., 2010, Persson et al., 2014). Note that recent extensions and advances in end-to-end modelling are not all covered in the peer-reviewed literature, and it is beyond the scope of this paper to provide more than a short overview of these models.

Three conceptually related models integrate oceanographic models, simplified nutrient and lower trophic level dynamics and bioenergetic models for certain pelagic fish species. APECOSM (Apex Predators ECOSystem Model; Maury, 2010) and SEAPODYM (Spatial Ecosystem And POpulations DYnamics Model; Lehodey et al., 2008) represent size-structured predation and movement in different tuna and related species, and have been used to investigate worldwide distribution shifts under climate change (Lefort et al., 2015, Lehodey et al., 2015). NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography - For Including Saury and Herring) has been developed to investigate climate regime effects on Pacific herring (*Clupea pallasii pallasii*, Clupeidae; Megrey et al., 2007, Rose et al., 2008) and Pacific saury (Ito et al., 2004).

OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) is an IBM representing multiple size classes and size-based interactions (Shin and Cury, 2004). Recent OSMOSE versions have been used to investigate combined effects of climate change and fisheries by coupling energy-dependent growth of early life stages to simple models of lower trophic levels (Travers-Trolet et al., 2014). Based on environmental driving from the NEMURO model, a recent multi-species IBM development for the California Current simulates dynamics of Californian anchovy (*Engraulis mordax*, Engraulidae) and Pacific sardine (*Sardinops sagax caerulea*, Clupeidae), linking to an agent-based fisheries model (Fiechter et al., 2015, Rose et al., 2015).

Atlantis is a modular end-to-end model aimed at the evaluation of management strategies (Fulton et al., 2004, Fulton et al., 2011). Fish stocks are age-structured, with average size and condition tracked, and different types of functional responses can be used to describe trophic interactions (Fulton, 2010, Kaplan et al., 2012). Effects of warming, acidification and salinity changes have been integrated on represented processes such as growth, reproduction, and movement (Griffith et al., 2012, Fulton and Gorton).

In principle, these comprehensive models possess a high potential for consideration of multiple drivers for different species and at various levels of description. However, the complexity of model structures causes a high work effort for estimating and analysing empirical parameters, the consideration of scaling issues and the coupling of modules may be limited by calibration issues and the propagation of uncertainties (Fulton et al., 2003, Rose, 2012, Voinov and Shugart, 2013, Evans et al., 2015).

As an alternative to the use of increasingly complex model structures, purposefully simplified end-to-end models can quantify climate change impacts and provide management advice. These have been termed 'models of intermediate complexity' (Hannah et al., 2010) and can be related to or based on multi-species population dynamic models (Plaganyi et al., 2014b). Recent examples have linked nutrient dynamics to fisheries management for the North Sea and Baltic Sea (e.g. Heath, 2012, Radtke et al., 2013). Also, Ecospace models (see 'Trophodynamic & mass-balance models') can be driven with spatial-temporal input from oceanographic models (Steenbeek et al., 2013) to investigate e.g.

interactions of hypoxia and fishing (de Mutsert et al., 2015). Lastly, in system dynamics modeling, which aims at a simplified representation of social-ecological systems (Costanza and Ruth, 1998), some examples for fish stocks in the Northwest Atlantic have incorporated habitat conditions and management elements (Ruth and Lindholm, 1996, Gottlieb, 1998).

From models to understanding and projections: Model choices and challenges for addressing questions of environmental change

Our compilation illustrates that modelling approaches have strongly diverging capacities to incorporate physiological and ecological processes under scenarios of climate change (Table 1). Most approaches concentrate on specific levels of organization and neglect others, although in many cases recently added features have improved capacities. The best choice of model thus depends on the primary question of interest, the relevant processes and the available data.

To exemplify relevant considerations when choosing or constructing a model, we consider five basic research questions asked by the scientific community. Questions 1 to 3 relate to advancing the fundamental understanding of biological responses of fishes to environmental changes (individual tolerance, population adaptation and ecological regime shifts). Questions 4 and 5 focus on projections of the future states of fish stocks (spatial distribution and links to socio-economic developments). We evaluate the capabilities of the presented model classes to treat these questions and suggest how these models may profit from integrating more experimental results and empirical data.

Question 1: What is the individual response and tolerance of fish to multiple changing environmental drivers?

Laboratory experiments contribute primarily to this research question by investigating organism level processes that determine the effect of multiple and combined environmental drivers (increasing temperature, acidification, hypoxia) on individual performance. Research on the cumulative effects of stressors, life stage-specific sensitivities and trade-offs between physiological processes can build the foundation for explaining the capacity for and the limitations of individual plasticity.

Bioenergetic models can represent individual processes in greatest detail. To project effects on higher-level processes, energy budgets have been successfully integrated in individual-based, trait-based, size-spectrum, species distribution and end-to-end models. Individual-based and trait-based models on the individual level are most directly parameterized with results from experiments, can consider inter-individual heterogeneity, and facilitate a mechanistic understanding of the effects of different constraining or enhancing factors on the performance of individuals. Due to detail richness and specificity of model formulations, these models are often not easily transferable to other species. When applied to multiple species and in a spatial ecosystem context, computational demands can be high.

Species distribution models and Ecospace offer comparatively straightforward integration of physiological performance curves into response functions to single and multiplicative drivers. Due to the implicit assumptions regarding upscaling to higher levels of organization, robustness and uncertainty of the applied response functions can be assessed e.g. by using results on sub-lethal physiological responses, which can be provided by laboratory experiments (Woodin et al., 2013). In single or

Table *1*: Overview on model classes for marine fish and their potential for representation of processes on various levels of biological organisation. Processes marked by an asterisk* are incorporated on an aggregate level or non-dynamically (state-independent). Processes in brackets ( ) can only be incorporated in a subset of models of the class or by using additional software features (see text for details). Coupled and end-to-end models can in principle incorporate all processes, and their specific capabilities depend on the model classes they are based on.

model class	**incorporated processes on level of description**				**main use in climate change context**
	Organism	**Population**	**Community**	**Ecosystem**	
1. Single-species population dynamic	growth* mortality* (development*)	recruitment (reproduction)	--	migration* dispersal*	stock management (no relevant stock interactions)
2. Multi-species population dynamic	growth* mortality* (development*) (foraging*)	recruitment (reproduction)	predation* competition*	migration* dispersal*	stock management (interactions important), community dynamics
3. tropho-dynamic & mass-balance	growth* mortality* (development*) foraging*	(recruitment) (reproduction*)	predation* competition* mutualism*	migration (dispersal) habitat *(all in Ecospace)*	community and ecosystem resilience, ecosystem-based management
4. species distribution (SDM)	growth* mortality* foraging* limitations*	recruitment*	(predation*) (competition) *(with size spectrum or trophic models)*	migration* (dispersal*) habitat	distribution range shifts, local fish catch potential

5. trait-based & size-spectrum	(plasticity) behaviour growth mortality development foraging (metabolism) energy allocation limitations	recruitment* reproduction adaptation	predation* competition*	habitat*	trade-offs in organismal processes, adaptation and community structure
6. individual-based (IBM)	(plasticity) behaviour growth mortality development foraging (metabolism) energy allocation limitations	recruitment* reproduction adaptation	predation competition mutualism*	migration dispersal habitat	larval dispersal, behavioural and population adaptation
7. bio-energetic	growth mortality (development) foraging metabolism energy allocation (limitations)	(recruitment) (reproduction) *(in IBMs)*	(predation) (competition) *(in size-spectrum models)*	(migration) (habitat) *(in IBMs or SDMs)*	trade-offs in organismal processes, linking of individual effects to community dynamics
8. coupled & end-to-end	[based on multi-species, size-spectrum, IBM, or bioenergetic]	recruitment* reproduction adaptation	predation competition mutualism*	migration dispersal habitat	ecosystem-based management, distribution and regime shifts

multi-species population dynamic and mass-balance models, experimental results can be used to adjust growth, consumption and mortality of (age/size) stages or cohorts. As this kind of aggregated integration of results does not account for individual variation in responses, robustness of these representations should be assessed over the range of responses in regard to interactions with other drivers and with processes on higher levels (such as predation and selection). This can be conducted e.g. by sensitivity analyses informed by physiological and ecological results, and by including multiple aggregate parameterisations to reflect some level of variation.

Advancements are necessary in the individual-level integration of multiple drivers, which can be informed by results from specifically designed experiments. Models will benefit from the integration of data on energy allocation and well-established physiological performance measures, such as aerobic scope, to define habitat suitability under driver combinations (Teal et al., 2015). These can be used to integrate experimental results directly into hydrodynamic and biogeochemical models (e.g. Cucco et al., 2012). Integrative concepts such as scope for activity (Claireaux and Lefrancois, 2007) and oxygen- and capacity-limited thermal tolerance (OCLTT; Pörtner, 2010) can be used to reduce complexity of representation and serve as a matrix for integration of multiple driver effects in order to generalize organismal performance and stress sensitivity (Pörtner, 2012).

Models should also increasingly incorporate dynamic responses, to account for acclimation and evolution. Laboratory measurements of organismal acclimation and phenotypic response variation within populations, as well as knowledge of the functional mechanisms underlying organismal responses, can help to estimate organismal adaptive capacity (see also question 2).

Question 2: How will climate change affect the population dynamics of fish stocks and what is their capacity for adaptation?

To assess fish stock responses to climate change, integration of the population level processes recruitment and reproduction, and of the adaptation capacity of populations is needed. Recent meta-analyses and statistical models show that for many stocks, recruitment may be strongly dependent on the environment (Ottersen et al., 2013, Szuwalski et al., 2014, Pecuchet et al., 2015). Data from different early life stages, the reproduction process and from trans-generational experiments can contribute to create a more mechanistic description of the environmental dependence of population dynamics and to determine the capacity of stocks to undergo adaptation.

Stage-structured single or multi-species population dynamic models can be used to investigate the impacts of environmental change on population size and age structure. The use of generalized stock-recruitment relationships or environmental carrying capacities entails strong assumptions, such as homogeneity of a cohort and of environmental conditions (Metcalfe et al., 2012), and the recruitment function can put considerable uncertainty on projections from these models (e.g. Cabral et al., 2013, Howell et al., 2013). An improved integration of environmental effects could be based on the explicit representation of different early life stages (e.g. eggs, non-feeding and feeding larval stages), as realized in some matrix projection models. To incorporate spatially resolved habitat drivers of population processes, increasing focus should also be put on the development of mechanistic SDMs that incorporate stage-structured population dynamic models, as they have been realized for terrestrial systems (e.g. Keith et al., 2008, Fordham et al., 2013, Lurgi et al., 2014).

For a more detailed investigation of population structure across life stages and to investigate population adaptation based on acclimation and evolution, trait-based models and IBMs making use of heritable, physiology-based traits will play an important role. While next-generation population genomic methods will help to link genotype and phenotype (Hemmer-Hansen et al., 2014), laboratory studies on organismal tolerance ranges and individual adaptation can help to identify plasticity and within-population variation in phenotypic traits. Investigation of adaption will advance further once gene expression can be more precisely linked to physiological functions and environmental performance, making use of transcriptomic data and transgenerational experiments (Munday, 2014, Logan and Buckley, 2015). This approach would improve mechanistic understanding of acclimation and evolution (Whitehead, 2012, Alvarez et al., 2015) and could be informed by data gained from 'common garden' experiments with fish from different environmental conditions (e.g. Oomen and Hutchings, 2015) and from laboratory experiments (Munday et al., 2013b). Investigations for early life stages can be complemented by large-scale manipulations conducted e.g. in mesocosms (cf. Munday et al., 2013b, Stewart et al., 2013).

Thus, using genetic data and physiological knowledge, exploratory studies about detailed scaling of key processes from organism to population level may succeed when using trait-based models or IBMs that integrate key traits for physiological mechanisms (cf. Reuter et al., 2008). Behavioural traits mediate a wide range of organism-organism and organism-habitat interactions in fish (Munday et al., 2013b, Nagelkerken and Munday, 2015), and thus may become valuable in modelling phenotypic variation and adaptive potential in the context of communities and ecosystems (e.g. Giske et al., 2014). Most trait-based models, however, currently include only a low number of different traits. In IBMs, 'super-individuals' can represent a variable number of real individuals (Scheffer et al., 1995). This concept can be used to scale up organismal properties to higher-level dynamics, maintaining self-organised population properties (Reuter et al., 2005) while limiting computational demands. It has been extended into grid-based approaches, for community size-spectra in OSMOSE (Shin and Cury 2004) and for sardine and anchovy in the Californian Current in NEMURO.FISH (Fiechter et al., 2015, Rose et al., 2015).

Question 3: Will marine food webs be resilient to climate change, or can regime shifts occur?

Regime shifts in marine ecosystems can have strong impacts on fish stocks and are difficult to predict (Frank et al., 2005, deYoung et al., 2008), but community responses to environmental drivers may be crucially determined by characteristics of food web interactions (Mangel and Levin, 2005, Hunsicker et al., 2011, Plaganyi et al., 2014a). Food web topology can be elucidated by analysing biochemical tracers such as stable isotopes and fatty acids (Young et al., 2015). Experimental results on feeding parameters, predation behaviour (e.g. prey switching) and size-dependence can help to detail the interactions and mechanistically describe changes in community-level processes under multiple climate change drivers (Stefansson, 2003, Persson et al., 2014, Nagelkerken and Munday, 2015).

In trophic mass-balance models such as EwE and in end-to-end models, different types of trophic control (bottom-up, top-down, or a mixture) can be integrated through vulnerability parameters (e.g. Ahrens et al., 2012), and network analysis indicators can be used to characterize the resulting food web dynamics and identify key functional groups (Heymans et al., 2014). Yet, aiming for a complete representation of food webs causes a comparatively high need for field data, especially when analysing dynamics over time.

Multi-species stock models are less data demanding and have been used to compare conditions for regime shifts and thresholds among different systems (e.g. Petrie et al., 2009, Plaganyi et al., 2014a). Their simplified structure should be informed by ecological knowledge, such as identification of major trophic pathways and selection of key components (Gilman et al., 2010, Shin et al., 2010), network analysis of more complex models (e.g. Metcalf et al., 2008, Livi et al., 2011), or 'ecotypes' that represent mixed ecological characteristics (Engelhard et al., 2010).

Size spectrum models can investigate food web dynamics based on size structure (e.g. Blanchard et al., 2010), but representation of other properties that affect interactions is currently limited. To quantitatively characterize the vulnerability of interaction processes to predator/prey or environmental changes, IBMs and trait-based models can use behavioural rules and inter-individual variability to produce emergent feeding interactions, instead of relying on a statistical functional response (Fiksen et al., 2007, Mariani and Visser, 2010). Understanding of marine ecosystem resilience under climate change could be advanced by trait-based models with a focus on ecologically functional traits (Bremner, 2008, Mouillot et al., 2013) and by multi-species IBMs that use empirical results on food uptake, energy allocation and predation behaviour to set parameter values (see 'Coupled and end-to-end models'). Predation and energy allocation are key processes to link fish models to lower trophic level changes (Cury et al., 2008), and a realistic two-way coupling is necessary to describe ecosystem dynamics, especially in top-down controlled systems (Travers et al., 2009, Daewel et al., 2014).

To provide data for parameterization of these models, more systematic experimental investigation of environmental influences on foraging and assimilation processes is necessary. The effects of different functional response formulations on model behaviour should be tested more routinely, and whenever feasible, relevant behavioural and habitat aspects be represented dynamically. Options include using integrative suitability or vulnerability settings (e.g. Kempf et al., 2010, Ahrens et al., 2012) and multi-dimensional functional responses (e.g. Büssenschütt and Pahl-Wostl, 2000, Dawes and Souza, 2013). These community models can then inform spatially resolved models to explore how local food web dynamics respond to changes in spatial distribution of species abundance.

Question 4: How will the spatial distribution and range of stocks change?

This research question combines data on different levels of biological organization (cf. Fig. 1), as individual responses to local environmental factors (e.g. temperatures, oxygen levels), adaptation and changes in recruitment, food web interactions, and dispersal and habitat availability all influence the distribution of fish stocks (Roessig et al., 2005, Rose, 2005, Hollowed et al., 2013).

Spatial variability is well represented in Species Distribution Models. SDMs have advanced considerably in incorporating details on organism-level processes, population dynamics, competition and spatial-temporal processes, and can be based upon experimental results on different levels, as exemplified for acidification and warming effects on a marine invertebrate species (Queirós et al., 2015). Underlying assumptions of steady-state relations in SDMs should always be critically examined (e.g. Guisan and Thuiller, 2005, Knudby et al., 2010). Additional empirical results should be used to consider potentially critical effects in processes not explicitly represented, e.g.

recruitment, population adaptation, migration and dispersal, and changes in species interactions (cf. Brander et al., 2013).

Further development of SDMs in the marine realm should also be inspired from extensive experience with related models in terrestrial applications, especially with respect to dynamic (state-dependent) integration of population and community level processes (Robinson et al., 2011, Fordham et al., 2013) and to physiological limits and adaptive evolution (Catullo et al., 2015), although not all concepts may be transferable to marine systems. The trophodynamic model Ecospace offers functionality similar to SDMs in its 'habitat capacity' response functions, with dynamic integration of spatial processes into the food web context and the option to link to spatial-temporal input (Steenbeek et al., 2013, Christensen et al., 2014a). As end-to-end models usually resolve spatial and community processes, they possess high capacity for more integrative projections of distribution changes (e.g. Rose et al., 2015).

IBMs have been used to describe larval growth and dispersal in high spatial resolution and integrate sampling data (Lett et al., 2010, Hidalgo et al., 2012). Energy allocation principles may be able to trace recruitment success and the evolution of spawning migrations, but need to be informed by more experimental research and coupled between all life stages (cf. Fiksen et al., 2007, Peck and Hufnagl, 2012). Integrative physiological concepts may be used to generalize changes in relative performance of interacting or competing species (Pörtner and Farrell, 2008, Pörtner, 2012). Additionally, more observational, telemetric and demographic data will be needed to improve incorporation of spatial structure and processes (Runge et al., 2010, Metcalfe et al., 2012).

The incorporation of active migration of later life stages and of spatially resolved and potentially patchy distribution of spawning habitat, and in general the integration of lower and higher level processes represent significant challenges in achieving reliable projections about spatial shifts of fish stocks under climate change. In the near future, these challenges will probably be handled using coupling of different modelling approaches and end-to-end models along with case-dependent strategies for reduction of complexity. In the meantime, adequate use of simpler representations will remain valuable for management and policy advice.

Question 5: What will be the socio-economic impacts and the implications for management of changing marine ecosystems?

Climate-mediated changes in marine ecosystems and fish stocks can have different socio-economic effects in different regions and affect a range of ecosystem services used by human societies (Cooley et al., 2009, Sumaila et al., 2011, Pörtner et al., 2014). Climate change effects can interact with human uses, e.g. by fishing, and can be modified by other short-term anthropogenic drivers such as eutrophication or pollution and amplified or even overridden by general socio-economic developments (Perry et al., 2010). Therefore, an analysis of ecosystem impacts of climate change in exploited marine systems, and especially the assessment of their socio-economic consequences, need to link biological and socio-economic research approaches, building on an identification of involved ecological processes and incorporating interactions with human societies (Le Quesne and Pinnegar, 2012, Hilmi et al., 2013).

Different model classes have been used to assess management or adaptation strategies to climate change effects for fish stocks and marine ecosystems, but societal dynamics have until recently received little attention (Barange et al., 2010). Socio-economic dynamics and background scenarios related to fish markets have been integrated into extended population dynamic or 'bioeconomic' models (e.g. Merino et al., 2010, Norman-Lopez et al., 2013), species distribution models (Cheung et al., 2010, Jones et al., 2014), mass-balance models (Christensen et al., 2015), size spectrum and trait-based models (Woodworth-Jefcoats et al., 2013, Barange et al., 2014, Zimmermann and Jorgensen, 2015) and the end-to-end model Atlantis (Fulton et al., 2011, Griffith et al., 2012).

Societies have a range of adaptation options to climate change-induced changes, e.g. increase of fishing effort, economic diversification, or change of fishing grounds (Perry et al., 2011). Incorporating adaptive societal responses and their social and cultural conditions, based on observations and models, can enable improved governance and increase resilience of marine social-ecological systems (Folke, 2006, Miller et al., 2010, Schlüter et al., 2012). Societal dynamics can be implemented e.g. using network models (Janssen et al., 2006) or arising from individual actor behaviour in 'agent-based' models (Gilbert and Terna, 2000).

The advancement of integrated models is promising to achieve more accurate projections of the future states of social-ecological systems (Österblom et al., 2013, Griffith and Fulton, 2014), and models for informing fisheries management under changing environmental drivers have been developed (e.g. Cooley et al., 2015). Advances are necessary in identifying specific societal adaptive capacities in response to regionally expected impacts of climate change, based on reliable quantitative data. Beyond fisheries, quantification of impacts of other marine industries and on the provision of other marine ecosystem services is needed, such as tourism, carbon sequestration, or coastal protection (cf. Beaumont et al., 2007, Liquete et al., 2013). Conceptual challenges relate to scale differences and the identification of processes which determine adaptive capacities of natural and social systems (Perry and Ommer, 2003, Griffith and Fulton, 2014).

Conclusions

The integration of physiological and ecological processes has great potential to advance ecological models for fish. Representation of mechanisms mediating climate effects can be increased by 1) identifying key processes for the question of interest across levels of organization, 2) using and coupling models which represent the key processes, and 3) incorporating experimental results from a range of conditions and across life history stages and generations.

For investigating the direct effects of multiple environmental drivers on fish, models should be adapted sensibly to integrate experimental data and investigate organism-level trade-offs and sensitivities, e.g. by making use of energy allocation principles. The investigation of changes in population dynamics can benefit from increased model detail in the representation of effects on early life stages and reproduction. Understanding of acclimation and evolution under climate change can be advanced by assessment of functional traits and specifically designed experiments. Marine community shifts under multiple drivers can be better anticipated by analysis of food web structure and quantification of functional responses. Research on stock distribution shifts and socio-economic impacts of changes in marine living resources should increasingly incorporate results on the co-determination of spatial movement and dispersal by behavioural fish responses and trade-offs in energy allocation and community interactions, and improve the integration of societal dynamics. Coupling of models to address these higher-order questions can be informed e.g. by data on food energy content and transfer, and by behavioural observations of fish and people.

Improvements in projection capacities by integrating these processes, and potential trade-offs e.g. with regard to parameter uncertainties, will have to be verified on a case-to-case basis. Scaling issues will have to be addressed to reduce the complexity of models while maintaining sensitivities across scales: a focus should be put on the identification of mechanisms and techniques that span levels of description and can couple specialized models without levelling out heterogeneity and variability at lower levels that may be decisive for higher level dynamics. Examples include the super-individual concept in individual-based models and physiological concepts for estimating organism sensitivity towards multiple drivers.

To this end, planning of experiments and structuring of models should be coordinated more closely in the research process and based on an improved dialogue between modellers and experimentalists. This will warrant meaningful physiological experiments and an improved integration of both empirical results and mechanistic understanding of effects into existing and future models.

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Paper 2: Stakeholder-Informed Ecosystem Modeling of Ocean Warming and Acidification Impacts in the Barents Sea Region

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Stakeholder-Informed Ecosystem Modeling of Ocean Warming and Acidification Impacts in the Barents Sea Region

Stefan Koenigstein[1]*, **Matthias Ruth**[2] **and Stefan Gößling-Reisemann**[1]

[1] Sustainability Research Center (artec) and Department for Resilient Energy Systems, University of Bremen, Bremen, Germany, [2] School of Public Policy and Urban Affairs, Department of Civil and Environmental Engineering, Northeastern University, Boston, MA, USA

Climate change and ocean acidification are anticipated to alter marine ecosystems, with consequences for the provision of marine resources and ecosystem services to human societies. However, considerable uncertainties about future ecological changes and ensuing socio-economic impacts impede the identification of societal adaptation strategies. In a case study from the Barents Sea and Northern Norwegian Sea region, we integrated stakeholder perceptions of ecological changes and their significance for societies with the current state of scientific knowledge, to investigate the marine-human system under climate change and identify societal adaptation options. Stakeholders were engaged through personal interviews, two local workshops, and a web based survey, identifying the most relevant ecosystem services potentially impacted and developing an integrated system dynamics model which links climate change scenarios to the response of relevant species. Stakeholder perceptions of temperature-dependent multiannual fluctuations of fish stocks, interactions among fish, marine mammal, and seabird populations, and ecological processes such as primary production are represented in the model. The model was used for a discourse-based stakeholder evaluation of potential ecosystem changes under ocean warming and acidification scenarios, identifying shifts in ecosystem service provision and discussing associated societal adaptation options. The results pointed to differences in adaptive capacity among user groups. Small-scale fishers and tourism businesses are potentially more affected by changing spatial distribution and local declines in marine species than industrial fisheries. Changes in biodiversity, especially extinctions of polar species, and ecosystem functioning were a concern from an environmental conservation viewpoint. When considering potential additional impacts of ocean acidification, changes observed in the model projections were more uniformly valued as negative, and associated with an increased potential for conflicts among user groups. The stakeholder-informed ecosystem modeling approach has succeeded in driving a discussion and interchange among stakeholder groups and with scientists, integrating knowledge about climate

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Beate M. W. Ratter,
University of Hamburg, Germany

Reviewed by:
Carolyn J. Lundquist,
National Institute of Water and Atmospheric Research, New Zealand
Edward Jeremy Hind,
Manchester Metropolitan University, UK

***Correspondence:**
Stefan Koenigstein
koenigstein@uni-bremen.de

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change impacts in the social-ecological system and identifying important factors that shape societal responses. The approach can thus serve to improve governance of marine systems by incorporating knowledge about system dynamics and about societal uses and values.

Keywords: participatory modeling, marine ecosystem services, marine systems, climate change adaptation, ocean acidification, Barents Sea

INTRODUCTION

Under global climate change, the oceans are undergoing profound changes. Ocean warming, acidification (decreasing pH values), deoxygenation (insufficient oxygen levels), and other physical and chemical changes are anticipated to affect marine species, drive changes in marine ecosystem structure and dynamics, and impact the productivity of marine ecosystems and the provision of ecosystem services to human societies (Pörtner et al., 2014; Gattuso et al., 2015). Ocean warming is already observed to lead to poleward shifts in the spatial distribution of marine organisms, facilitating species invasions into regional ecosystems, and causing local or regional extinctions by exceeding the thermal tolerance limits of organisms (Poloczanska et al., 2013). Ocean acidification, the decrease in water pH via increasing solution of atmospheric CO_2, is anticipated to impact different organism groups in marine ecosystems (Kroeker et al., 2013). Increased mortality and structural damages observed in laboratory experiments with early life stages of fish under future ocean pH values cause concern about the future of fish stocks (Munday et al., 2010; Denman et al., 2011).

Nevertheless, considerable uncertainty compounds the analysis of ecosystem-level effects of multiple climate change drivers, and their interactions with anthropogenic impacts and human uses (Gattuso et al., 2015; Riebesell and Gattuso, 2015). Ecological models are increasingly playing an important role in an integrated assessment of these effects in marine social-ecological systems (Perry et al., 2010; Osterblom et al., 2013). A wide range of human uses and activities will be affected by climate change impacts on marine systems (Allison and Bassett, 2015). Economic and nutritional dependence on marine resources, and vulnerability toward change differs strongly among countries (Allison et al., 2009). While societies have a range of options to adapt to changes in marine living resources, e.g., increase of exploitation efforts or economic diversification, these depend on economic, social and cultural conditions (Perry et al., 2011; Haynie and Pfeiffer, 2012). The ecosystem services concept (Millenium Ecosystem Assessment, 2005) can serve as a framework for assessing changes in societal benefits provided by marine ecosystems, like food provision from fisheries and aquaculture, carbon uptake and climate regulation, bioremediation, and nutrient cycling, or recreation and cultural services (Beaumont et al., 2007). To improve the scientific basis for quantifying changes in the provision of these services and important trade-offs among services, assessment methodologies must be equipped to capture the multidimensional nature of the value of ecosystems, to enable better informed individual and institutional decisions and improve governance mechanisms (Daily et al., 2009; Kittinger et al., 2014). Since ecosystem services are ultimately defined by society and governance decisions should be more effective when supported by affected societal groups, there is strong rationale for stakeholder participation as an integral part of ecosystem assessment processes.

We present a regional case study on climate change impacts on ecosystem service provision in the Barents Sea and Northern Norwegian Sea area. In Norway, the oceans play an important economic and cultural role. The fisheries sector with a production of 2.3 million tons of fish and 12.800 employees in 2011 makes the country the world's second-largest seafood exporter after China (FAO, 2013), divided between industrial off-shore fishing, aquaculture mostly of Atlantic salmon, and small-scale coastal fisheries. Main capture fish species are Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), capelin (*Mallotus villosus*), Atlantic mackerel (*Scomber scombrus*), saithe (*Pollachius virens*), and other whitefish. Norway's national fisheries management is generally seen as well-regulated, science-driven, internationally cooperative and sustainable (FAO, 2013, 2014). Fishers participate in management via national and regional fisheries associations and provide catch information (Johnsen, 2013; Jentoft and Mikalsen, 2014). In recent years, good management and favorable environmental conditions under ocean warming have facilitated large fish stock sizes such as of Barents Sea cod (Eide et al., 2013; Kjesbu et al., 2014). Nevertheless, future climate change represents a considerable challenge for Norwegian fisheries management (Harsem and Hoel, 2012), and recent integrated, ecosystem-based coastal zone management plans recognize important knowledge gaps with regard to the impacts of climate change and ocean acidification (Hoel and Olsen, 2012).

The Barents Sea is projected to experience rapid ocean warming in the next decades, which together with a reduced extent of Arctic sea ice is already leading to pronounced changes in ecological community composition, spatial distribution and biomass of fish stocks, and thus, fisheries provision (Hollowed and Sundby, 2014; Fossheim et al., 2015; Kortsch et al., 2015). At the same time, Arctic and subarctic areas will be affected by the strongest pH changes expected worldwide until the end of the century, with Arctic waters becoming corrosive to some shell-producing organisms. Thus, changes in food web structure and also direct impacts on fish stocks are expected, but still subject to high scientific uncertainty (AMAP, 2013). The comparatively simple food web in the Barents Sea is expected to be more vulnerable to impacts on certain keystone or bottleneck species than ecosystems with higher species diversity (Wassmann et al., 2006; Duarte et al., 2012).

We constructed an ecological model of the expected impacts of ocean warming and acidification on marine ecosystem services in the Barents sea region, based on input from potentially affected stakeholder groups (Costanza and Ruth, 1998; Voinov and Bousquet, 2010). We incorporated stakeholder input regarding which ecosystem elements and processes to include in the model, and used stakeholder perceptions to assess which human uses and societal groups may be impacted by environmental changes in the region. Thus, stakeholders served as representatives of society, to integrate local knowledge and concerns, identify relevant ecosystem elements and services, evaluate projected changes under scientific uncertainties, and identify societal adaptation options (Walker et al., 2002). This integrated social-ecological systems approach is applied with the aim of increasing resilience of marine-human systems and improving adaptive capacity (Hughes et al., 2005), to discover governance options for a more sustainable use of marine resources under climate change.

MATERIALS AND METHODS

Stakeholder Consultation

For an initial compilation of potential ecosystem changes under climate change in the focus area, the scientific literature was screened for an overview of the problem (reviews on regional ecosystems and on climate change and ocean acidification impacts, reports of expert groups, news, and outreach products produced by regional scientific institutes). To compare these findings to relevant topics of concern for the users, internet-based news portals aimed at regional stakeholders, archives of newspapers of general interest and for user groups (e.g., fisheries magazines) were screened for recent prominent topics. Ten interviews with regional scientific experts with a background in marine ecology, governance of marine resources and areas, oceanography, ecosystem modeling, fisheries science, and other disciplines, further helped to identify potentially affected ecosystem services and stakeholders. Interviews with 25 stakeholders of potentially affected groups from Norway and Russia were conducted in different locations in Norway (Oslo, Bergen, Tromsø, Bodø, Lofoten Islands, Finnmark, Svalbard) or via email between March and September 2013. Stakeholders included representatives from fishing associations and aquaculture companies, individual small-scale fishers, tourism operators (hotels/camps, sport fishing, whale watching), non-governmental organizations (including environmental conservation and indigenous Sami groups), and governmental agencies (Fisheries and Environmental Directorates). The personal interviews aimed at identifying (1) the general socio-economic situation of participants, (2) perceptions and concerns about regional ecosystem impacts of climate change, (3) the communication between science, politics and stakeholders about expected impacts, (4) societal impacts and adaptation options to climate change, and (5) management options and political adaptation strategies (Supplemental File S1: Interview questionnaire). Participants were also asked for their personal opinion on further potentially affected societal groups, to open up the investigation to ecosystem services and user groups not initially identified.

The most frequently mentioned ocean uses, climate-related concerns, and ecosystem interactions from stakeholder interviews which could be linked to elements of the marine ecosystem, were compiled to form the basis of the model (**Table 1**). A model-building workshop with stakeholders was held in Bergen, Southern Norway in October 2013, where stakeholders were introduced to the topics of the research project and the current state of scientific knowledge about climate change impacts on marine ecosystems. A draft of the model structure based on the identification of relevant ecosystem services and elements from the interviews was presented. Stakeholder comments on the model structure and requests for further elements and services to be included were collected to inform further model development (Koenigstein and Goessling-Reisemann, 2014).

Integrative System Dynamics Model

A system dynamics model (Costanza and Ruth, 1998) was developed in the modeling software STELLA 9.1, and later converted to STELLA Professional 1.0 (www.iseesystems.com). Its structure was based on the most relevant ecological elements and processes that can be linked and quantified using empirical biological results. Graphical icons for species and ecosystem services were designed and integrated into the model interface to make the model structure more easily accessible to stakeholders. The model was based on a multi-species population structure, with biological processes governing population dynamics of the integrated species, and interactions among species represented by predation and consumption (**Figure 1**).

The model structure incorporates the marine species of high importance to the various stakeholder groups, and the most commonly mentioned biological processes. Some ecologically similar species were aggregated to groups ("other baleen whales," seals, "other seabirds") to limit model complexity, and/or combined in modules (tooth whales, baleen whales, seabirds) in the model interface. Aggregate representations of lower trophic levels (one phytoplankton and three zooplankton groups) were used to base the biomass flow through the food web on a primary production process, integrating stakeholder concerns about primary production and the ecosystem services of carbon uptake and export (**Figure 1A**). Due to the importance of fish stock recruitment in stakeholder concerns, fish populations were divided into two to four life stages and embedded in a self-enhancing feedback of reproduction and recruitment processes.

Ocean warming and acidification were incorporated as changes in fish and zooplankton consumption and growth, based on physiological thermal growth windows (Pörtner and Farrell, 2008) and assuming an increasing loss of metabolic energy under acidification reaching up to 10% of the total energy uptake (**Figure 1C**). Driver scenarios for temperature and pH were incorporated based on IPCC (Intergovernmental Panel on Climate Change) ensemble earth system model projections for the Barents Sea under the RCP (Representative Concentration Pathway) 8.5 ("business-as-usual") emission scenario (AMAP, 2013; Bopp et al., 2013; Collins et al., 2013). Temperature was additionally adjusted to undergo seasonal fluctuation and an inter-annual oscillation with a period of 8 years (**Figure 1B**),

TABLE 1 | Stakeholder concerns and observations with regard to climate change impacts on marine ecosystems, from personal interviews with stakeholders from the fisheries sector (F), tour providers and other tourism businesses (T), and environmental and other non-governmental organizations (E), ranked by sum over sectors (seven participants for each sector, one additional aquaculture representative for the fisheries sector).

Species of interest and/or concern	*F*	*T*	*E*	*Σ*
Atlantic cod	7	5	5	17
Mackerel	6	5	5	16
Kelp/Seaweeds	2	1	4	7
Herring	6		1	7
King crab	2		3	5
Capelin	3		1	4
Atlantic Halibut	1	2	1	4
Haddock	2		2	4
Shellfish (mussels, scallops, etc.)	2	1	1	4
Zooplankton	2		1	3
Sea urchins		1	2	3
Blue whiting	3			3
Lobster	0	1	1	2
Shrimps	2			2
Atlantic salmon			2	2
Seabass	1		1	2
Saithe	1		1	2
(Cold water) corals	1		1	2
Dolphins and pilot whales		2		2
Minke whales	1	1		2
Orcas		2		2
Redfish	1	1		2
Seabirds		1	1	2
Seals		1	1	2
Sperm whales		1	1	2
Total: marine mammals	1	7	2	10
Total: fish	30	14	20	64
Total: benthic organisms	12	4	12	28

General ecosystem observations	*F*	*T*	*E*	*Σ*
Feeding interactions/competition	8	3	3	14
Fish larvae/spawning/stock recruitment	5	5	2	12
Natural fluctuations in abundance	5	2	2	9
Primary production	4	1		5
Phenology/migration patterns	2	1	2	5
Local fish declines in fjords			3	3
Regime shifts			2	2
Fish size	1	1		2
Fish more distant to coast		1		1
Observations and concerns linked to climate change				
Fish stock abundance or productivity changes	6	4	4	14
Distribution range shifts	7	2	4	13
Ocean warming	6	2	3	11
Immigrating species	4	3	3	10
Ice melting/ice coverage	4	1	3	8
Sea level rise/wave height		4	3	7
Ocean acidification	3		2	5
Oceanic currents	2		1	3
Threatened Arctic species		1	2	3
International disputes	3			3
Habitat reduction		1	1	2
Snow melt		2		2
Increased precipitation and nutrient influx			2	2
Harmful algae blooms			2	2
Extreme weather events	1		1	2
Milder winters	1			1
Fish migrations to deeper waters	1			1
Anoxia in fjord depths			1	1

Number of instances mentioned across interviews for species of interest or concern (only species mentioned more than once), general ecosystem observations, and observations or concerns explicitly linked to climate change impacts (detailed interview questions given in Supplemental File S1).

mimicking the natural fluctuations linked to the North Atlantic Oscillation (Ottersen et al., 2001) as mentioned in the stakeholder interviews. Marine mammal and seabird populations were modeled without direct effects of warming or acidification, as empirically observed changes are mostly indirectly caused through food web changes (Sandvik et al., 2005; Simmonds and Isaac, 2007). Fishing was incorporated as an additional biomass extraction process for fish and minke whales (*Balaenoptera acutorostrata*), defined as fixed relationships between stock sizes and landings in the following year, based on past quota agreements. Details of model parameterization, calibration and validation will be described in a separate publication, as we focus on the incorporation of stakeholder perceptions into the model and their assessment of the results here. The graphical interface of the model included dynamic displays of the states of the relevant biomass compartments and other indicators in the model over time, grouped in combined graphs aimed at each of the three stakeholder groups in the model valuation workshop (**Figure 1D**).

Model Evaluation and Identification of Adaptation Options

A web-based online survey was prepared to evaluate the relative importance of socio-economic framing factors identified in the interviews, created in a Norwegian and an English version using the platform Limesurvey by the provider Limeservice (www.limeservice.com). This served to prepare input for the discussions in the second workshop and helped the creation of framing scenarios at a later time. Factors already included in the model (e.g., ocean temperature or marine organism abundances) were not surveyed.

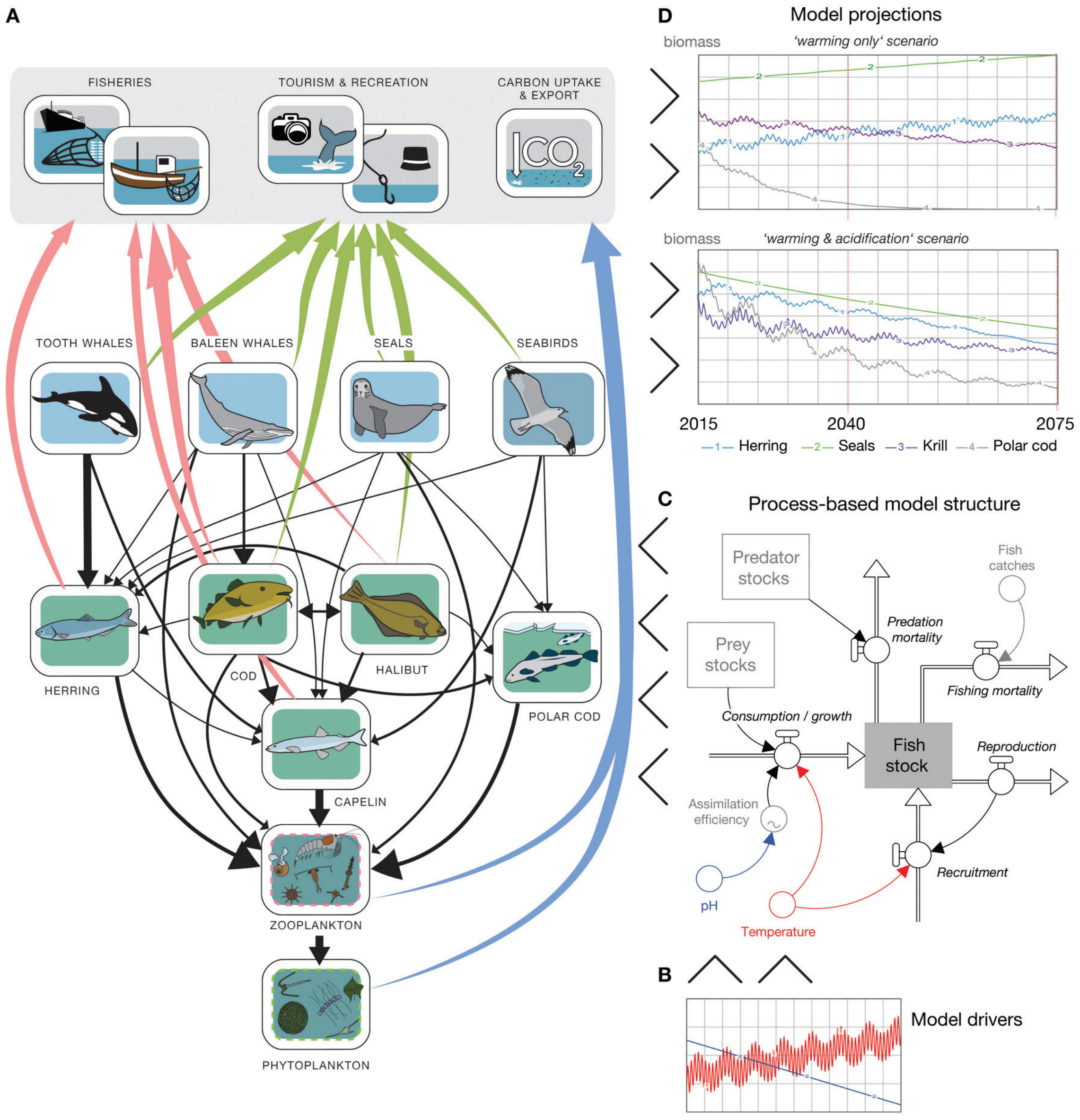

FIGURE 1 | Structure, drivers, and exemplified projections of the developed system dynamics model. (A) Top-level interface of the model, with modules of the most relevant species interacting in the marine food web, and links to provided ecosystem services (gray shaded top row). Thin black arrows mark predation on other species in the food web, wide colored arrows mark connections to the ecosystem services fisheries (pink), tourism (green), and carbon uptake and export by primary production and plankton mortality (blue). Icon design for organism and ecosystem services by Leonard Rokita, Bremen. **(B)** Temperature and pH over model time frame as drivers of the model, affecting biological processes. **(C)** detailed structure of the species included in the model in system dynamics notation, based on biomass flows (thick arrows) which determine the state of each fish stock and the dynamic links to other stocks in the model (boxes), and are influenced by the environmental drivers temperature and pH, and by fish catches (circles, thin arrows). **(D)** examples for resulting model projections under "warming only" and "warming and acidification" scenarios (different biomass scales), which qualitatively reproduce natural fluctuations and were evaluated by stakeholders at two time points, the model years 2040 and 2075 (red dotted lines).

A second stakeholder workshop for model valuation was held in Tromsø, Northern Norway in June 2015 with representative stakeholders from fisheries, tourism and environmental conservation. Structure and functioning of the parameterized model was explained, model assumptions and scientific uncertainties discussed, and model runs performed under two scenarios, driven by ocean warming alone, and warming and acidification combined, respectively. At two time points in the simulation—the year 2040 and at the end of the simulation in the year 2075—model runs were stopped and stakeholders asked to discuss the developments in stock levels and ecosystem indicators in groups by sector. Stakeholders agreed on a rating in terms of the significance for their business and interests on a scale of +5 to −5, where: +5 refers to a high preference, i.e., the best imaginable event for participants' business or interests; 0 is neutral, and −5 is catastrophic for economic survival or the stakeholders' main interests.

Then, stakeholders were asked to decide whether they needed to change their business, take organizational decisions or other steps to adapt to the projected ecosystem changes. Groups discussed and proposed possible adaptation options for their sector. Finally, general societal adaptation options were discussed among all stakeholders, and common policy recommendations developed among the participants of the different sectors. During this process, stakeholders had access to all model variables and indicators (dynamics of species abundance and processes, biodiversity and ecosystem indicators, etc.), which together reflect the complexity of the underlying ecosystem.

RESULTS

Stakeholder Perceptions and Concerns

Marine species most often mentioned by stakeholders with regard to ecosystem changes in the interview series were the fish species Atlantic cod, mackerel and herring, as well as kelp and seaweeds, king crabs, and followed by other fish species (**Table 1**). Stakeholders exhibited a high level of ecological knowledge in their observations and concerns about marine organisms. The most prominent environmental changes linked to climate change were distribution range shifts of fish and other marine species, changes in fish abundance or productivity of fish stocks, an increased occurrence of newly immigrated species such as mackerel, and the factor which was attributed as the main cause of these changes, ocean warming. When describing their observations and/or concerns, stakeholders frequently mentioned ecological processes, mainly feeding interactions, e.g., among herring, cod and capelin, fish stock spawning and recruitment, and inter-annual environment-related fluctuations and variability of fish stocks. Ocean acidification as a relatively newly discovered additional factor was known to fewer stakeholders, but was incorporated as a model driver as it was a central topic of the project, and because it could be linked to warming effects via physiological mechanisms. Upon presentation of scientific results from laboratory experiments on ocean warming and acidification at the workshops, acidification was perceived as an additional concern, but uncertainty with regard to effects in the ecosystem was recognized.

A compilation of stakeholder statements and backgrounds on the topics in the interviews and the first workshop was published in an open-access report (Koenigstein and Goessling-Reisemann, 2014). Based on these interview results and discussions at the model-building workshop, the ecosystem elements and services of highest relevance to stakeholders, and which were suitable for integration in a foodweb-based model consistent with ecological knowledge, were selected to represent ecosystem service provision in the model. These were the commercially harvested fish stocks Atlantic cod, herring, capelin and halibut, as well as minke whales for food provision via fisheries. Mackerel, which was regularly mentioned in interviews as a newly immigrated fish species in Northern Norway, was not integrated because data on feeding interactions is not yet available. For tourism and recreation services, baleen whales (Humpback whales, *Megaptera novaeangliae*, and fin whales, *Balaenoptera physalus*), sperm whales (*Physeter macrocephalus),* killer whales (*Orcinus orca*), Atlantic puffin (*Fratercula arctica),* and other seabirds, as well as Greenland halibut (*Reinhardtius hippoglossoides*) and Atlantic cod stocks relevant for sports fishing were integrated. To represent a potentially threatened Arctic species dependent on sea ice, and because experimental data on warming and acidification impacts was available, Polar cod (*Boreogadus saida)* was also included. Lower trophic levels (phyto- and zooplankton) integrated primary production and food availability for fish. These elements thus represent the ecosystem services of food provision to industrial and small-scale fisheries, tourism and recreation as income-generating and cultural services (sports fishing, tours for whale, sea lion, and seabird watching, and other nature-related activities), and regulating and supporting services by carbon uptake via primary production and carbon export via sequestration. Species diversity (Shannon index) was incorporated as an indicator of ecosystem state on demand of stakeholders from the environmental sector in the model valuation workshop.

In the interviews, the most prominent socio-economic concern unrelated to climate change was pollution by oil drilling, mining sewage, dumping, or other sources, followed by fish market prices and labor availability. In the web-based survey conducted to gain additional insights on socio-economic factors and to prepare the valuation workshop, participants (12 completely answered surveys) rated sustainability-oriented management of resources, oceanographic changes, fish price, global economic growth and fishing quota as the most important external factors for their business or interest, with differences in importance among sectors (**Figure 2**).

Stakeholder Valuation of Model Projections

Stakeholder valuations of model projections in the second workshop differed markedly among stakeholder groups (Supplemental File S2: stakeholder valuations). Stakeholders noted that their valuations of the model projections depend on the trend displayed up to the stop in simulation time, i.e., the same stock level was rated more negatively when stock levels had been descending to this level as opposed to when they had ascended. The full development was only revealed after the simulation restarted to complete the run, reflecting uncertainty about the future in decision making in real life.

Projected changes in the warming-only scenario included increases in most fish stocks, orcas and "other seabirds," and decreases in sperm whales, seals, krill, and carbon export associated with zooplankton mortality. This scenario was rated as positive for fisheries, but as negative by tourism stakeholders due to decreased sperm whale levels, and caused concern for environmental conservation due to declines in species diversity and the collapse of Polar cod (**Table 2**). In the "warming and acidification" scenario, most species showed declines due to the energetic loss under ocean acidification incorporated in the model. Stakeholders from the fisheries sector viewed the projections for 2040 as "economically painful," given locally strong socio-economic impacts for fishers, and possible conflicts

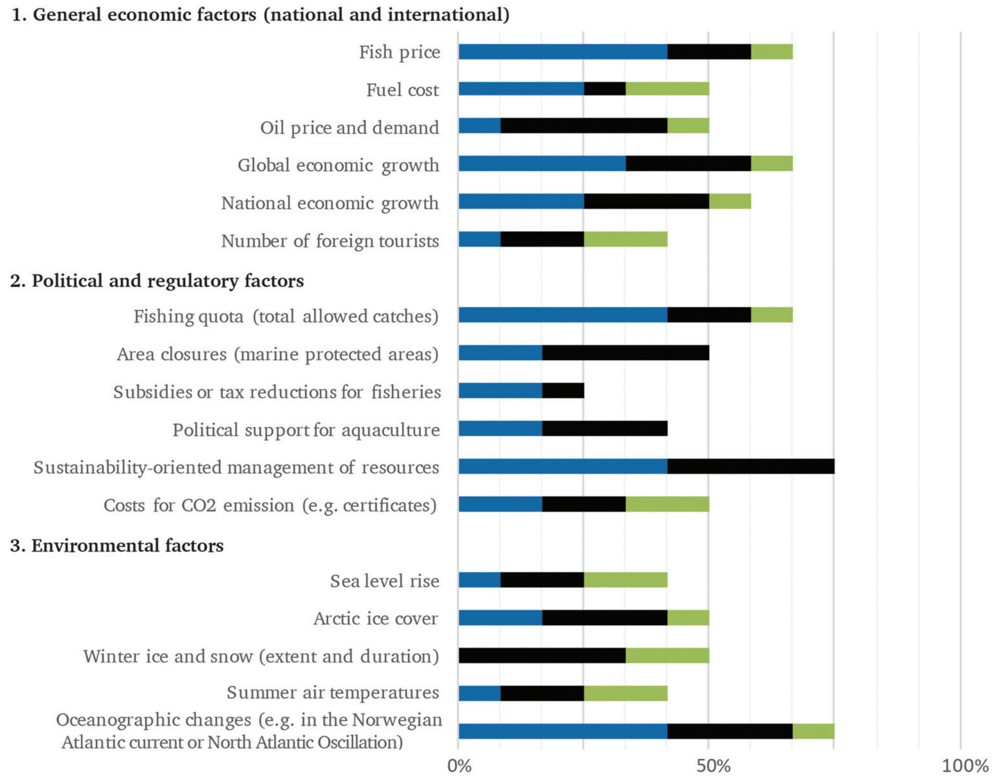

FIGURE 2 | Importance of selected economic, political and regulatory, and environmental framing factors for the business or interest of regional stakeholders (percentage of stakeholders denoting factors as "important") from a web-based survey, *N* = 12. Colors indicate self-designated sectors of participants: fisheries (blue, five participating stakeholders), environmental conservation (black, four persons) and tourism (green, three persons).

between large vessels and small-scale fishers. Further decreased stocks and the collapse of the Atlantic cod stock toward the end of the simulation in the year 2075 were perceived as leading to strong socio-economic impacts and a challenge for fisheries policies. At the model valuation workshop, present stakeholders from the fisheries sector noted that haddock, saithe, and the increasingly immigrating mackerel were also important species for regional fisheries (or expected to become important in the future), and should be added to the model.

Adaptation Options

Continued adjustment of fishing quota and intensified regulation of stock management were proposed as an adaptation option to climate change effects for fisheries in the interviews and the valuation workshop. Stricter quotas in times of declining stocks, potentially aided by a diversification of quotas and the regulation of by-catches may support a recovery of stocks. Larger vessels can also respond by moving further out to open waters, following moving fish stocks. In the valuation workshop, switching fisheries to other species (e.g., crab, mackerel, mollusks) was viewed as an additional option for reducing economic losses. Also, in the opinion of the stakeholders, increased fines for illegal fishing and catch limitations for tourist fishing may become necessary. Increased research on and investment in aquaculture as an alternative for food provision was discussed as a further adaptation option with explicit mention of sustainable and multi-species aquaculture, including species such as seaweeds and sea urchins, depending on market demand and cultural acceptance, and research into zoo- and phyto-plankton as a food source.

The tourism sector would also suffer from local collapses of small-scale fisheries, and generally decreased fish stock levels. One of the suggested adaptation options was to change marketing, focusing less on marine animals and more on cultural heritage and landscapes, and possibly on winter business to make use of the modest declines projected for orcas, and strengthen networking with small-scale fishers. The potential impacts of aquaculture on tourism and the possible use of aquaculture facilities as a tourist option could be explored. Stakeholders from environmental conservation called for an extension of marine protected areas, e.g., for nursery grounds of polar cod and whales, to mitigate ecological impacts of warming and acidification, and a stricter regulation of additional anthropogenic stressors, e.g., pollution by the deposition of mining wastes in fjords.

Commonly agreed policy recommendations of the participants of the second workshop for the projected warming and acidification scenarios were to explore the potential of increased seaweed farming and other alternative aquaculture food. For this, creating training and education, and conserving local economies by appropriate government strategies and incentives would be necessary. Abandoning the consumption

TABLE 2 | Stakeholder concerns about socio-economic impacts on their business or interest, and societal and personal adaptation options to climate change impacts, from personal interviews with stakeholder from the fisheries sector (F), tour providers and other tourism businesses (T), and environmental and other non-governmental organizations (E), ranked by sum over sectors (Σ), seven participants for each sector (one additional aquaculture representative for F).

	F	*T*	*E*	Σ
SOCIO-ECONOMIC CONCERNS AND OTHER IMPACTS ON BUSINESS				
Oil drilling pollution	5	1	1	7
Garbage dumping and other/unspecified pollution	3	2	1	6
Fish market prices	5			5
Mining discharges pollution	1		3	4
Labor market	3		1	4
Ecological impacts of aquaculture	1		2	3
Increasing aquaculture activity	1	1		2
Bad weather		2		2
Unfair distribution of fishing rights			2	2
Heavy metals/seafood health effects	1		1	2
General economic situation		1		1
Seismic exploration		1		1
CO_2 storage	1			1
ADAPTATION OPTIONS TO CLIMATE CHANGE IMPACTS				
Quota adjustments	6	4	1	11
Increase vessel search area	4	2		6
Protected areas/local management	1	1	2	4
New technologies	2		1	3
Reduce or compensate CO_2 emissions	2		1	3
Change target species	2			2
Move business to other location		1		1
Change profession		1		1

Number of instances mentioned across interviews (detailed interview questions given in Supplemental File S1).

of seagull eggs, seals and whales may be advisable, and would necessitate some cultural changes. Under the projected strong stock declines, renegotiations of fishing rights and quotas may become necessary. This would call for the respective political will and actions for conflict resolution among fisheries in Norway.

DISCUSSION

Integration of Stakeholder Perceptions about Climate Change and Ocean Acidification Impacts

All interviewed stakeholders reported plausible climate change effects on marine species, thus their personal accounts substantiated recent scientific results (Fossheim et al., 2015). However, many participants also pointed to the great variability in marine ecosystems in the region, especially fish stocks, which makes it difficult to distinguish environmental fluctuations from long-term change, and thus increases uncertainty about climate-related trends (Johannesen et al., 2012). Because of the high importance of ecological processes and species interactions for stakeholders in the initial interview series, the ecosystem model was based on the foodweb interactions among pelagic and demersal species in the Barents Sea (Bogstad et al., 2015), explicitly integrating the biological processes of interest (Koenigstein et al., 2016). This enabled the incorporation of a large fraction of the species of interest to the stakeholders into the model, and also allowed us to incorporate fishing quotas as the most important adaptation option and anthropogenic driver initially identified in the interviews. However, this choice of model structure came at the expense of being unable to consider spatially explicit distribution shifts and benthic species such as macroalgae, shellfish, or echinoderms. These are often restricted to coastal and fjord habitats and undergo highly localized conditions, e.g., with regard to freshwater influx or hypoxia. In comparison to mental models or other probabilistic models often used in participatory modeling, the deterministic ecosystem model developed here resolves to some degree the emergent behavior of the ecosystem under different conditions, and enables the integration of scientific knowledge, assessing dynamic trade-offs in effects among species and among biological processes under future climate change conditions (see subsection “Towards ecological realism...”).

The main non-climate related concern was pollution, caused by oil and gas exploration, residues from mineral mining along the coasts, or shipping. For whale watching companies, noise pollution from shipping and seismic exploration was a prevalent concern. Due to high scientific uncertainty and highly localized ecological impacts, these concerns could not be incorporated into the model. Also, as aquaculture is not directly linked to marine foodwebs, and was not often mentioned as a factor or concern by the stakeholders in the interview phase, the aquaculture sector was not further considered at this point. Melting of the Arctic sea ice and sea level rise, although of high relevance in the interviews, were also not incorporated due to unclear links to the marine organisms in the model. The scenario-based incorporation of pollution, sea ice and aquaculture is planned for a future extension of the model.

Although impacts of marine ecosystem changes on tourism are far less prominently covered in the scientific literature and the media, the relevance of shifts in marine food ecosystems was immediately obvious to most interviewed stakeholders from the tourism sector. Worldwide, biodiversity loss and reduced aesthetic value of landscapes are expected to impact tourism under climate change, among a range of other factors (Simpson et al., 2008). Tourism in our study region is to a high degree dependent on certain locally abundant species (sperm whales, cod, halibut, seals), thus pointing to highly localized climate change impacts on tourism and recreation, and to the necessity for a detailed assessment of local conditions. Biodiversity and cold-water coral reefs were also mentioned as threatened by climate change, and valuation studies point to a very high willingness-to-pay of the Norwegian public to conserve cold-water coral reefs (Aanesen et al., 2015). Stakeholders of all sectors had agreed in the model-building workshop on conserving the protected status of coral reef areas (e.g., prohibition of trawl fisheries) and not including reefs in the model, putatively reflecting the cultural and existence value of this reefs, but also low economic importance of these areas for fisheries.

Adaptation Options for Stakeholders to Projected Ecosystem Changes

Stakeholder valuations and discussions at the valuation workshop showed that small-scale fisheries and tourism businesses have less, or more constrained adaptation options for the ecological changes projected by the model (cf. **Table 3**). For instance, small-scale fishers often cannot follow moving fish stocks far away from the coast, or have the funds to invest in different gear. The commercially relevant whale-watching and other tour activities in the area are heavily dependent on the sighting probability of certain species (e.g., sperm whales). Adaptation options for sightings decreasing below a critical level would entail drastic changes in the character of tourism activities, with probable reductions in customer numbers and income.

Fishing quota adjustments were seen as the primary adaptation option by fisheries and tourism stakeholders. However, small fishing boat owners, often located in more remote areas and with a partial income from sports fishing tours, perceived quota adjustment as less likely to be a sufficient measure for climate change impacts than stakeholders organized in fisheries associations. In a situation with reductions in several co-used fish stocks, as projected under the combined warming and acidification scenario, suggested adaptation options ceased to be sector-exclusive, and conflicts were expected to increase among industrial, small-scale, and sports fishing, when catch efforts would be increasingly concentrated on the remaining stable species (e.g., halibut). Conflict potential among and within sectors led to the recognition of the need for increased cooperation and networking among user groups. Increased investment in aquaculture was a heavily discussed adaptation option at the valuation workshop, which is very relevant worldwide in the context of securing food provision under overfishing of many fish stocks (FAO, 2014). Yet, there was a range of concerns from stakeholders with regard to the ecological impacts of aquaculture (pollution from nutrients and antibiotics, escaped individuals and parasites, spatial use conflicts). Also, the viability of this option depends on economic factors and the continued provision of small pelagic fish by capture fisheries for fish meal production. Stakeholders agreed on the need for increased research on ecological impacts and more sustainable methods of aquaculture production.

Environmental conservation stakeholders adopted a broader view on ecosystem functioning, asking for inclusion of a biodiversity indicator during the valuation workshop, and thus brought a precautionary aspect into the discussion. Declines in zooplankton and phytoplankton biomass levels were also negatively rated by stakeholders from the fisheries sector, reflecting concerns about indirect impacts on fish stocks. The discussion among different stakeholder groups was also shaped to some extent by implicit societal values, as e.g., the high cultural importance of the Atlantic cod fishery in Northern Norway and the significance of marine species for the coastal indigenous Sámi were mentioned. In the discussion of societal adaptation options, a focus on options which were undisputed among the workshop participants was observed, while options which would have more potential for conflicts (e.g., total catch bans or area closures for certain uses) were avoided topics. The group evaluation approach thus reproduced certain factors and constellations which govern societal decision-making, e.g., implicit valuing, social agreement, and power balances among stakeholders.

These results point to considerable differences in adaptation capacities to climate change impacts among stakeholders in the Northern Norwegian Sea and Barents Sea region, with less resilient small-scale fishers and tourism businesses. Potential food-web mediated impacts e.g., on whales and seabirds or lower trophic levels would thus lead to governance-relevant trade-offs among fish provisioning and other ecosystem services. As model development is ongoing and valuations are based on a preliminary, not finally validated version of the model, projections and societal adaptation options at this stage should be regarded as describing possible paths of system behavior. As framing and limiting conditions for stakeholder decisions have been identified during the valuation workshop, stakeholder decisions will be transferrable to validated projections as these become available.

Toward Ecological Realism in Assessments of Climate Change Impacts on Ecosystem Services

The participating stakeholders' main ecological concerns and the most relevant ecosystem services have been integrated into the developed ecosystem model, considering the scientific knowledge

TABLE 3 | Projected ecological impacts of climate change and ocean acidification for which a need for adaptation measures was recognized among 18 stakeholders during a model valuation workshop.

	Impact	Stakeholder rating (2040/2075)	Adaptation option	Condition/drawback
"WARMING ONLY" SCENARIO				
Fisheries	Increased fish stock levels (decreases in capelin 2075)	+4/+3	None (continue good fisheries management)	–
Tourism	Declines in sperm whales and seals, robust fish stocks, increases in orcas	–2.5/–3	Increase tour/search distance	Customer acceptance, increased fuel consumption
Conservation	High biomasses, but decreasing species diversity and polar species	–3/–4	Protect nursery areas (e.g. of polar cod and whales)	Political will
	Decreases in krill and carbon export	–3/–4	–	–
"WARMING AND ACIDIFICATION" SCENARIO				
Fisheries	Fish stock declines/cod stock collapse, zooplankton declines	–2.5/–4	Stricter catch regulations	Social quota redistributions
			Switch target species	Adaptation of catch gear and vessels
			Increased investment in aquaculture	Research on ecological impacts and market acceptance, conflict with fisheries
Tourism	Fish stock declines	–2/–3	Strengthen networks/cooperation with fishers	Resolution of conflicts with fishers
	Decreases in mammals and seabirds	–3/–5	Change tour focus	Customer acceptance for less ecological attraction
Conservation	Decreases in fish, mammals, zooplankton, and biodiversity	–4/–5	Area closures	Use conflicts
			Stricter regulation of other stressors	Economic impacts

Relevant aspects of impacts, with stakeholder rating on a scale from +5 to –5, adaptation options suggested by stakeholder groups, and conditions or potential drawbacks given for these adaptation options. Stakeholder rating +5 reflects an extremely beneficial effect on stakeholder group, –5 reflects a catastrophic effect.

on interactions among ecosystem elements and processes, and helping to build trust in the model. Importantly, this model structure also enables the assessment of indirect ecological climate change impacts (e.g., on marine mammals and seabirds relevant for tourism), thus exploring possible trade-offs among ecosystem services. The process-based structure of the developed model thus enables a more realistic representation of biodiversity (Queirós et al., 2015) and improves the potential for integrating empirical data into climate change projections (Koenigstein et al., 2016).

Models used in ecosystem service assessment are usually highly simplified in order to be easily understandable, and it is a challenge to communicate scientific uncertainty (Ruckelshaus et al., 2013). Our stakeholder-informed ecosystem model development represents an intermediate approach between participatory modeling of stakeholder perceptions without a direct empirical basis of ecosystem behavior, and the use of models e.g., in fisheries management, where a pre-developed model is often brought to the stakeholders and explained by scientists. The model developed and used here reproduces the inter-annual variability in ecosystem dynamics and interdependent fluctuations in fish populations observed by the stakeholders, which are governed by climatic fluctuations linked to the North Atlantic Oscillation (Ottersen et al., 2001; Dalpadado et al., 2012). The reflection of their perceptions in the model enabled the participants to "play" with it during the workshop, exploring effects that were in some cases not expected by the model developers, and finding their own explanations for model behavior. Importantly, it was understood and accepted that the model is not a scientifically proven prediction of the future, but has a range of internal uncertainties e.g., in parameter ranges and structural reliability, and depends on uncertain external parameters with regard to climatic and economic factors. The observed influence of the displayed trend in model projections on stakeholder valuations indicates that stakeholders implicitly extrapolate model trends (and fluctuations) into the future, incorporating the perceived uncertainty into their decision.

A focus on ecosystem services during model development helped to limit model complexity to ecosystem elements that can be linked to societal uses. The ecosystem service concept promises to improve the participation of stakeholders in the management and conservation of marine areas and resources (Kittinger et al., 2014; Leenhardt et al., 2015). However, ecosystem services have been criticized as being too simplistic and too much focused on monetization (Norgaard, 2010; Silvertown, 2015), and cultural services are often not considered in ecosystem service assessments (Chan et al., 2012). We addressed these issues through the use of a process-based ecosystem model, taking into account ecological complexity and variability, and dynamic trade-offs among ecosystem services. Cultural and ethical values were implicitly considered in the discourse-based valuation, which should improve the perceived legitimacy of the derived recommendations (Wilson and Howarth, 2002).

Altogether, our approach to combine stakeholder consultation and ecosystem modeling has been successful in conveying scientific backgrounds and associated uncertainties of climate change processes to stakeholders, motivating stakeholders to participate in the evaluation of impacts and the identification of societally acceptable adaptation options. In a next step, insights on environmental and socio-economic framing factors gained in this study will be integrated into consistent scenarios, and stakeholders will again be involved in finding adaptation options under these scenarios using an extended and validated version of the model. This forms a methodological basis for developing adaptation strategies under scientific uncertainties, that are informed both by knowledge about ecosystem dynamics and by societal uses and values. Characterization of societal responses in connection with the identified properties of the social-ecological system (e.g., species composition, ecological dynamics, human uses and user groups) can yield insights for research in situations with lower data availability and lower level of knowledge of stakeholders, where a comparably high model detail may not be possible.

CONCLUSIONS

Our integrative ecosystem model was designed to consolidate the dynamic simulation of climate change impacts with stakeholder perceptions and concerns. By reflecting the complexity of the biological processes underlying ecosystem dynamics, individual scientific results of ocean warming and acidification research can be integrated and communicated, interactions and uncertainties discussed with affected stakeholders, and trust gained in long-term projections under climate change. Stakeholder-informed ecosystem modeling and discourse-based evaluation are thus useful tools for ecosystem service assessments with multiple user groups, investigating trade-offs and balancing interests under multiple system drivers. Integrative models of intermediate complexity, like the one developed in this work, have the potential to improve understanding of regional social-ecological systems, and help to identify options for adaptive governance of marine systems under climate change and human use.

AUTHOR CONTRIBUTIONS

SG conceptualized the work program. SK conducted and evaluated the interviews, SG and SK conducted and evaluated the stakeholder workshops. SK, MR, and SG conceptualized, developed and validated the simulation model. SK drafted the manuscript, MR and SG contributed to the manuscript and reviewed the final version.

ETHICS STATEMENT

All human participants took part voluntarily and gave oral or written informed consent to participate. They also consented to the use of their statements for the study after anonymization. The purpose and background of the study and the planned use of the results were made transparent prior to interviews, surveys and workshops. The confidentiality of personal information and the right to omit uncomfortable questions or withdraw from the interview at any stage were provided.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00093

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

Supplementary Material S1: Participatory Ecological Modelling of Climate Change and Ocean Acidification Impacts on Marine Ecosystem Services in the Barents Sea Region

Stefan Koenigstein*, Matthias Ruth, Stefan Gößling-Reisemann
*Correspondence: koenigstein@uni–bremen.de

Stakeholder interview questionnaire

Note: The questionnaire was adjusted to stakeholder backgrounds and not all questions posed to every stakeholder. Additionally to the listed questions, follow-up questions were used to validate specific examples for e.g. climate change effects (II.-1.), economic impacts (IV.-1.) and adaptation options (V.-1.), and to further investigate topics of interest.

I. General situation

1. Are you satisfied with how your yields or gains have developed in the last years? Why / why not?
2. What are your biggest concerns about the future development of your business?
3. Which parts of the marine ecosystems are important for you? Which parts do you use?
4. Have you observed changes in the ecosystem in the last years/decades? Which changes?
5. What are your biggest concerns about the future development of the ecosystems?
6. Are you concerned about the effects of climate change on marine ecosystems? Do you think the observed changes may be connected to climate?

II. Climate change & ocean acidification

1. What impacts of climate change are you most concerned about?
2. Which society groups or users of ecosystems do you expect to be first or most strongly impacted?
3. Have you heard about ocean acidification? What?
4. How do you think climate change and ocean acidification could impact marine ecosystems?
5. What consequences might that have for you or your work?
6. How could you / your company react in order to mitigate consequences?

III. Science communication

1. Do science and politics support you / cooperate with you sufficiently?
2. What information do you need from science to plan ahead in the face of possible changes?
3. How should uncertainty of scientific statements be communicated?

IV. Climate change & society

1. What might be the main impacts of climate change on Norwegian societies? Which economic consequences have to be considered?
2. Which might be options for the society to adapt to climate change?
3. What obstacles exist for adaptation strategies?
4. How is the public perception of threat from climate change?
5. How high is the willingness to change one's behaviour or pay costs for the prevention of climate change consequences?

V. Management options

1. Which adaptation strategies / regulation measures (examples) decided by politics would you accept? Which not?
2. What factors and whose interests are relevant in decisions about adaptation strategies?
3. Which social or cultural backgrounds influence the acceptance of adaptation strategies?
4. Which other (national/international) dependencies have to be considered when developing strategies or making decisions?

Supplementary Material S2:

Participatory Ecological Modelling of Climate Change and Ocean Acidification Impacts on Marine Ecosystem Services in the Barents Sea Region

Stefan Koenigstein*, Matthias Ruth and Stefan Gößling–Reisemann

***Correspondence:** koenigstein@uni–bremen.de

	'warming only' scenario				*'warming + acidification' scenario*			
Species		Stakeholder rating				Stakeholder rating		
	biomass change	***Fisheries***	***Tourism***	***Env. protection***	biomass change	***Fisheries***	***Tourism***	***Env. protection***
Atlantic cod	+100% +110%	+4 +3			–20% –90%	–2 –5	–2 –5	–2 –5
Herring	+60 % +100%	+4	+2 +2		–20% –30%	–3 –3	–2 –3	–2 –3
Capelin	–5% –10%	0 –1			–20% –30%	–2 –3	–2 –3	–2 –3
Halibut	0% 0%		0 0		+10% 0%	0	+1 0	
Polar cod	–15% –50%			–3 –5	–10% –20%			
*All fish stocks**		+4 +4		+1 +1			–2	–4 –5
Sperm whales	–10% –15%		–2 –3		–15% –30%		–4 –5	
Orcas	+30% +100%		+1 +2		+40% +25%		+1 –1	
Minke whales	+20% +25%				–5% –15%		0 –1	
Other baleen whales	– 15% –30%		–1 –2		–10% –20%		–3 –3	
Seals	–15% –20%		–2 –2		–15% –30%	+2 +2	–1 –2	
Puffins	+10% +15%		+2 +2		–10% –20%		0 –1	
Other seabirds	+10% +15%		+2 +3		–15% –30%		0 –1	–3 –4
*All mammals & seabirds**			–2.5 –3					–3 –4
Zoo- / Phytoplankton	+15%/ –10% +30%/ –15%			–3 –3	–15% / ± 0% –30% / + 5%	–2 / 0 –3 / 0		–3 / 0 –4 / 0
Species diversity	–5% –10%			–3 –3	–25% –50%			–3 –4
Carbon export	–10% –15%			–2 –3	–15% –20%			

Supplementary Table 2. Ecosystem model projections in relative biomass changes of represented species and species groups, with regard to levels for the year 2015, and stakeholder ratings of these changes on a scale from –5 to +5, under a 'warming only' and a 'warming + acidification' scenario for the model years 2040 (upper lines) and 2075 (lower lines). *Stakeholders were asked for an additional group rating of 'All fish stocks' and 'all mammals and seabirds', to reflect their personal weighting of species.

Paper 3: Forecasting future recruitment success for Atlantic cod in the warming and acidifying Barents Sea

Forecasting future recruitment success for Atlantic cod in the warming and acidifying Barents Sea

Stefan Koenigstein[1,2], Flemming T. Dahlke[1,2], Martina H. Stiasny[3,4], Daniela Storch[2], Catriona Clemmesen[3,4] & Hans-Otto Pörtner[1,2]

[1]University of Bremen, PO Box 33 04 40, D-28334 Bremen, Germany; [2]Alfred Wegener Institute (AWI) Helmholtz Centre for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany; [3]GEOMAR Helmholtz Centre for Ocean Research, Düsternbrooker Weg 20, D-24105 Kiel, Germany; [4]University of Kiel, Wilhelm-Seelig-Platz 1, D-24118 Kiel, Germany

Abstract

Productivity of marine fish stocks is known to be affected by environmental and ecological drivers, and global climate change is anticipated to alter recruitment success of many stocks. While the direct effects of environmental drivers on fish early life stage functioning and survival can be quantified experimentally, indirect effects in marine ecosystems and the role of evolutionary adaptation are still highly uncertain.

We developed an integrative model for the effects of ocean warming and acidification on the early life stages of Atlantic cod in the Barents Sea, termed SCREI (*Simulator of Cod Recruitment under Environmental Influences*). Experimental results on temperature and CO_2 effects on egg fertilization, egg and larval survival and development times are incorporated. Calibration using empirical time series of egg production, temperature, food and predator abundance reproduces age-0 recruitment over three decades. We project trajectories of recruitment success under different scenarios and quantify confidence limits based on inter-individual variation in experiments.

Severe reductions in average age-0 recruitment success of Barents Sea cod are projected under uncompensated warming and acidification towards the middle to end of this century. Although population stochasticity is high, considerable rates of evolutionary adaptation to acidification and shifts in organismal thermal windows would be needed to buffer impacts on recruitment. While increases in food availability may mitigate short-term impacts, an increase in egg production achieved by stock management could provide more long-term safety for cod recruitment success.

The SCREI model provides a novel integration of multiple driver effects in different life stages, enables an estimation of uncertainty associated with inter-individual and ecological variation, and improves the prospects of quantifying impacts under future climate change. The model thus helps to advance towards an improved empirical foundation of climate change impacts on marine fish recruitment, relevant for ecosystem-based assessments of climate change impacts on marine systems.

Introduction

Environmental conditions drive the productivity of marine fish populations, and changing environmental drivers under global climate change will impact recruitment of fish populations via direct and indirect ecological effects, with considerable consequences for marine ecosystems and fisheries. Meta-analyses and statistical models show substantial influence of environmental drivers on fish stock recruitment (Pécuchet *et al.*, 2015; Szuwalski *et al.*, 2015). Ocean warming, changes in primary productivity and fisheries exploitation are already, mostly negatively, affecting recruitment of marine fish stocks (Rijnsdorp *et al.*, 2009; Britten *et al.*, 2016). Ocean acidification due to increasing atmospheric CO_2 levels has only recently been recognized as an additional concern for fish stock recruitment (Denman *et al.*, 2011; Le Quesne & Pinnegar, 2012). While experimental studies have shown ocean acidification acting alone or together with increased temperatures to negatively affect survival of eggs and larvae of some fish species (Baumann *et al.*, 2011; Flynn *et al.*, 2015; Stiasny *et al.*, 2016; Dahlke *et al.*, 2016a), it remains unclear how these effects can be extrapolated to potential impacts on fish populations within marine ecosystems.

As early life stages of marine fish are affected by a wide range of dynamically interacting environmental and ecological drivers over different temporal and spatial scales, fisheries biology approaches to forecasting climatic influences on stock recruitment using stock-recruitment functions and statistical correlation have been largely unsuccessful (Hare, 2014; Rice & Browman, 2014; Subbey *et al.*, 2014). Underlying recruitment variability is the increased sensitivity to environmental conditions of embryo and larval stages, which thus constitute bottlenecks in the tolerance to climate change of marine fish (Melzner *et al.*, 2009; Rijnsdorp *et al.*, 2009; Pörtner & Peck, 2010). Also, selection during these high-mortality stages plays an important role in transgenerational and evolutionary adaptation of the population, determining actual climate change impacts on marine fish populations (Reusch, 2013; Crozier & Hutchings, 2014). To advance understanding of climate change impacts on marine fish, an improved interdisciplinary integration of ecological processes and empirical data over early life stages is thus necessary (Houde, 2008; Metcalfe *et al.*, 2012; Koenigstein *et al.*, 2016).

The Northeast Arctic cod stock in the Barents Sea is of high socio-economic importance and a prominent historical example for research on biotic and abiotic drivers of fluctuating fish stock recruitment (Hjort, 1914). Barents Sea cod recruitment is known to be influenced by temperature, predation, food availability, and physico-oceanographic factors, producing climate-dependent variability of the stock (Ottersen *et al.*, 1994; Sundby, 2000; Ottersen *et al.*, 2014). Northward shifts in spawning habitat along the Norwegian coast have historically been observed in warmer years (Sundby & Nakken, 2008). Interactions with other fish species in the Barents Sea that are also subject to large inter-annual fluctuations mediate indirect environmental effects on the cod stock (Gjøsæter *et al.*, 2009; Bogstad *et al.*, 2015a). Significant statistical correlations have been found among water temperature, cod recruitment, and abundances of different life stages of capelin, herring and zooplankton (Dingsør *et al.*, 2007; Hjermann *et al.*, 2007; Stige *et al.*, 2010). Survival of cod larvae depends on the environmental, food and predator conditions encountered during the drift into the Barents Sea (Hidalgo *et al.*, 2012; Kristiansen *et al.*, 2014; Stige *et al.*, 2015). Direct and indirect effects on cod populations are thus expected under climate change (Pörtner *et al.*, 2008; Mieszkowska *et al.*, 2009; Brander, 2010).

We present a dynamic recruitment model for Atlantic cod *Gadus morhua*, termed *SCREI* (**S**imulator of **C**od **R**ecruitment under **E**nvironmental **I**nfluences; *Skrei* is the Norwegian word for the mature Barents Sea cod), which integrates experimentally quantified effects of temperature and $p\mathrm{CO}_2$ on various early life stages. A biologically detailed description of ontogenetic development in the model enables the integration of experimentally quantified egg and larval mortality rates and stage durations. We assume that survival in the field, in addition to experimentally recorded mortalities, is affected by foodweb-mediated (predation and starvation) and non-temperature-related natural mortalities (e.g. by the factors UV radiation and dispersal into unfavorable conditions). To estimate the contributions of these environmental factors, the model is calibrated to empirical survey estimates of cod age-0 abundance in the Barents Sea, using estimates of total egg production, predator abundance and food availability. Trajectories of future cod age-0 recruitment are then projected under future ocean warming and acidification and scenarios of population adaptation and food-web changes. The model demonstrates an approach for the integration of empirical data from experiments conducted under current and projected future environmental conditions and long-term field observations, making SCREI a valuable tool for advancing projections of climate change impacts on marine fish stock recruitment in an ecosystem-context.

Materials and methods

Early life stage model structure

A detailed model of Atlantic cod early life stages was constructed in the system dynamics modelling software STELLA Professional 1.0, which constructs finite difference equation systems from a graphical 'stocks and flows' annotation (www.iseesystems.com). Different ‘conveyor’ stock elements in a row were used to model daily cohorts of individual cod eggs and larvae, with temperature-dependent egg hatching and larval development times in days as the ‘transit time‘ (number of sub-stocks in the conveyor), and temperature- and CO_2-dependent daily mortalities modelled as ‘leakage‘ flows of the conveyors (**Figure 1**). This is conceptually equivalent to stage-structured fish stock assessment models (Deriso *et al.*, 1985; Fournier *et al.*, 1998). To provide good fits to experimentally quantified data, substocks are calculated with linear leakage fractions for eggs, as

$$E_i(t) = E_i(t - dt) + (I_i(t) - I_0 \frac{M_e}{t_e}) * \ dt$$

and with exponential leakage fractions for larvae as

$$L_i(t) = L_i(t - dt) + (I_i(t) - I_i(t) * M_l) * \ dt$$

where E_i (t) and L_i (t) are the number of developing eggs or larvae in position i of the substock at time t; I_i (t) is the inflow of eggs and larvae from the previous sub-stock, I_0 is the number of newly hatched eggs and t_e is the number of substocks (hatching time in days) for eggs, and M_e and M_l are total egg and larval mortality rates. The content of each sub-stock at i becomes the inflow I_{i+1}

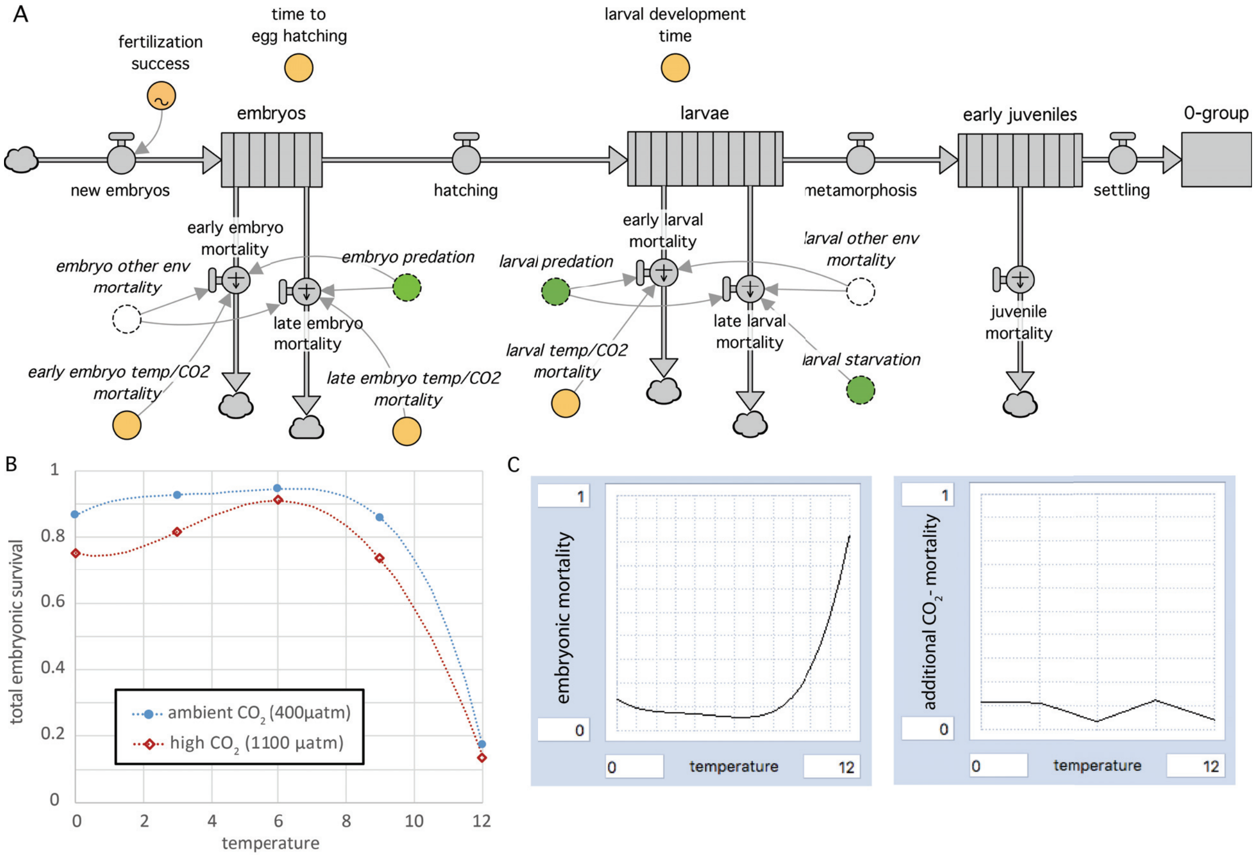

Figure 1: Structure of the dynamic model for Atlantic cod early life stage survival and incorporation of experimentally quantified mortalities. (A) Model structure in systems dynamics notation: Conveyors (split boxes) hold cohorts of individuals for three separate developmental stages, embryos (successfully fertilized, developing eggs), larvae (non-feeding yolk sac and feeding larvae) and early juveniles (up to age 5 months). Flows (wide arrows) transfer individuals to the next stage or extract individuals as daily mortalities (leakage flows). Convertors (circles) manipulate flows connected by thin arrows, incorporating temperature- and CO_2-dependent mortalities from aquaculture experiments (yellow circles), constant other environmental mortalities (white circles), and predation and starvation mortalities fitted to empirical predator and food abundance time series (green circles). (B) Experimentally quantified egg mortalities under 5 different temperatures under ambient and high pCO_2 conditions (Dahlke et al. submitted, Supplemental File S1). (C) Incorporation of quantified mortalities into the model using 'graphical functions' for temperature-dependent mortalities and for additional mortalities under increased CO_2

(t) of the next sub-stock at $i+1$ every 8 time steps (daily), and equations were solved for a *dt* of 1/8 d using Runge-Kutta 4th order integration. Daily mortality rates are

$$M_e = (n_e + e_{eTt} + a_{eTtCt} + p_eP_t) * dt$$

for eggs and

$$M_l = \left(n_l + e_{lTt} + a_{lTtCt} + p_lP_t + \frac{s}{F_t}\right) * \ dt$$

for larvae, composed of a constant (natural) mortality rate n, an environmental mortality rate e mediated by the current temperature T_t; an additional stressor mortality a (in this case caused by ocean acidification) dependent on projected pCO_2 (C_t) and temperature T_t, which is separately set for early and late egg and larval stages (set to 0 for late larval stages); a predation mortality rate p linearly dependent on predator abundance P_t; and finally, for the late larval stage, a starvation mortality rate s inversely related to food abundance F_t.

Temperature- and acidification-mediated mortalities *e* and *a*, and durations ('transit time') of conveyors were based on experimental observations and physiological knowledge of cod ontogenetic development. Egg mortalities were split between the critical phase of the first 30% of the embryonic development time ('early mortality' rate from day 1 after fertilization to the end of gastrulation), where a major part of the mortality is recorded, and the remaining 70% with considerably lower mortality (Dahlke *et al.*, 2016b). Larval mortalities were separated between the yolk sac stage (before the gut is completely developed), estimated as the first 60% of the larval development time (corresponding to 210 degree days), and the feeding stage in the second 40% of larval development, completed with metamorphosis after 350 degree days (Herbing *et al.*, 1996; Falk-Petersen, 2005). After metamorphosis, larvae enter a third stock as early pelagic juvenile fish, until 5 months of age, when age-0 cod settles to its demersal habitat in the Barents Sea (Ottersen et al., 2014).

Experimentally determined mortality rates and development times

Temperature- and CO_2-dependent egg fertilization success, egg and larvae mortality rates and development times were quantified in experiments conducted at the Centre for Marine Aquaculture (formerly National Cod Breeding Centre), Tromsø, Norway, with offspring of Atlantic cod *Gadus morhua* caught in the Barents Sea (Dahlke et al. submitted; Stiasny *et al.*, 2016). While numbers of living embryos declined linearly over time in two distinct phases, a negative exponential function was fitted for larval survival (Supplemental File S1: Figs. S1, S2).

Additional mortality under high pCO_2 conditions in our experiments with embryos was lowest at optimum temperatures, and increased with departure from the thermal optimum (decreasing again under very high temperature-related mortalities; Fig. 1b,c). This matches with a physiologically-based description of interactive effects of temperature and CO_2 on organismal performance (Pörtner & Farrell, 2008). For deriving quantitative temperature-survival curves, 4th order polynomial functions were fitted to the experimental mortalities under ambient CO_2 for cod embryos and larvae (Fig. 1b). Temperature-dependent background mortalities and additive temperature-dependent acidification mortality rates were then implemented into the model using the 'graphical function' feature of the STELLA software (Fig. 1c). Acidification mortalities at each temperature were linearly interpolated between the 500 and the 1100μatm CO_2 value for intermediate CO_2 values, starting at certain CO_2 thresholds for the adaptation scenarios (see section 'scenarios and sensitivity').

Model calibration to empirical temperature and food-web data

Using predation, starvation and 'other environmental' mortality calibration factors for egg and larval stages together with historical temperature, prey and predator time series, the model was calibrated to reproduce empirical 0-group estimates for the Barents Sea cod stock from total egg production estimates for the years 1983–2009 (Marshall *et al.*, 2006; Bogstad *et al.*, 2015b). Early juvenile mortality was adjusted to a constant rate of 0.04 d^{-1}, as estimated by population regression analysis of empirical data (Langangen *et al.*, 2014; Bogstad *et al.*, 2015b).

Temperature data used was for the ‘Barents Sea Opening’ sampling area integrated over 0–400m depth for the month of May (NOAA, 2014), corresponding to the main Barents Sea cod spawning period and area around Lofoten. Starvation mortality of late (feeding) larvae was incorporated as a negative linear relation to time series of zooplankton biomass of the size range 180–2000 μm in the Barents Sea in autumn, mainly comprised of copepods (Dalpadado *et al.*, 2002; ICES WGZE, 2013), which constitute the main feed of newly hatched cod larvae (Fossum & Ellertsen, 1994; Ottersen *et al.*, 2014).

The contribution of predation mortality for eggs and larvae was tested for time series of different potential predators in the Barents Sea: The maturing part of the Barents Sea Capelin stock, Atlantic herring, and Greenland halibut (ICES, 2015; ICES WGWIDE, 2015). Calibration to the Greenland halibut stock biomass produced the best fit. Although this is presumably an indirect link, as no accounts of Greenland halibut as a relevant predator of cod eggs or larvae have been found, we used this correlation for further improving fit to the empirical data.

The values for ‘other environmental’, predation and starvation mortality factors resulting in the best explanation (adjusted R^2 values; Supplemental File S1: Tab. S1) of empirical 0-group data for Barents Sea cod (ICES, 2015) were used for further analyses.

Scenarios and sensitivity analysis

Projections of future 0-group recruitment success were driven by temperature and CO_2 trends based on IPCC (Intergovernmental Panel on Climate Change) ensemble earth system models projections for the Barents Sea under the RCP 8.5 scenario (Representative Concentration Pathway, corresponding to 'business-as-usual' emissions). Under this scenario, increases of annual average water temperature by 3.5°C and average surface $p\mathrm{CO}_2$ from 400μatm to 1100μatm until the year 2100 are anticipated in the Barents Sea region (Bopp et al. 2013; Collins et al. 2013; AMAP 2013).

Inter-individual variation from our experiments was used to estimate the capacity for selection of tolerant individuals and derive confidence intervals for recruitment success by sensitivity analysis. Experimentally quantified mortalities were varied in 1000 model runs for each temperature/CO_2 combination, using a normal distribution with the standard deviation from the average early egg and late egg survival in each experimental treatment, with produced mortalities lower than zero adjusted to zero. For larvae, the standard deviation from larval experiments at 10°C was applied for all temperatures. For future projections under warming only, standard deviations from the 6°C ambient $p\mathrm{CO}_2$ treatment were used, and for all other projections involving acidification, standard deviations from the high $p\mathrm{CO}_2$ treatments at 6°C were used.

Two adaptation scenarios were constructed to explore the potential impact of evolutionary and behavioral population adaptation on projections. Both assume an adaptation capacity to ocean warming of 1°C, implemented as an upward shift in the thermal survival curve when the optimum temperature is reached. This can represent either a physiological adaptation (shift in metabolic and enzymatic optima) or a change in the temperature experienced by the organism due to a spatial shift in the spawning habitat. The assumed thermal adaptive capacity corresponds to the difference in the optimum survival temperature quantified for Barents Sea cod eggs and larvae (6°C) and the maximum water temperature observed for the North Sea cod spawning areas (7°C). For acidification, as we only integrate direct mortality effects and no sub-lethal effects in terms of reduction in organismal performance are considered, thresholds of $p\mathrm{CO}_2$ at which acidification-mediated mortality starts to occur were set at 700μatm and 900μatm $p\mathrm{CO}_2$ for the “moderate adaptation” and high adaptation” scenarios, from which mortalities increase linearly up to the effects quantified at 1100μatm. As no estimates of evolutionary adaptation rates to ocean acidification in fish are currently available, compensation of acidification mortality by 5% and 20% per cod generation (7 years) were arbitrarily assumed for the two adaptation scenarios.

Total egg production, food and predator abundance were set to average values from the calibration interval 1983–2009 for base scenarios. Scenarios for increasing food availability and egg production under climate change and different management strategies were constructed by assuming a linear increase in food (copepod) abundance to 200% until the year 2100 and a constantly increased level of egg production at 150%.

Results & Discussion

Integrated temperature- and CO_2-dependent age-0 recruitment success of Barents Sea cod

The calibrated model reproduced historical 0-group estimates from the Barents Sea with a coefficient of determination R^2=0.61 (**Figure 2,** Supplemental File S1). After adjustment for the increased number of independent model variables, the model has R^2_{adj}=0.46, while we calculated R^2_{adj}=0.269

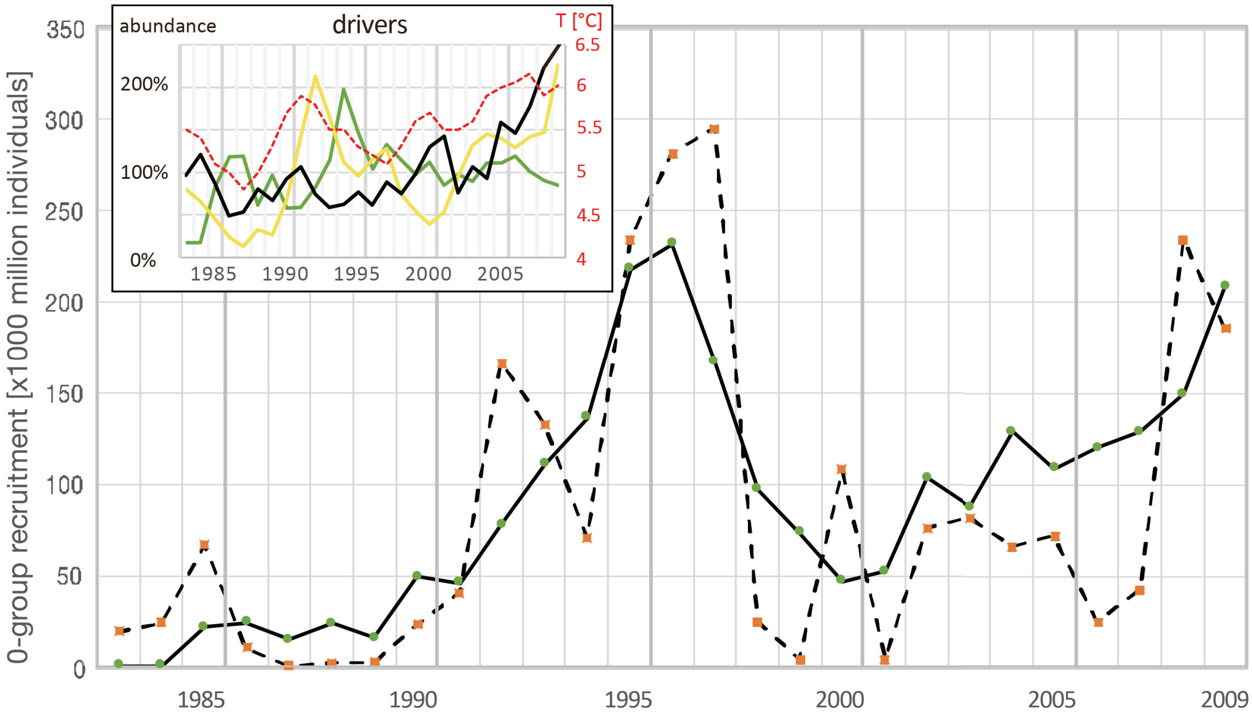

Figure 2: Model fit for the calibration time period 1983–2009, R^2 = 0.61. Model-projected number of age-0 individuals (solid line) compared to empirical estimates of Barents Sea cod 0-group abundance (dashed line) from Norwegian/Russian ecosystem surveys (Eriksen, 2015). Box: Time series of water temperature (dashed red lines), egg production (yellow), food (green) and predator abundance (black) during the calibration interval (see section ‘model calibration…’ for data sources).

for the original total egg production and 0-group data (R^2 = 0.298; Bogstad et al. 2015b). The model thus provides a substantially improved explanation of age-0 recruitment for Barents Sea cod with regard to using only the egg production data provided by Bogstad *et al.* (2015b), capturing the main historical fluctuations in age-0 recruitment in the calibration period. For instance, the phase of very high 0-group abundance in the years 1995–1997 is not explained by a single beneficial factor, but reproduced from the combination of relatively high levels of both egg production and food availability, and low predator abundance (cf. Fig. 2).

The optimal temperature range for good cod 0-group recruitment success (70% or more of the maximum) under normal CO_2 conditions is projected around 3.5–7° C (**Figure 3**). The experimentally quantified temperature-dependent egg and larvae survival rates thus have been slightly shifted towards lower temperatures by the calibration to food and predator field data. This temperature range fits well with the core thermal habitat of 4–8°C for age-0 Barents Sea cod at the end of summer, as estimated by statistical models (Eriksen et al., 2012).

As we apply the inter-individual variation in daily mortalities from our experiments to all

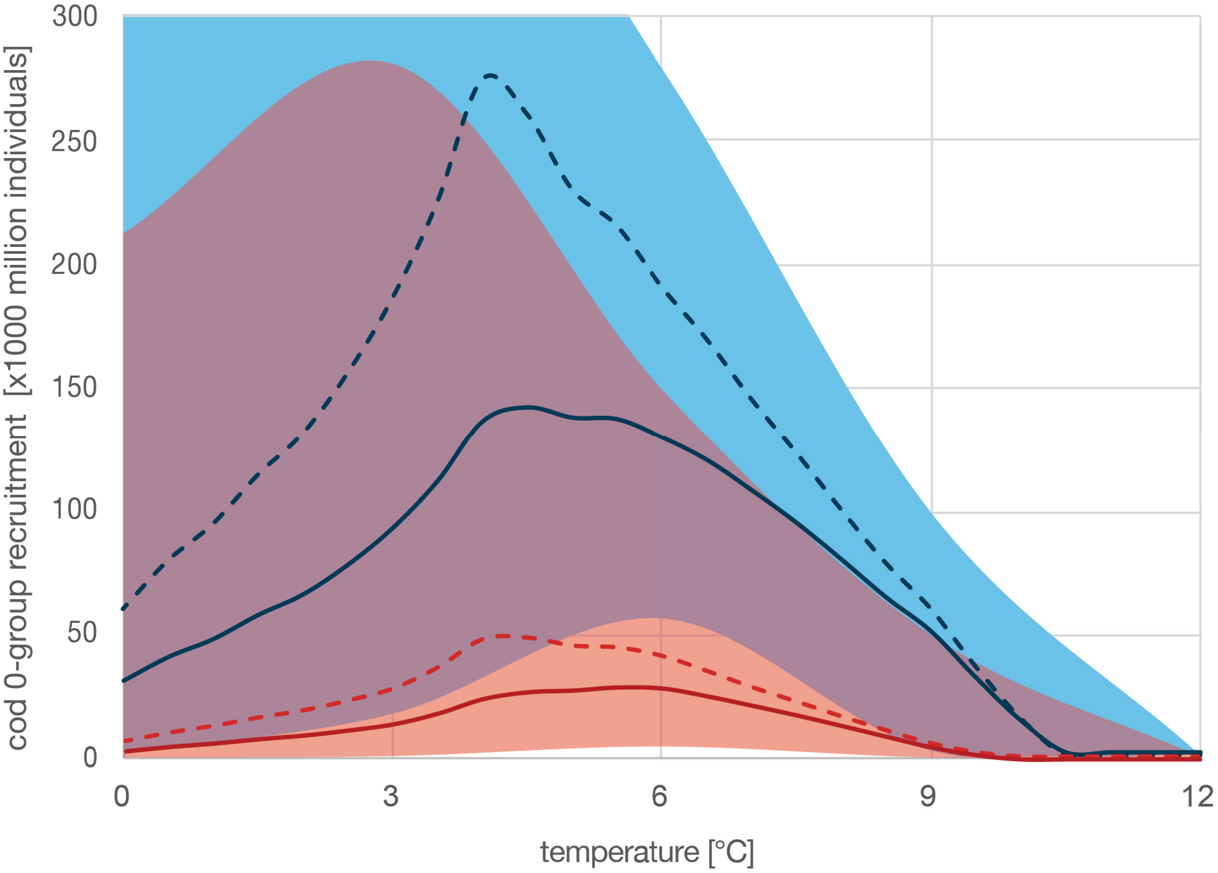

Figure 3: Atlantic cod 0-group recruitment over water temperatures, modelled for current (400–500μatm, solid blue line) and future (1100μatm, solid red line) pCO_2 levels, with 95% confidence limits (colored areas, grey area is overlap) based on inter-individual variation. Based on experimentally determined fertilization success, egg and larval survival rates, and calibration to empirical time series of temperature and cod 0-group, predator and prey abundance (1983–2009). Dashed lines give average temperature-dependent recruitment for maximum food availability (copepod abundance) during the calibration period under current and future CO_2 levels.

projected temperatures for larvae, long development times putatively cause an overestimation of confidence intervals under low temperatures by the model (cf. Fig. 3). Under high temperatures, fixed daily mortality rates in conjunction with decreasing development times lead to some compensation of total mortality, and the right flank of the recruitment curve is consequently less steep than in typical individual curves of temperature-dependent physiological performance or survival. Warmer temperatures have indeed been found to positively affect recruitment through the decreasing duration of vulnerable, high-mortality early life stages in cod and other fish (Otterlei *et al.*, 1999; Ottersen & Loeng, 2000). An individual-based model for North Sea cod has also found trade-offs among stage duration and temperature-correlated mortality by predation (Akimova *et al.*, 2016).

Based on the experimental results, we incorporated pCO$_2$-dependent (acidification) mortality as an additive temperature-dependent mortality, which leads to severely decreased average age-0 recruitment, of 22% at the optimum temperature under high pCO$_2$ conditions (1100μatm; cf. Fig. 3). Confidence intervals based on inter-individual variability show that in the best case, recruitment may be sustained at the level of the long-term average even under high CO$_2$ conditions. In the worst case however, recruitment at optimal temperatures may be reduced to 3% under high CO$_2$ levels, while a minimum recruitment of 40% is sustained under current CO$_2$ levels. Under high food availability, survival can be expected to be increased by almost 100% at temperatures around and lower than the optimum, but this effect is quickly diminished with additional mortality induced by higher temperatures and increasing acidification.

The SCREI model thus enables the derivation of environment-recruitment relationships from experimentally quantified stage-specific survival rates, providing a quantification of the extent to which an additional stressor such as ocean acidification can narrow thermal survival windows of marine fish across different life stages (Pörtner & Peck, 2010). The thermal survival curve integrated over life stages and calibrated to ecological drivers takes on a slightly different form than typical single-stage curves. The model calibration also integrates potential interactions with species and other factors for which we have not tested time series data. Mechanistic detail and explanatory power of the model may be further improved by increasing the spatio-temporal resolution of temperature, copepod abundance and food-web links in the Barents Sea (Sundby, 2000; Dingsør *et al.*, 2007). More experimental work under multiple environmental drivers and different food abundances to investigate trade-offs among growth, feeding and survival would further help to mechanistically separate direct and indirect drivers.

Projected Barents Sea cod recruitment success under environmental and ecological scenarios

Forecasts of future age-0 recruitment driven by temperature and CO$_2$ trends projected under IPCC RCP 8.5 show differential effects of the two drivers and the potential influence of adaptation (**Figure 4**).

Under projected ocean warming only, average age-0 recruitment success nearly linearly decreases to 26% of the long-term mean (calibration interval 1983–2009) in 2100. Application of the experimentally

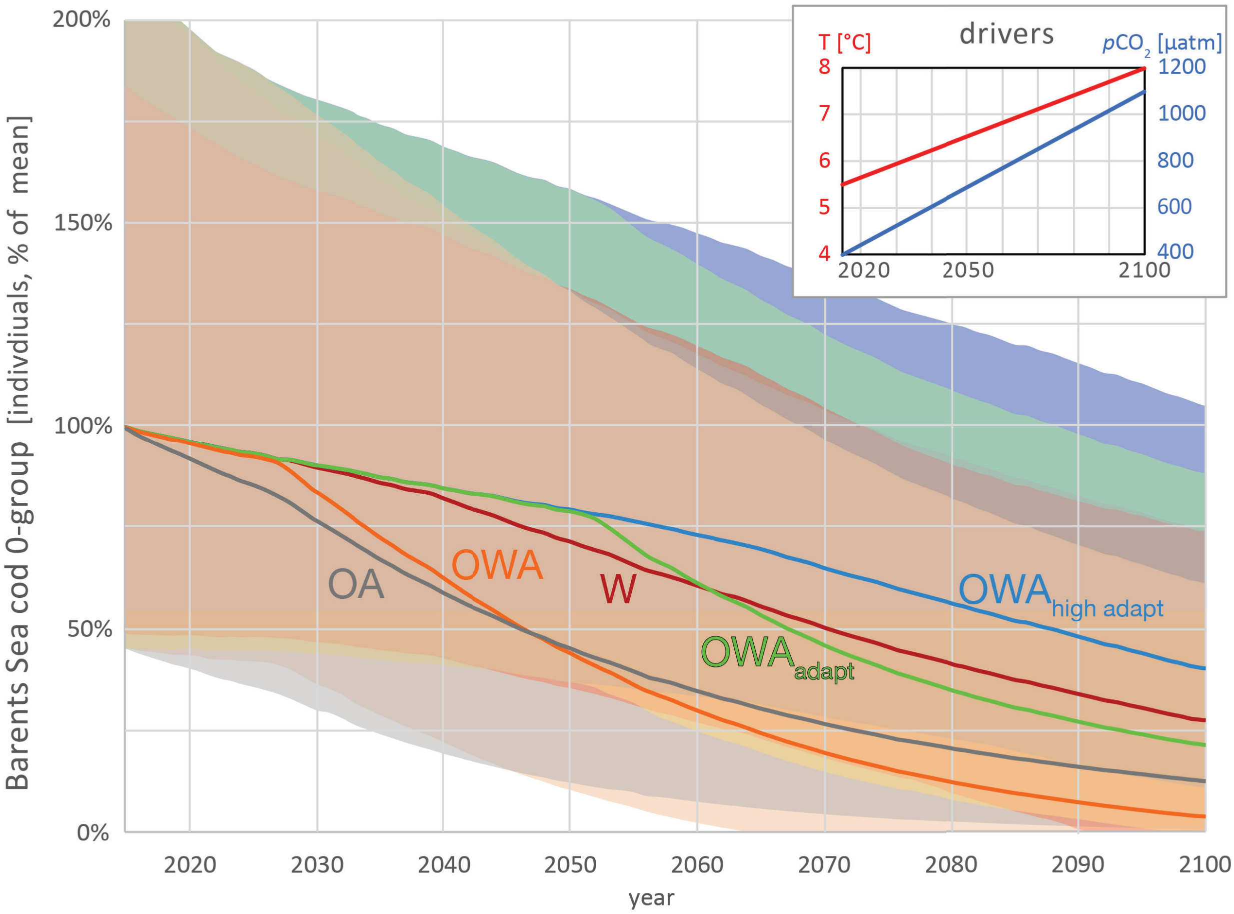

Figure 4: Projections of Barents Sea cod age-0 recruitment success over the course of the century, under different ocean warming and/or acidification scenarios. Given as percentage of long-term mean age-0 abundance (1983–2009), assuming average food availability and predator abundance. Projections are given for full ocean acidification and warming impacts (OAW), theoretical impacts of ocean acidification only (OA) and warming only (W), and moderate (OAW_{adapt}) and high ($OAW_{high\ adapt}$) potential for population adaptation to warming and acidification. Colored areas give 95% confidence intervals for the respective scenarios, based on inter-individual variation in experiments. Box: Trends in water temperature and surface pCO_2 used as model drivers, based on projections for the Barents Sea under IPCC RCP 8.5.

quantified ocean acidification effects on egg and larval survival leads to earlier decreases to 50% already in 2045, reaching 13% of the long-term mean in 2100. Under combined ocean warming and acidification, acidification impacts are slightly compensated for by warming in the short-term until 2045, but severely affect recruitment after that, reducing recruitment to an average 5% of the long-term mean by 2100. In this scenario, 95% confidence limits indicate that age-0 recruitment will constantly fall below the long-term average after 2070, while in the worst case, recruitment success reduced to 5% may already occur in 2055.

The two different adaptation scenarios to ocean warming and acidification project average recruitment to decrease to 20% and 40% in 2100 for moderate and for high adaptation rates, respectively, while the upper confidence limit for these scenarios falls below the long-term average towards the end of the century. Under the moderate adaptation scenario, impacts become evident after 2050, when the assumed thermal adaptation range and acidification effect threshold are passed. The adaptation rate of 5% mortality compensation per cod generation (7 years) employed in this scenario is not sufficient to compensate long-term impacts on recruitment towards the middle to end of the century. In contrast, the 20% adaptation rate in the “high adaptation” scenario would completely buffer later acidification effects, but the departure from optimum survival temperatures leads to increasing mortality by ocean warming and significantly reduces recruitment potential at the end of the century.

The positive effect of warmer water temperatures on recruitment success has putatively co-produced the historically high

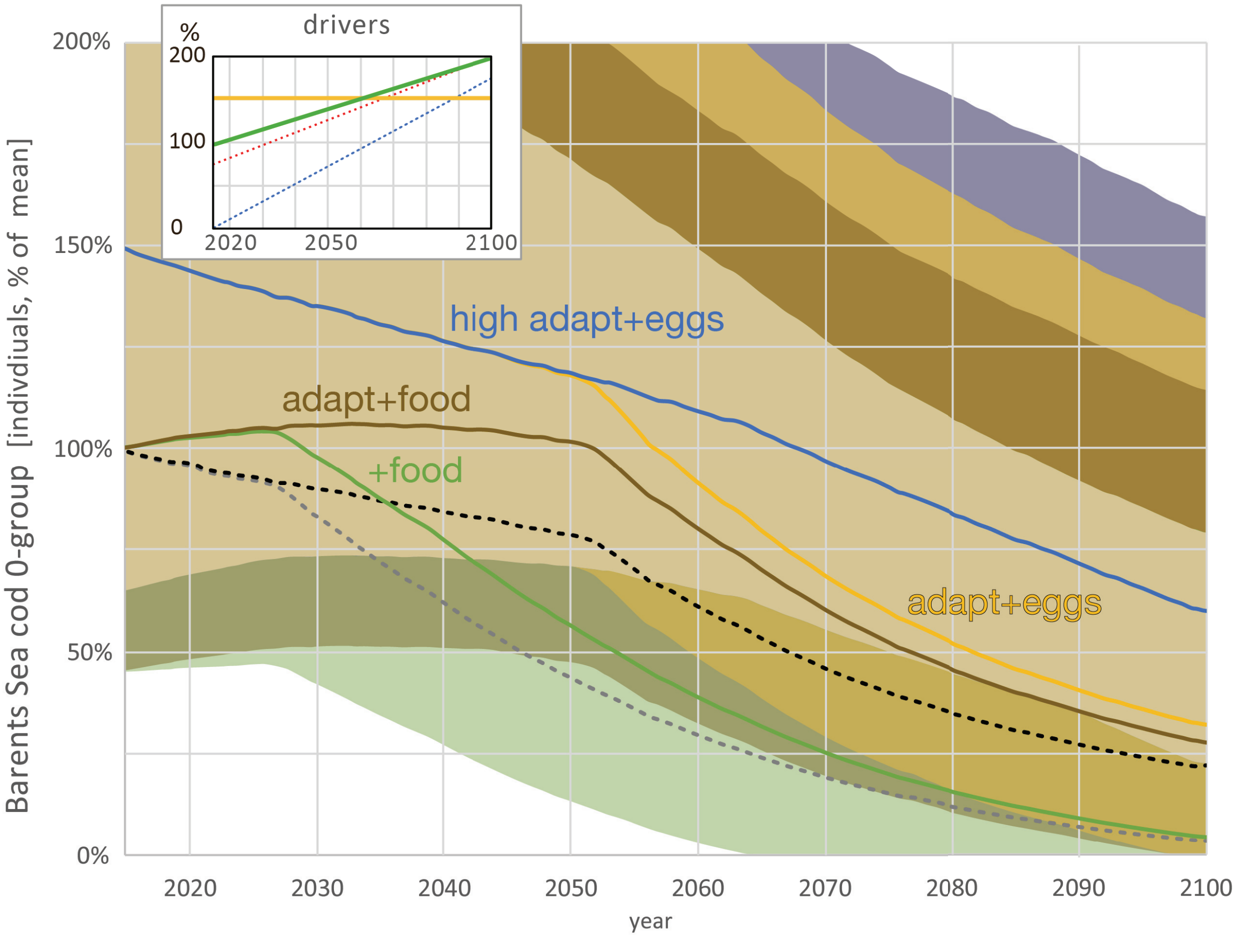

Figure 5: Projections of Barents Sea cod age-0 recruitment success in the course of the century under ocean warming and acidification trends, and different scenarios of increases in food availability and egg production. Given as percentage of long-term mean 0-group abundance (1983–2009) for full ocean warming and acidification (OWA) impacts under linearly increasing food availability (+food), moderate adaptation to ocean warming and acidification and increasing food (adapt+food), and yearly egg production constantly increased under moderate (adapt+eggs) and high adaptation scenarios (high-adapt+eggs). Colored areas give 95% confidence intervals for the respective scenarios, based on inter-individual variation in experiments. For comparison, dotted lines give projections under uncompensated OWA and under moderate adaptation, without food or egg production increases. Box: Applied trends in the additional model drivers food availability (green line) and egg production (yellow line) as percentage of the long-term averages, and underlying trends in water temperature and surface pCO_2 (dotted lines, cf. Fig. 4 for scale)

levels of the Barents Sea cod stock in recent years (Kjesbu et al., 2014). Based on experimentally quantified current temperature-dependent survival, our model shows that optimum temperatures for cod early life stage survival may already have been reached, and this positive trend could be reversed in the coming decades under continuously increasing water temperatures. Recruitment potential may constantly fall below the long-term average towards the middle to end of the century, if physiological adaptation to ocean warming and spatial shifts in spawning habitat do not exceed the 1°C shift in the thermal survival optimum assumed here. Based on the experimental results on cod egg and larval mortalities incorporated into our model, ocean acidification may put considerable additional pressure on Atlantic cod recruitment in the second half of the 21^{st} century, if population adaptation does not happen at a high rate (20% mortality compensation per generation). As these projections assume a constant egg production of the cod stock, they do not consider reductions in the spawning stock that would appear as a long-term result of reduced recruitment, nor potential density-dependent compensation of these effects in later life stages, or reductions in fitness by sub-lethal effects of temperature and pH that may become relevant in the field.

We used field data in the calibration interval for an exploratory analysis of potential effects of changes in indirect ecological drivers. Future cod age-0 recruitment may be improved under increased food availability in the short to mid-term, while warming and acidification are buffered by adaptation, but will progressively be overridden by direct warming and acidification effects in the second half of the 21^{st} century (**Figure 5**). In contrast, a constantly higher level of egg production at 150% would buffer negative effects to a greater extent, keeping average recruitment above the long-term mean until the middle of the century and, according to the lower confidence limit, secure recruitment above 30% until 2070 under the moderate adaptation scenario. This may be achieved by management measures sustaining the cod stock at a higher spawning stock biomass and would improve the chances to secure sufficient recruitment in the long-term, i.e. in the second half of the century.

The present work provides first insights into the dynamic interactions of multiple drivers of fish stock recruitment that can be expected in the course of this century, and creates a basis for incorporating estimates of inter-individual variability, population adaptation rates and ecological changes into model projections. More research involving multi-generational experiments and genetic analysis of relevant traits and neutral genomic markers is needed to provide more robust estimates of evolutionary adaptation rates and possible maternal effects on egg quality, and to assess the appropriate representation of the genetic variability in the spawning stock in experimental animal samples.

Perspectives: Integration among models and empirical studies to investigate marine fish stock recruitment under climate change

The SCREI model serves as a proof-of-concept that biological knowledge and experimentally quantified rates possess high potential to improve dynamic projections of environmental driver effects on fish stock recruitment. Environmental and predation- and starvation-mediated mortalities offer integrative measures for investigating effects of climate-related drivers in the context of changing marine community dynamics.

The approach could be used to complement single- and multi-species population and life cycle models in assessing future recruitment to the fished stock, incorporating density-dependent processes in juvenile and adult stages, and the influence of other factors such as fishing pressure on age structure and egg production (Ohlberger & Langangen, 2015; Pepin, 2016). It provides a novel option for bridging existing models of zooplankton production and higher trophic level models (Carlotti & Poggiale, 2010; Mitra *et al.*, 2014). The fine-scaled biological structure and temporal resolution (daily time-step) enable the incorporation of changes in cod spawning timing and copepod presence, offering a tool for investigating possible shifts in seasonal timing (match-mismatch dynamics) for climate effects on the high-latitude Atlantic cod stocks (Mertz & Myers, 1994; Beaugrand & Kirby, 2010; Kristiansen *et al.*, 2011). Together with growth potential for the juvenile and adult population in relation to temperature and other environmental drivers (Butzin & Pörtner, 2016), this would lead to a greatly improved description of environmental effects over the life history of Atlantic cod, advancing understanding of future climate change impacts on this and other marine fish populations.

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Supporting Information S1: Experimental setups, model validation and calibration

Experimental setups

Temperature- and CO_2-dependent egg fertilization success, egg and larvae mortality rates and development times were quantified in experiments conducted at the National Cod Breeding Centre, Tromsø, Norway, with offspring of Atlantic cod *Gadus morhua* caught in the Barents Sea (70°15'N, 19°00'E) in March 2014.

Fertilization success was derived from six fertilisation trials with eggs from different females (n = 6) at ten different water temperatures (-1.5 to 12 °C) and two different pCO_2 treatments (400μatm and 1100μatm), with approximately 150 eggs per treatment combination (Dahlke et al. 2016b in preparation; data available at *doi.org/10.1594/PANGAEA.868126*).

Embryo mortalities and time to peak hatch were determined in fertilized batches at five different temperatures (0, 3, 6, 9 and 12°C) with the two respective seawater pCO_2 conditions established in temperature-controlled reservoir tanks. Dead eggs were removed daily and embryo mortality recorded until all individuals within an incubator had either died or hatched as larvae. Egg developmental time until hatch followed a similar, negative exponential relationship to temperature as reported before (Ellertsen et al., 1987 and references therein). Increased pCO_2 caused temperature-dependent additional mortality, which was lowest at optimum temperature and increased with lower and higher

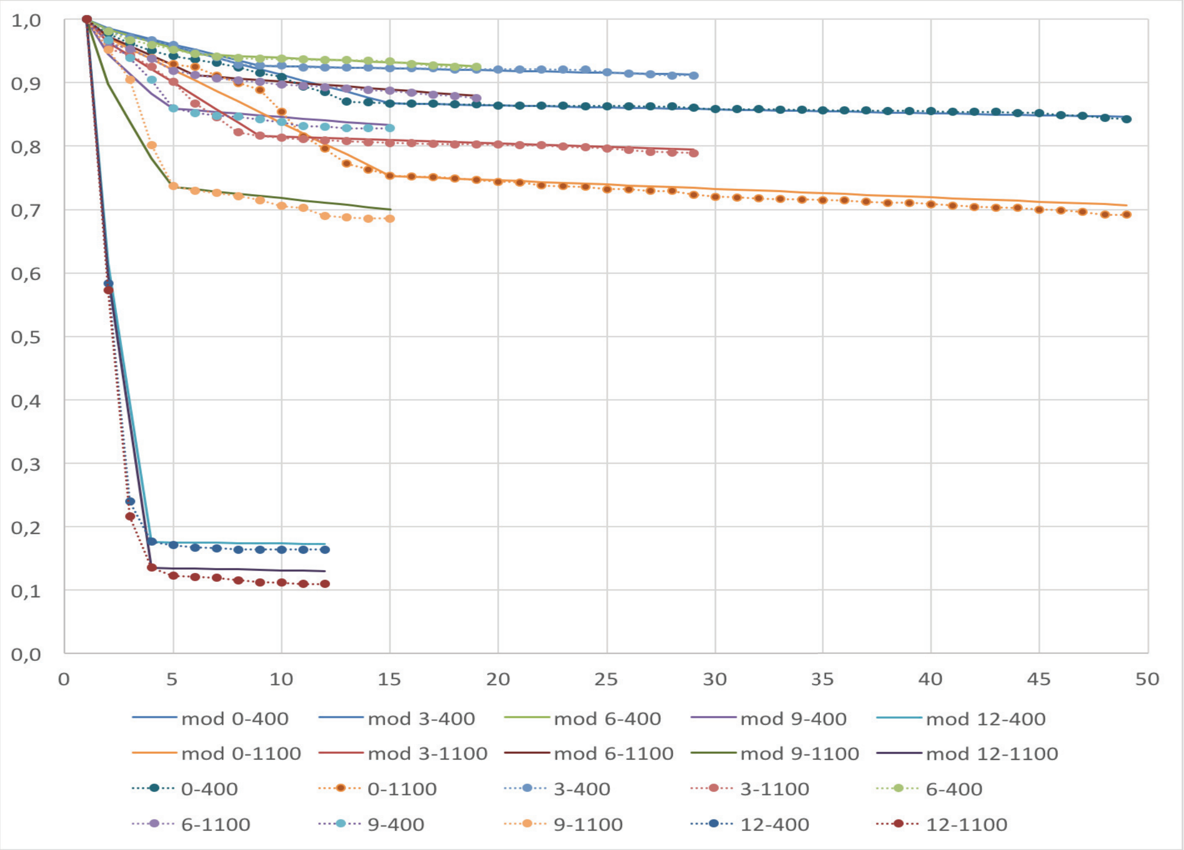

Figure S1: Validation of model structure for egg development: Experimentally quantified egg survival over days post fertilization (dots; fraction of living embryos at day-x post fertilization relative to the initial number of fertilized eggs on day 1), and relative modelled embryo numbers for a single egg input at time one (solid lines).

temperatures (Dahlke et al. submitted).

For quantifying larval mortalities, eggs were incubated under either ambient fjord water (500µatm CO_2) or increased CO_2 (1180µatm CO_2) concentrations, and 11,000 hatched larvae transferred into each of twelve 190 L rearing tanks, with a constant flow-through of water from a common header tank at 10°C, in six replicates for the high CO_2 treatment and five for the ambient treatment (Stiasny et al., 2016). Starting on day 8 post-hatch the survival was measured every four to six days until day 22, counting larvae across five water samples from each tank over the whole water column, across treatments with different feeding levels in which survival was not significantly different. A negative exponential function was fitted for each larval replicate tank, calculating mean daily mortality coefficients for ambient and high-CO_2 treatments of 7% and 13%, respectively (Stiasny et al., 2016). Temperature-dependence of larval mortality was derived from literature values at 4, 6, 10 and 12°C (Otterlei et al., 1999) and the additional acidification-induced mortality rate assumed as constant over temperatures.

Validation of stage-specific outputs and mortalities

The model structure was validated by running egg and larval stages separately under the experimental temperatures and CO_2 values, with a single input of egg or larvae, and setting 'other environmental', predation and starvation mortalities to zero (Figs. S1 and S2).

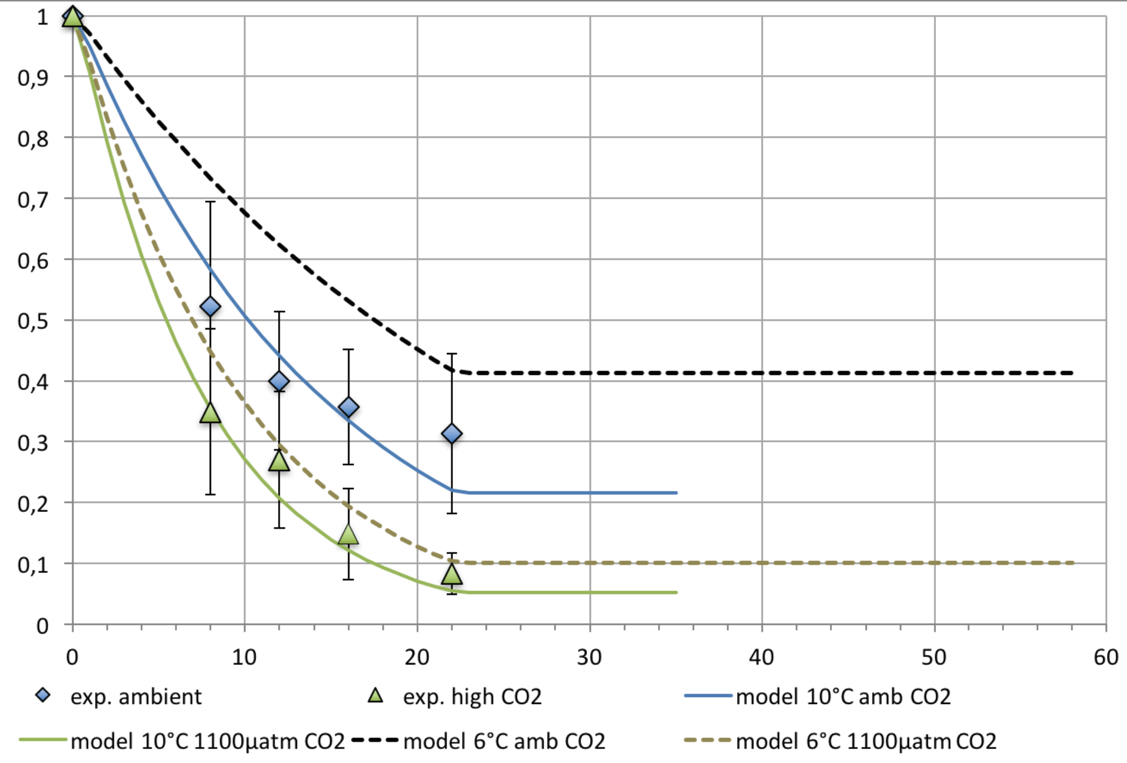

Figure S2: Validation of model structure for larval development: Experimentally quantified larval survival at 10°C over days post hatch, as fraction of initial larvae number (diamonds and triangles with standard deviation among experimental treatments), and modelled larval survival for 10°C (solid lines) and for 6°C (dashed lines) for a single larvae input at time zero (without additional mortality factors for the early and late larval stages used in calibration and projections)

Driver time series	Mortality scenario	Egg mortalities (early + late total rates)		Larval mortalities (exponential daily rates)			***R^2***	***Adjusted R^2 (no. of variables)***
		Environ-mental	Predation	Environ-mental	Predation	Star-vation		
Copepods (prey only)		0.7	-	0.01	-	0.03	***0.56***	***0.45 (5)***
Halibut + copepods	Egg	0.6	0.13	0.007	0.009	0.021	***0.61***	***0.46 (7)***
	Larvae	0.19	0.087	0.015	0.0004	0.022	***0.60***	***0.46 (7)***
Herring + copepods	Egg	0.62	0.15	0.01	0	0.03	***0.58***	***0.42 (7)***
	Larvae	0.35	0	0.011	0.035	0.02	***0.57***	***0.41 (7)***
Capelin + copepods	Egg	0.75	0	0.012	0.012	0.02	***0.57***	***0.42 (7)***
	Larvae	0.45	0	0.028	0.024	0.03	***0.52***	***0.34 (7)***

Table S1: Values for calibration factors for different combinations of prey and predator time series as food-web drivers of cod 0-group survival. R^2 values calculated for model output to empirical data over the years 1983–2009, and R^2 adjusted for the number of independent variables.

Model calibration

The model was calibrated for prey abundance in the same year (zooplankton biomass < 2 mm; Dalpadado *et al.*, 2002; ICES WGZE, 2013), and the predators Barents Sea capelin, Norwegian spring-spawning herring and Greenland Halibut for the years 1983–2009, as abundance indices in autumn shifted to the following year of recruitment (ICES WGWIDE 2015, ICES AFWG, 2015). For each predator and without any predator (only prey), sensitivity analyses over the whole plausible value range were conducted, varying all 'other environmental' and predation/starvation mortalities from 0 to a value corresponding to a total mortality close to 1 (0.95 total rate for early and late egg mortalities, 0.06 daily exponential rate for early and late larval mortalities), and calculating the deviation (sum of squares) in output to the 0-group data.

For all predators, best fit to empirical time series was obtained for two different optima of calibration factor combinations, either high egg mortalities and low larval mortalities, or moderate egg mortalities and moderate larval mortalities. Exact parameter values for both optima were found by running PEST version 13.6 (*Model-Independent Parameter ESTimation and Uncertainty Analysis*; Watermark Numerical Computing; pesthomepage.org) for the whole value range, and separately for 'other environmental mortalities' <0.5 and >0.5 (Tab. S1).

Fitting starvation mortality to copepod data without predation mortalities provided an R^2 value of 0.56. Additional use of capelin or herring abundance data improved R^2 slightly, but not more than to be expected by using two additional variables (adjusted R^2 values; Tab. S1). Use of halibut abundance data improved fit significantly and was subsequently used to drive predation mortality. The 'high egg mortality' scenario was chosen for projections, as it coincides better with field observations for Barents Sea cod, providing egg mortalities in the range of survey–based estimates (Langangen et al. 2014, Bogstad 2015b).

Paper 4: Impacts of ocean warming and acidification on marine food web dynamics in the Barents Sea

Effects of ocean warming and acidification on marine food web dynamics in the Barents Sea

Abstract

The arcto–boreal seas are subject to high climatic variability and anticipated to be impacted early by global climate change, with uncertain consequences for the dynamics and composition of their marine ecosystems and the provision of marine ecosystem services to human societies.

We present a process–based dynamic multi–species model of the Barents Sea, a shelf sea known for its high fish biomass and inter annual climate-dependent variability. The model reproduces biomass fluctuations of the main species in the food web from their interactions and temperature preferences, and extrapolates impacts of continuing ocean warming for the rest of the century. The effects of ocean acidification on food web dynamics are considered by incorporating an additional loss of metabolic energy for increased ion and acid-base regulation.

The model shows a continuation of the typical biomass fluctuations arising from species interactions, and projects shifts among species composition under progressive warming. Shifts among zooplankton groups, with increasing copepod and krill versus declining amphipod abundance, are projected to cause impacts on the levels and fluctuations of the main fish species capelin, cod, herring, haddock and polar cod. The additional energetic loss by acidification would cause divergent impacts across the food web, depending on trophic position and diet composition. Mammals and seabirds are impacted through changes in prey availability, and fisheries landings may decrease moderately towards the end of the century.

The model provides a novel description of food web dynamics over time in a highly climate–sensitive system, calibrated with empirical data. It highlights the relevance of both organismal temperature preferences and feeding interactions in shaping food web dynamics in marine ecosystems and explores the possibility to use historical ecological fluctuations to advance the understanding of the role of climate variability in marine ecosystems and the development of regime shifts, thereby projecting potential shifts in ecosystem service provision under future climate conditions.

Introduction

Arctic and subarctic regions are hotspots of climate change impacts in the ocean (Denman et al. 2011; Hoegh-Guldberg et al. 2014; Pörtner et al. 2014). Marine ecosystems in arctic and subarctic areas are being affected by warming of waters and decreasing sea ice extent (Darnis et al. 2012), and changes in oceanic and atmospheric circulations and increased uptake of atmospheric CO_2 are expected in the course of this century. Arctic food webs are progressively changing from typical polar towards boreal communities (Kortsch et al. 2015). Ocean acidification may affect lower trophic level productivity and some fish stocks, and thereby alter food web structure and energy transfer (AMAP 2013). Direct environmental effects on marine organisms are modulated by species interactions in the food web, leading to indirect effects on other species, and changing ecological community dynamics (Kordas et al. 2011). Thus, investigation of climate change effects on marine ecosystems has to integrate the organism, population, and community levels (Doney et al. 2012; Sydeman et al. 2015).

The Barents Sea is a high–latitude shelf sea with high biological productivity, home to several important pelagic and demersal fish stocks, but comparatively low species diversity (Wassmann et al. 2006; Loeng & Drinkwater 2007; Olsen et al. 2010). Climate variability on multi-annual and decadal scales is known to influence biological productivity and ecosystem dynamics (Yaragina & Dolgov 2009; Drinkwater 2011). Historical observations and statistical time-series analyses show a high correlation among the productivities and abundances of the fish populations in the Barents Sea, i.e. the Northeast Arctic cod, Norwegian spring-spawning herring, Atlantic capelin and other fish stocks (Hamre 1994; Cury et al. 2008; Bogstad et al. 2015). These fluctuations are driven by changing oceanic regimes with regard to Atlantic and Arctic water masses, and resulting fluctuations in temperature and food availability (zooplankton transport onto the Norwegian shelf; Sakshaug et al. 1994; Loeng & Drinkwater 2007), and can be linked to the North Atlantic Oscillation (NAO; Ottersen & Stenseth 2001; Dalpadado et al. 2002; Orlova et al. 2005).

The Barents Sea has experienced substantial warming in recent years, with increases in the biomass in fish and Northern krill (Eriksen et al. 2017), and is projected to experience further warming in the coming decades, leading to shifts in the spatial distribution, productivity and biomass of fish stocks, and thus, socio-economic impacts on fisheries (Stenevik & Sundby 2007; Hollowed & Sundby 2014; Fossheim et al. 2015). Under future climate change, changes in zooplankton species composition from those associated with Arctic waters to predominantly Atlantic species are expected (Dalpadado et al. 2012). These changes affect the provision of food energy to the fish stocks, may alter food-web functioning and dynamics in the Barents Sea, and change the relative contribution of top-down and bottom-up trophic controls (Johannesen et al. 2012). On the other hand, changes in fish abundance, together with the reduction in sea ice, are affecting bird and mammal species in the Barents Sea region (Descamps et al. 2017).

This region thus represents a suitable study area for the impact of climate variability and change on marine living resources (Michalsen et al. 2013), and exemplifies how the resilience of marine fish populations can be determined by the interactive effects of the drivers fishing and climate (Lehodey et al. 2006; Perry et al. 2010; Planque et al. 2010). The resilience of marine systems is determined by the emergent properties arising from their components and their interactions (Link et al. 2015). Both stabilizing interactions, e.g. from predator-prey feedbacks (Gardmark et al. 2013), and sudden regime shifts by positive feedback cycles (Pedersen et al. 2016) are possible. Especially in systems with some degree of top–down (predator) control like the Barents Sea, direct impacts on one element of the food web can trigger cascading effects, and lead to regime shifts and food web restructuring under climate change (Mangel & Levin 2005). The food webs in the Barents Sea are expected to be more vulnerable to impacts on certain keystone or bottleneck species than marine ecosystems with higher species diversity, constituting potential tipping points (Wassmann et al. 2006; Duarte et al. 2012). The relative contribution of direct abiotic effects and indirect food web–mediated effects under warming is determined by the relationships of organismal metabolic rates, resource requirements and resource availability (Kordas et al. 2011). Thus, resolving trophodynamic links and the relative contributions of bottom-up and top-down trophic controls is vital for understanding the resilience of marine ecosystems to environmental variability and climate change (Frank et al. 2006; Stock et al. 2017).

Anthropogenic impacts, such as the extraction of biomass by fisheries, exacerbate the pressure by climate change on marine ecosystems (Brander 2012). In recent years, increased efforts are undertaken to establish ecosystem–based management regimes of the ocean and its resources (Browman & Stergiou 2005; Katsanevakis et al. 2011; Long et al. 2015). Norway is one of the nations that is actively pursuing the establishment of this approach, and the potential impacts of climate change and ocean acidification are explicitly acknowledged as relevant knowledge gaps in the ecosystem–based management plans for the Barents Sea–Lofoten area (Hoel & Olsen 2012; Sainsbury et al. 2014; Gullestad et al. 2014).

To assess climate change impacts on marine fish and ecosystems, and identify societal adaptation and governance strategies, ecological simulation models are important tools (Rose & Allen 2013; Koenigstein et al. 2016). Multispecies models incorporate predation and competition processes among a moderate number of species assumed to be sufficient to describe regional food web dynamics, and different multi–species models have been used to investigate interactions among fish stocks in the Barents Sea (Howell & Bogstad 2010; Rindorf et al. 2013). They focus on top-down effects (predation mortalities by top predators), and the inclusion of bottom-up effects (varying food abundances for fish) could improve understanding of the system (Bogstad et al. 2015). Through an improved basis of biological process knowledge, models can make better use of experimental and observational data to extrapolate impacts of changing environmental drivers (Pörtner & Peck 2010; Metcalfe et al. 2012), and incorporate management–relevant system indicators, e.g. keystone species, biodiversity indices, and energy flux across trophic levels (Griffith & Fulton 2014; Queirós et al. 2015), facilitating development of early-warning signs for climate change impacts on marine ecosystems with socio–economic consequences (Brander 2010).

We present an integrative system model of intermediate complexity for the Barents Sea region, which was derived from a participatory approach, incorporating input from stakeholders in the area (Koenigstein et al. 2016b). We focus on the regional marine–human system under changing external driver scenarios, assuming that feedbacks from this system to the earth system (e.g. by altered CO_2 uptake) are negligible. The model structure integrates direct physiological drivers of organism performance and indirect food–web effects, and is used to investigate the combined effects of projected ocean warming and acidification regimes in the area and anthropogenic impacts through biomass extraction by fisheries. The model is based on the assumption that species' thermal windows represent an organismal adaptation to the environment, i.e. a basic limitation of organismal performance which determines the fundamental ecological niche of a species and can be quantified under suitable experimental conditions (Pörtner 2008; Pörtner et al. 2014). Food–web structure and dynamics then represent indirect effects and biotic limitations, which constrain and determine the realized niche in the ecosystem, and can be quantified by empirical field data.

Material & Methods

Modeled region and data input

The Barents Sea–Lofoten system

The modeled region is mainly comprised of the Barents Sea, a shelf sea under influence of Arctic waters (Fig. 1). The northernmost part of the Norwegian Sea, i.e. the region off Lofoten where the North Atlantic current enters the Barents Sea on an extended shelf, is used for spawning by the main Barents Sea fish stocks, and is thus commonly included as part of a 'Barents Sea–Lofoten regional marine system‘ in

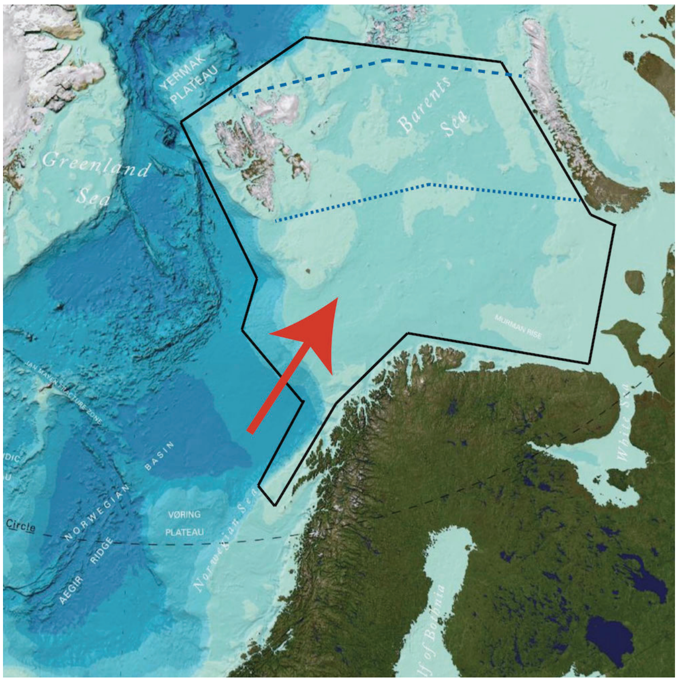

Figure 1: Geographical location, system boundaries and main oceanographic features of the modeled marine system, the Barents Sea–Lofoten regional marine system. Blue lines give the approximate position of the ice edge in summer (dashed) and winter (dotted), red arrow indicates Atlantic water inflow, the main supply of heat and advected plankton into the system.

Norwegian ecosystem–based management plans and forms the ICES (International Council for the Exploration of the Sea) 'Ecoregion Barents Sea', comprising a total area of 1.800.000 km^2.

Species and biomass estimates

Selection of species included in the model was based on importance in terms of biomass, observed ecological interactions, and relevance for stakeholders in the Barents Sea–Lofoten region (Koenigstein et al. 2016b). Abundance of fish in different age classes and 0-group fish abundance are survey-based estimates from ICES working group reports (ICES WGWIDE 2015; ICES WGIBAR 2016; ICES AFWG 2016). We included the major fish species in the Barents Sea, Northeast Arctic Cod (*Gadus morhua*), Norwegian Spring-Spawning Herring (*Clupea harengus*), Northeast Arctic Haddock (*Melanogrammus aeglefinus),* the Barents Sea stock of Atlantic Capelin (*Mallotus villosus*), and Polar cod (*Boreogadus saida*). Whenever available, we used survey–based data, in order to minimize additional assumptions of model–based data. For the spatially highly variable spawning stock of NSS herring, VPA (Virtual Population Assessment) model-derived estimates were used.

The biomass values (initial stocks and time series used for calibration) for species with only a partial distribution in the modeled area were reduced. Young Norwegian Spring-spawning herring is an important predator for 0–group fish and prey for cod and other fish species. Mature herring leaves the Barents Sea, spends its life in the Norwegian Sea and returns to the Lofoten area only for spawning, reducing interactions with the species in the Barents Sea, therefore, biomass of ages 3+ was divided by 5 in the model. As the stock has been at a low level and no reliable estimates are available before 1988, the low biomass values for 1988 were used for the years 1983–1987. The stock of adult haddock was divided by 2, since half of the stock is located in the Norwegian Sea (Olsen et al. 2010).

Marine mammal populations were incorporated based on population and sighting models and estimates. Seals were represented by the dominant population in the Barents Sea, the ‚east ice’ harp seal (*Phoca groenlandica*) population breeding in the White Sea (ICES WGHARP 2016). Minke whales (*Balaenoptera acutorostrata*), the most abundant whale species in the area (Skaug et al. 2004), were considered as a separate group, while fin whales (*Balaenoptera physalus*), Humpback whale (*Megaptera novaengliae*) and Blue whales (*Balaenoptera musculus*) were grouped together as 'other baleen whales' (Skaret & Pitcher 2016). Among the two main groups of toothed whales, orcas (*Orcinus orca*) enter the Barents Sea for feeding, while sperm whales (*Physeter macrocephalus*) occur only up to the Northern Norwegian Sea, thus abundance estimates of the latter species were divided by

10. Population biomass estimates for whales are based on estimates of population numbers and average body weight, and adjusted to the Barents Sea area for those North Atlantic species that stay in the Barents Sea only part of the year (Dommasnes et al. 2000; Skaret & Pitcher 2016).

The four most abundant seabird species in the Barents Sea were included: Brünnich's guillemot *Uria lomvia,* Northern fulmar *Fulmaris glacialis,* Black-legged kittiwake *Rissa tridactyla*, and Atlantic puffin *Fratercula arctica.* Due to a higher proportion of fish in their diet, Atlantic puffin was incorporated as a separate group (ICES WGSE 2013; Dommasnes et al. 2000; Barrett et al. 2002).

Consumption estimates, diet composition and lower trophic level biomass

Lower trophic levels were represented by one phytoplankton compartment, dependent on net primary production, which is around 100 g C/m^2 y in the Barents Sea (Wassmann et al. 2006; Dalpadado et al. 2014), and the three major zooplankton groups in terms of biomass in the modeled region, copepods (*Calanus finmarchicus, C. hyperboreus* and *C. glacialis*), pelagic amphipods *(Themisto libellula, T. abyssorum* and *T. compressa*) and Northern krill (*Meganyctiphanes norvegica*, *Thysanoessa inermis* and *T. longicaudata*) (Dalpadado et al. 2002; Dalpadado et al. 2012).

Estimates of consumption and diet composition were adjusted to match those used in holistic trophodynamic models of the Barents Sea, based on data from stomach content analysis and estimates of energy demand. All feeding linkages among species in our model which contribute at least 1% of the diet were considered, with diet fractions estimated for prey stock levels of the year 2000 (Dommasnes et al. 2000; Skaret & Pitcher 2016).

We used thermal performance curves (Fry, 1971) for adjusting the productivity (assimilated biomass per population biomass, Q/B) over different water temperatures for the fish species in the model (**Figure 2**). These thermal windows can serve to describe organismal performance or productivity under multiple environmental drivers, and the extent of competition between two species is co-determined by the overlap of their performance windows (Pörtner & Farrell 2008; Pörtner et al. 2014). The sensitivity of a species to future ocean warming can be described by the distance from the temperature for optimum organismal performance (T_{opt}) and the

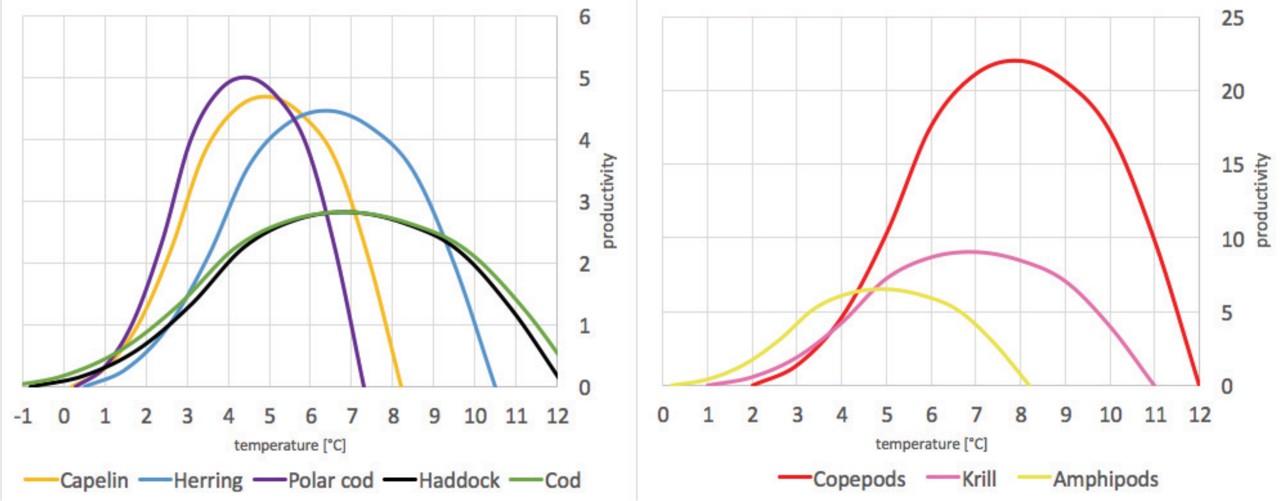

Figure 2: Productivity (assimilated biomass per population biomass) over temperature for the species in the model, for A) Fish (depicted for adult stages), B) Zooplankton groups. Based on idealized thermal performance windows, range and optimum of preferred field temperatures (core thermal habitat; Eriksen 2015), and age–specific field consumption estimates at the preferred temperature.

temperature for subsistence living (T_{crit}; Farrell 2016). As experimentally determined thermal curves are not available for all species in our model, and T_{opt} determined under ad libitum feeding conditions may diverge strongly from those under natural conditions, we adjust T_{opt} to match the statistically determined core thermal habitats of the fish species in the Barents Sea (Eriksen et al. 2012). The width of thermal windows (lower bound to upper bound) was generally assumed at 10°C, and adjusted to 8°C for the more stenothermal, cold-water associated capelin and amphipods, and to 7° for Polar cod.

Model structure

Basic model structure and integrated biological processes

The model was constructed as a multi-species model in the system dynamics modeling software STELLA Architect V. 1.22 (www.iseesystems.com). Each biomass stock is determined by in- and outflows which represent biological processes, with aging (biomass flow to the next age stock), reproduction and recruitment governing population dynamics of the integrated species, and interactions among species represented by predation and consumption, determined by the predator and prey stocks (**Figure 3**).

Table 1a: Consumption per biomass per year (Q/B) and diet composition (fraction of consumption for each prey) of the species included in the model

	Q/B	Cod0	Cod1	Cod3+	Had0	Had3+	Her0	Her1	Her3+
Minke whales	**8.14**	0.02		0.2	0.02	0.005	0.02	0.31	0.05
Sperm whales	**4.55**							0.03	0.1
Orcas	**12.75**							0.28	0.7
Baleen whales	**14.6**	0.02						0.11	0.02
Harp seal (0-1)	***16.49***	0.02		0.04		0.005	0.01	0.1	
Harp seals (1+)	**15**	0.02		0.04		0.001	0.01	0.1	
Atlantic puffins	**160**	0.02			0.1		0.29	0.03	
Other seabirds	**112.32**				0.01		0.02	0.02	
Atlantic cod (0-1)	***8***						0.01	0.02	
Atlantic cod (1-3)	***8***						0.01	0.02	
Atlantic cod (3+)	**2.82**	0.03			0.01		0.03	0.04	0.04
Haddock (0-2)	***7.95***							0.01	
Haddock (3+)	**2.82**							0.01	0.06
Herring (0-1)	***39.92***								
Herring (1-2)	***9.83***								
Herring (3+)	**4.47**						0.01		

Table 1b: Consumption per biomass (Q/B) and diet composition (fraction of consumption for each prey) of the species included in the model (continued)

	Q/B	Pco0	Pco1+	Cap0	Cap1	Cap2+	Kri	Amph	Cope	Phyt
Minke whales	**8.14**				0.015	0.07	0.242			
Sperm whales	**4.55**				0.01	0.05				
Orcas	**12.75**									
Baleen whales	**14.6**				0.03	0.11	0.632	0.06		
Harp seal (0-1)	***16.49***	0.05	0.1			0.17	0.166	0.1		
Harp seals (1+)	**15**	0.04	0.08			0.17	0.1683	0.1		
Atlantic puffins	**160**			0.03	0.11					
Other seabirds	**112.32**	0.02	0.06	0.05	0.16		0.09	0.1		
Atlantic cod (0-1)	***8***	0.01	0.02		0.015	0.14	0.29	0.33		
Atlantic cod (1-3)	***8***	0.01	0.02		0.015	0.14	0.29	0.33		
Atlantic cod (3+)	**2.82**	0.01	0.02		0.06	0.25	0.12	0.14536		
Haddock (0-2)	***7.95***				0.02		0.232	0.19		
Haddock (3+)	**2.82**				0.01	0.19	0.17	0.04		
Herring (0-1)	***39.92***						0.01	0.01	0.33	
Herring (1-2)	***9.83***			0.01			0.06	0.14	0.64	
Herring (3+)	**4.47**						0.06	0.13	0.65	
Polar cod (0-1)	**5**						0.55	0.32	0.07	
Polar cod (1+)	**5**						0.55	0.32	0.07	
Capelin (0-1)	***21.34***						0.03	0.02	0.5	
Capelin (1-2)	***7.83***						0.65	0.14	0.2	
Capelin (2+)	**4.7**						0.69	0.15	0.15	
Krill	**9**								0.05	0.8
Amphipods	**6.5**						0.02		0.47	
Copepods	**22**									0.9

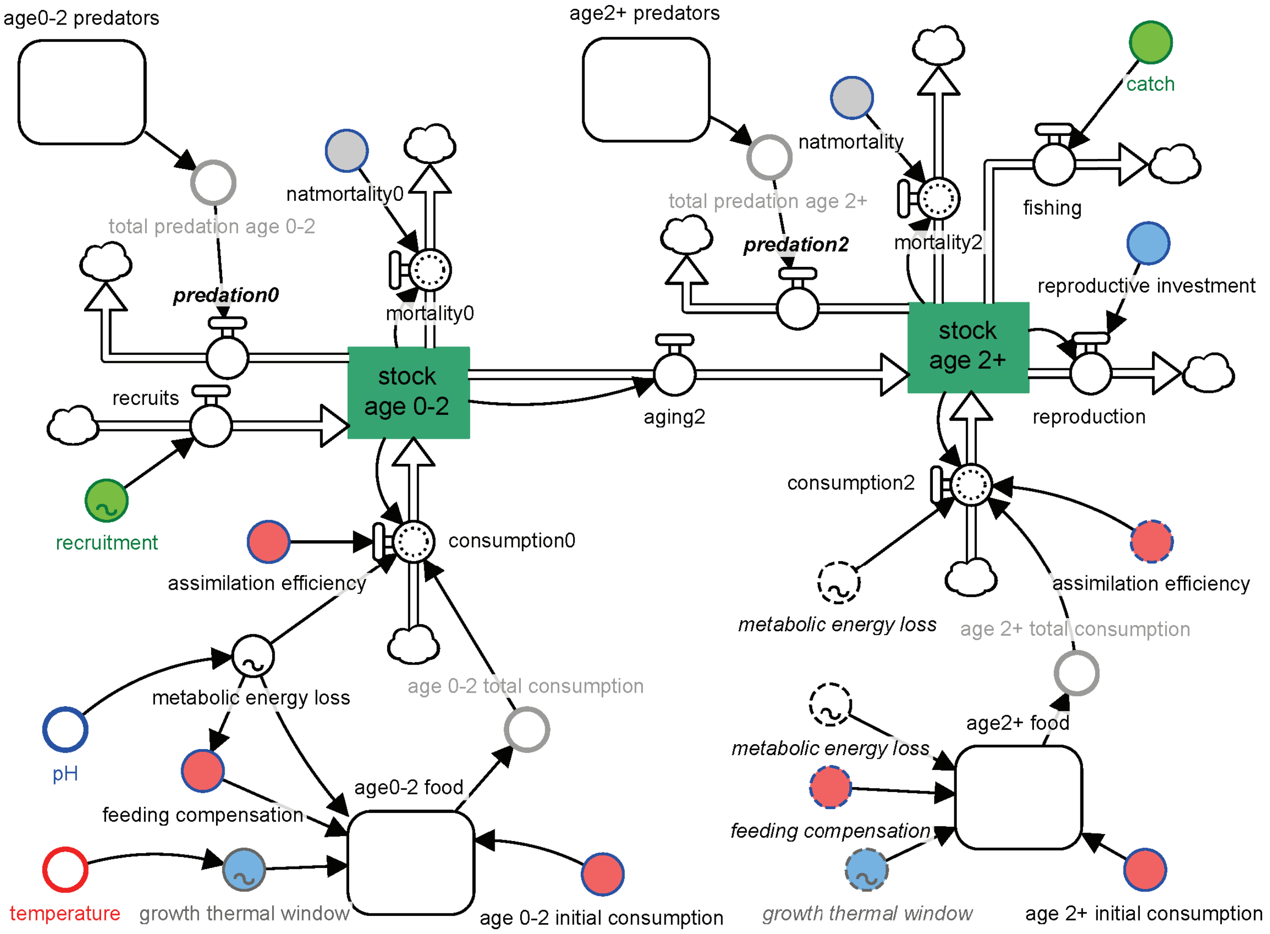

Figure 3: Generalized depiction of model structure used for fish stocks and determining processes (biomass flows), exemplified for two age classes. Biomass stocks (green boxes) are determined by biomass in- and outflows (thick arrows). Model parameters (circles) affect flows and other parameters (thin arrows). Filled circles are parameters based on ecological (red), physiological (blue) and field observational data (green), and and calibration parameters (grey). The model drivers temperature and pH (circles with thick lines) determine energy input, and total consumption and total predation (grey circles) are determined in model submodules (round boxes) based on diet composition, state of the prey/predator stocks and a functional response (see text). Circles with dashed outlines are copies of parameters calculated for all life stages.

Fish species in the model and harp seals are divided into two or three age classes, while plankton groups, other mammals and seabirds are modeled as stable single biomass compartments, without reproduction and recruitment flows.

Each stock is thus calculated as a finite difference equation

$$B_i(t) = B_i(t-dt) + (r(t) + (g(t) - a(t) - d(t)) * B_t + i(t) * B_{i-1}(t) - p(t) - n(t) * B_i^2(t) - f(t)) * dt$$

where B_i *(t)* is biomass in tons of the stock of the age class *i* at time *t*, $B_i(t-dt)$ is biomass at the previous time step, *r(t)* is biomass inflow by recruitment for the age 0 stock, *g(t)* is stock growth (biomass accumulation per stock biomass), *a(t)* is outflow through aging to the next age group for all but the adult stock, *d(t)* is investment in reproduction of the adult stock, *i(t)* is inflow through aging of the previous age group B_{i-1}, *p(t)* is total predation (sum of partial consumptions $\Sigma\ q_s\ (t)$ of the stock's predators), *n(t)* is a natural mortality rate, and *f(t)* is biomass extraction by fishing. Equations are solved for a *dt* of 1/4 week using Runge–Kutta 4th order integration.

The ‘natural mortality‘ term describes predation mortality by species not included in the model and other causes, is represented as a yearly rate multiplied with the squared stock biomass (quadratic mortality; Fulton et al. 2003) and used to calibrate the model to fit time series of biomass estimates for each stock. Reproductive investment of the stock, representing the energy invested into maturation and egg production and thus lost to somatic biomass production, was assumed as a yearly rate of 20% of stock biomass.

Productivity, consumption and predation (food web interactions)

Population productivity (net assimilated biomass per population biomass) is determined by

$$g(t) = (q(t) * w(t,T) * E_A) * dt$$

where q is prey consumption per biomass, $w(t, T)$ is the organismal growth performance dependent on current temperature (thermal window, cf. **Figure 2**) of the species, and E_A is assimilation efficiency of the species.

Consumption of each prey item is calculated in a submodule for each species, and subsequently used to determine the predation process for each prey species, thus linking the stocks in the model (cf. **Figure 3**). Consumption per predator biomass is described by an asymptotic Holling 'Type II' functional response (Holling 1959), following the form

$$q_i(t) = \frac{q_{max} * P_i}{k + P_i}$$

where $q_{\max}$ is maximum consumption per predator biomass, k is a half-saturation constant, and P_i is biomass of one prey species. To improve biological significance of the parameters, we used a ‘sensitivity’ factor

$$S = \frac{q_{max}}{q_0}$$

to define asymptotic consumption as a multiple of the estimate of initial consumption q_0, at the start of the calibration process set to S = 2 (i.e. each predator can double its per-biomass consumption under increasing prey). We transformed k to refer to the initial reference prey biomass of the consumption estimate

$$k = \frac{S}{2} * P_0$$

Inserting eqs. (4) and (5) into (3) gives

$$q(t) = \sum_i \frac{P_i \, S \, q_0}{\frac{S}{2} * P_0 + P_i} * y_i$$

as the functional response for multiple prey species (cf. Magnússon 1995), where y_i is the fraction of the prey in the diet of the predator and P is the reference biomass of the prey at which the initial consumption estimate q_0 has been determined.

Model calibration and scenarios

Model calibration

To drive the model in the calibration interval 1983–2015, the temperature time series from the Kola section (0–200m depth) was used, which is representative for the Barents Sea temperature conditions (Ottersen et al. 2005). Primary production was adjusted to 100g C/m^2 and a carbon–wetness ratio of 1:20 assumed.

As advection of external zooplankton production from the Norwegian Sea comprises an important contribution to zooplankton biomass in the Barents Sea (Yaragina & Dolgov 2009), and total biomass estimates for zooplankton groups are more difficult to obtain due to high spatio-temporal variability, we used empirical abundance indices for zooplankton groups (Dalpadado et al. 2012) and a group-specific productivity calibration factor, to match estimated long-term averages of zooplankton biomasses (Eriksen 2015). Yearly fisheries landings for fish stocks were taken from ICES reports, and the considerably lower minke whale catches adjusted at a constant 5700 tons. Fish recruitment was calibrated to match empirical 0-group abundance indices from the Norwegian-Russian ecosystem survey in autumn, corrected for capture efficiency (Eriksen 2015).

Model calibration was conducted using a step–wise, hierarchical approach considering model structure and data sources on different levels of description (cf. Kubicek et al. 2015; Oliveros-Ramos et al. 2017), aiming to reproduce the amplitude and wavelength of empirical biomass fluctuations over time in the calibration interval 1983–2015, with a burn-in period starting in 1970. Natural mortalities of species, trophic level sensitivity factors, assimilation efficiencies and advection of zooplankton groups were adjusted to reproduce survey-based biomass time series, with age-0 recruitment of fish stocks forced by using 0-group time series. Predators on higher trophic levels were initially deactivated by setting their consumption to zero, and in iterative steps, were progressively added and natural mortalities on lower levels reduced, until reproducing empirically observed biomass fluctuations of fish stocks and estimated abundances of marine mammals and seabirds.

Table 2: Final values of food web calibration factors after model fitting.

	production (t biomass /a)	**natural mortality rate**	**assimilation efficiency**	**sensitivity**
Phytoplankton	1350000000	0	–	–
Copepods	5000000	3.00E-09	0.1	2
Amphipods	100000	9.00E-09		
Krill	300000	9.00E-09		
Capelin (0-1)		1.60E-07	0.2	1.6
Capelin (1-2)		1.40E-07		
Capelin (2+)		1.00E-07		
Herring (0-1)		0		
Herring (1-2)		5.00E-07		
Herring (3+)		3.00E-06		
Polar cod (0-1)		5.00E-06		
Polar cod (1+)		5.00E-06		
Atlantic cod (0-1)		0.0002	0.54	2.13
Atlantic cod (1-3)		3.00E-05		
Atlantic cod (3+)		2.20E-06		
Haddock (0-2)		9.00E-06		
Haddock (3+)		1.00E-05		
Minke whales		3.00E-07	0.1	20
Baleen whales		5.00E-07		
Sperm whales		1.10E-07		
Orcas		6.00E-05		
Harp seal (0-1)		0.00015		
Harp seals (1+)		9.00E-07		
Other seabirds		1.09E-05	0.1	20
Atlantic puffins		5.49E-05		

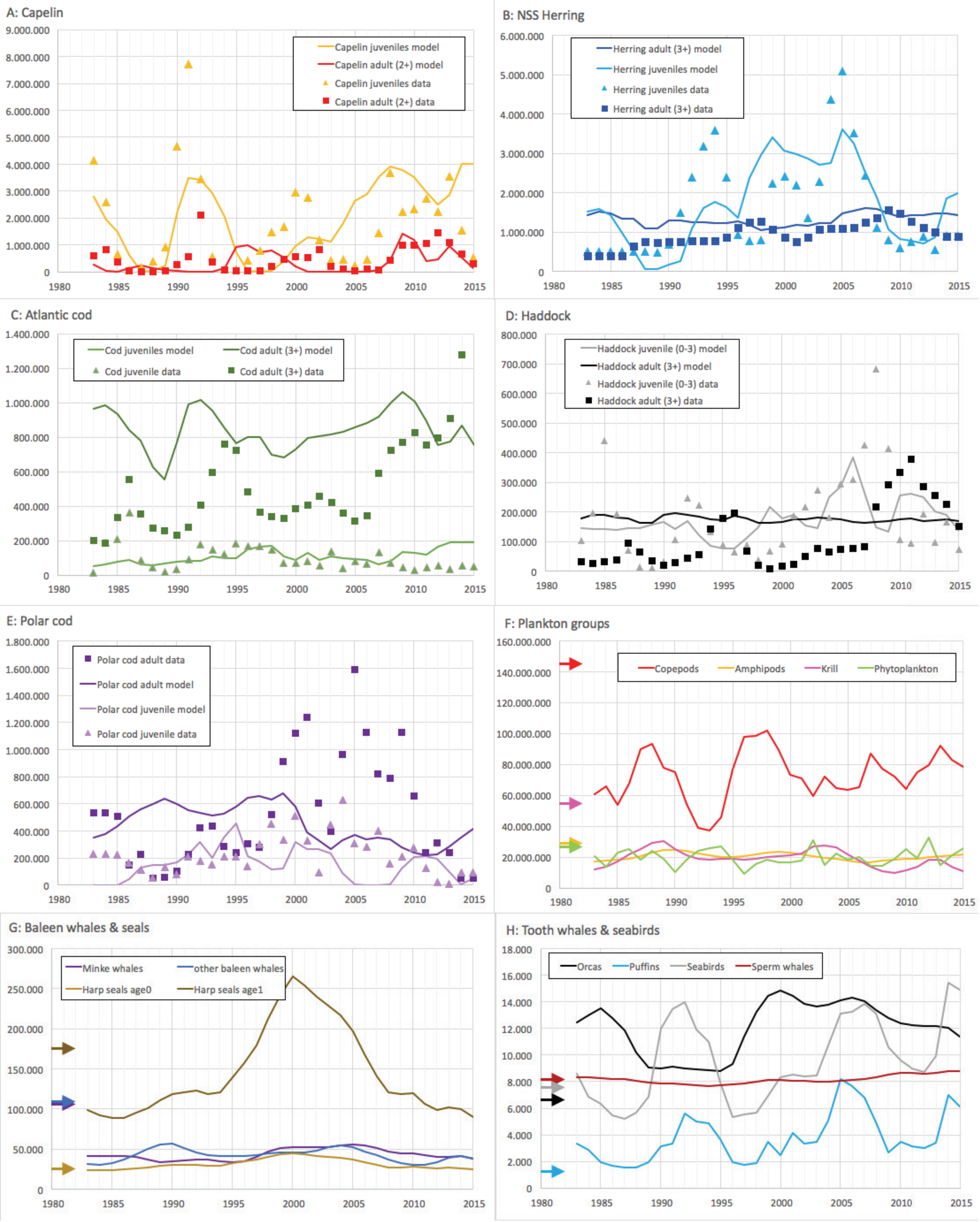

Figure 3: Fluctuations of the modeled species in the Barents Sea (yearly averaged population biomass in tons) in comparison to empirical estimates during the model calibration interval 1983–2015. A–E) Major fish species (lines) in comparison to empirical survey-based estimates (symbols), for adult populations (darker lines, squares) and for juveniles (lighter-colored lines, triangles), A) Capelin, B) Herring (biomass scaled by 1/5), C) Atlantic Cod, D) Haddock (biomass scaled by 1/2), and E) Polar cod. F) Biomass of lower trophic levels (copepods, krill, amphipods, and phytoplankton), G) Baleen whales (Minke whales and other baleen whales) and Harp seals, H) Toothed whales (Sperm whales and Orcas) and seabirds (Atlantic puffins and other seabirds). Arrows give mean biomass estimates for mammals, seabirds and lower trophic levels (see text for data sources).

After adjusting values by hand to find a rough fit, more exact parameter values were found by running PEST version 13.6 (*Model-Independent Parameter ESTimation and Uncertainty Analysis*; Watermark Numerical Computing; pesthomepage.org). Finally, the calibrated model was run under stable conditions (constant temperature) to assess the internal fluctuations of the model (Supplemental **Figure 8**). The combination of calibration values shows increasing natural mortalities, assimilation efficiencies and feeding sensitivities on higher trophic levels (**Table 2)**. The calibrated model describes food web behavior in the calibration period reasonably well, providing a good quantitative fit to biomass levels, amplitude and wavelength of biomass fluctuations in comparison with empirical data (**Figure 4)**. Some biomasses on higher and lower trophic levels (copepods, krill, and baleen whales) are lower by around 50% in comparison to combined area-based estimates for the Norwegian and Barents Sea, but stable during the calibration interval.

Scenarios and model sensitivity analysis

Climate change projections were driven by temperature and CO_2 trends based on IPCC (Intergovernmental Panel on Climate Change) ensemble earth system models projections for the Barents Sea under the RCP 8.5 scenario (Representative Concentration Pathway, corresponding to 'business-as-usual' emissions). Under this scenario, increases of annual average water temperature by 3.5°C are anticipated in the Barents Sea region (Bopp et al. 2013).

Multi-annual temperature fluctuations are a distinct feature of physical conditions in the Barents Sea, and have been used in other attempts to forecast the Barents Sea cod stock (Howell et al. 2013). To simulate these temperature fluctuations connected to oceanographic and atmospheric forcing, e.g. by the North Atlantic Oscillation (Ottersen & Stenseth 2001), we forced temperature projections with sinus waves of wavelengths 9.3y and 18.6y (amplitudes of 0.4°C and 0.5°C) connected to lunar cycles, which have been shown to provide a good description of the fluctuations of Barents Sea temperature in the Kola section (Yndestad 2003).

Ocean acidification, through increased uptake of anthropogenic atmospheric CO_2, will increase average surface pCO_2 in the Barents Sea from 400μatm to 590μatm in 2065 and approximately 1100μatm until the year 2100, as estimated under business-as-usual emission scenarios by regional models for the Nordic and Barents Seas, corresponding to a pH decrease of 0.0033 y^{-1} (Skogen et al. 2014; AMAP 2013). Increased seawater CO_2 levels will increase the need for compensatory metabolic processes to maintain the internal pH in marine fish, thus leading to additional losses in their energy budget (Fabry et al. 2008; Pörtner et al. 2010). We tested the potential impacts of ocean acidification by assuming a linear decrease in pH to 7.8 in the year 2100, and a linearly decreasing growth performance of up to –20% at the final simulation pH of 7.8.

We currently do not assume direct environmentally driven changes in primary and secondary production in the projection. Although it has been argued that increases in primary production can be expected in the Barents Sea due to decreasing ice cover in the Northern part, ocean model simulations demonstrate that this may be impeded by decreased nutrient supply from deeper waters under ocean warming (Slagstad et al. 2011). Nevertheless, import of production from the Norwegian Sea through advection may increase (Wassmann & Reigstad 2011).

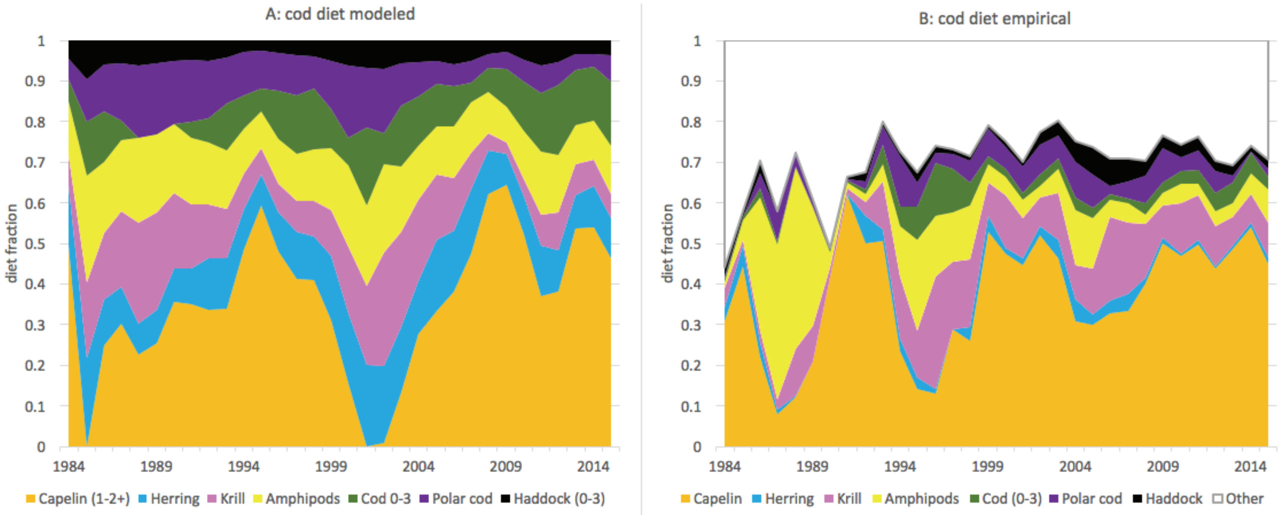

Figure 4: Diet composition of adult Atlantic cod (stacked lines give cumulative fraction of each prey in annual cod consumption) during the calibration period in the model (A), and according to empirical data from the Norwegian-Russian stomach content database (B; ICES AFWG 2016)

Future fisheries landings were assumed to follow the current management regime. This was incorporated by a linear relation of total fisheries landings to stock biomass in the previous year, determined for the calibration period with a good fit for herring, cod and haddock (R^2= 0.67–0.75; Supplemental **Figure 9**). For capelin, landings were assumed to follow the current management rule of leaving a surviving stock of 200,000 tons (ICES AFWG 2016).

For sensitivity analysis, empirically estimated consumption, 0-group recruitment and primary and secondary production rates were varied in 1000 model runs, using normal distributions with two standard deviations corresponding to the 95% confidence intervals of their estimates, at +/– 0.15 for the primary production estimate (Dalpadado et al. 2014), ranging from 0.19 to 0.45 for the different fish 0-group abundance estimates as averaged among years (ICES AFWG 2016), and an assumed confidence interval of 0.5 for secondary production.

Results

Model behavior

After calibration, the model reproduced the biomass levels of fish stocks, lower trophic levels and top predators, and exhibits some of the characteristic fluctuations of the major fish stocks in the Barents Sea (Supplement Figure 1, **Figure 4**). Juvenile stocks generally show higher variability, and oscillations are shifted with regard to adult stocks, reflecting the biomass transfer through the aging process. Species that rely on a single prey species show oscillations in form of sinus curves that are anti-correlated to their prey, corresponding to classical Lotka–Volterra type dynamics. In species that have a more equilibrated diet, more complex fluctuations are produced as a combination of the prey availabilities.

Realized diet composition over time in the model compared to empirical data from stomach content analyses shows that the fluctuations of diet composition are comparable to empirical data. In years with a high capelin stock, capelin forms the main component of the diet of adult cod, while in low-capelin years, cod compensates for the losses by increasing consumption of krill, amphipods, polar cod, herring and its own juveniles (Bogstad et al. 2015). The general pattern in the empirical diet data is thus reproduced, although the model shows a constant slight overestimation of herring consumption and an underestimation of capelin consumption in low-capelin years.

Biomass projections under continuing ocean warming

Under the ocean warming scenario, assuming a linear increase in temperature by 3.5°C until 2100, the model projects continuing biomass oscillations and some shifts among species in the food web in the course of the century (**Figure 7**). In lower trophic levels, a shift in dominance among groups is projected in the second half of the century, with copepods increasing their biomass towards a long-term average of 200 mio. tons, krill increasing to 20 mio. tons, and cold-water associated amphipods showing a marked decrease after 2040 to a biomass of about 7 mio. tons. These changes in grazing pressure reduce the variability in phytoplankton biomass and reduce it to an inter-annual average of 5 mio. tons at the end of the century.

Capelin is projected to decrease in average biomass from 4 mio. tons to 1 mio. tons, with dampening multi-annual fluctuations. Herring remains at the same average level, but increases in inter-annual variability. While haddock remains stable over the projection interval, biomasses of cod and polar cod exhibit downward trends after 2050–70.

Among the top predators, decreases are projected on average for harp seal biomass, and marked reductions with decreased variability for the ‚Other seabirds' group. Toothed whales (sperm whales and the more variable orcas) remain at stable level, but show moderate negative impacts towards the end of the projection. The 'other baleen whales‘ group, and to some extent minke whales, show moderately positive trends in average biomass. A short-term capelin reduction in the year 2060, caused by a fast decrease in our oscillatory temperature forcing, shows marked repercussions in the food web, with short-term reductions in baleen and toothed whales and seabirds. Confidence intervals for these projections quantified by sensitivity analysis show a relation to the amplitude of inter–annual fluctuation, increasing for highly variable species.

Under stable harvest control rules, fisheries yield in the Barents Sea will be moderately affected by the continuing warming. The principal impact is seen in capelin catches in years with a high capelin biomass, which are projected to decrease progressively from around 2 mio. to 2–400.000 tons. Cod and herring catches show moderate decreases in the second half of the century, while haddock fisheries remain stable.

Impacts of ocean acidification

Under the applied ocean acidification scenarios, effects differ among species, and based on the degree of compensation (50% or 90%) of the assumed energy losses by an increase in feeding (cf. **Figure 6**). Copepods, krill and amphipods are progressively negatively affected by the ocean acidification–mediated energy loss in the model, whereby we did not assume feeding compensation for these zooplankton groups. Herring, cod and haddock are negatively affected, to a greater extent when assuming lower (50%) compensation by increased feeding. In contrast, polar cod benefits from the release in feeding competition by the other fish species, and is positively affected under the ocean acidification scenarios even when polar cod itself also loses energy. These overall reductions in prey species show repercussions among all mammals and seabirds as top-level predators, with ameliorated increases in baleen whales and reinforced reductions in toothed whales, harp seals and seabirds.

Figure 5: Projections of future changes (yearly averaged population biomass in tons) in the marine food web of the Barents Sea under ocean warming and acidification scenarios in the course of this century. Shown for warming only (solid lines), and for combined warming and acidification, 90% compensated by increased feeding (dashed lines) and 50% compensated (dotted lines). A) Minke whales, other baleen whales and harp seals, B) Sperm whales, Orcas, Atlantic puffins, and Other seabirds; C+D) fishes: Atlantic cod (dark green, shown on two different scales), Capelin (orange), Herring (blue, biomass scaled by 1/5), Haddock (black, biomass scaled by 1/2), and polar cod (violet). E+F) Plankton groups: Copepods (red), krill (pink), amphipods (yellow) and phytoplankton (green, shown on two different scales). Boxes at the right edge of graphs depict 95% confidence intervals for end points of the respective projections under the warming scenario, quantified by sensitivity analysis.

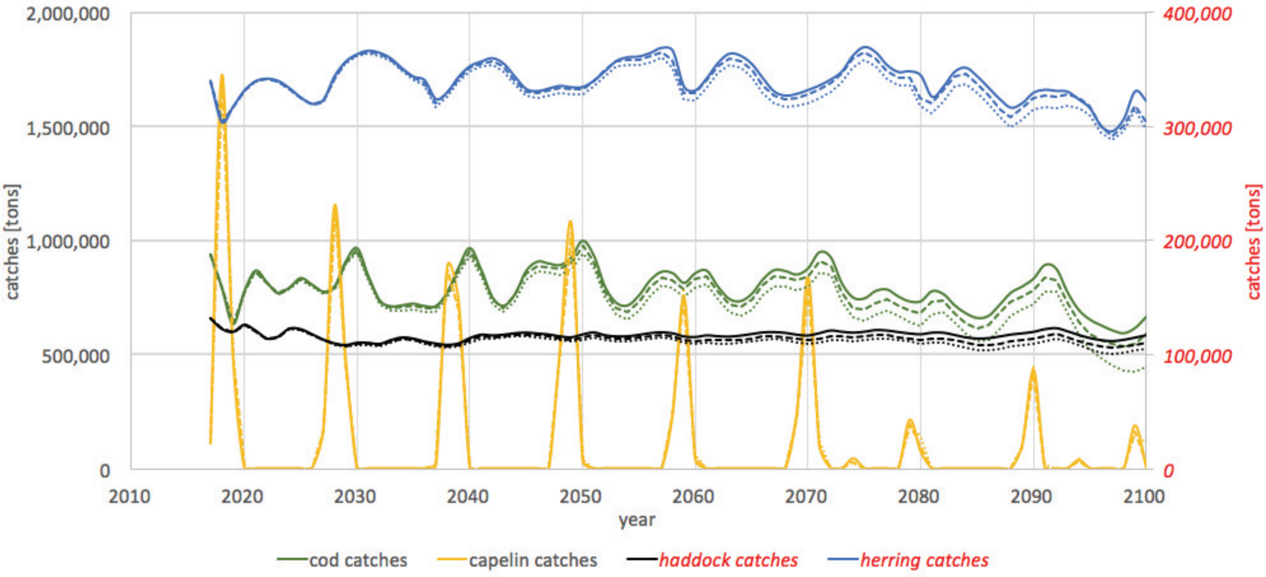

Figure 6: Projected fisheries catches (fished biomass in tons) in the Barents Sea, for Atlantic cod (green, left scale), Barents Sea capelin (yellow, left scale), Northeast Arctic Haddock (black, right scale, catches scaled by 1/2), and Norwegian spring-spawning herring (blue, right scale, catches scaled by 1/5).

Additional effects of ocean acidification generally lie within the confidence intervals of the warming projections, except for cod, harp seals and baleen whales. For these species, significant negative impacts are projected under both scenarios of feeding compensation (50% or 90%). The negative ocean acidification effects on cod, herring and haddock biomass affect the projected fisheries yields, with slight losses in catches under the 90% compensation scenario, which approximately double under the 50% compensation in cod (**Figure 7**).

Discussion

How well does the model reproduce empirical biomass fluctuations in the Barents Sea?

The calibrated model reproduces the average biomass levels of the fish stocks and a range of interdependent fluctuations among species in the Barents Sea–Lofoten system. Thus, based on organismal thermal performance curves and food–web interactions, the model provides a semi-quantitative explanation of the empirical biomass fluctuations recorded in the years 1983–2015, over several shifts in ecosystem state and three capelin collapses. The drastic fluctuations in the capelin stock with links to the cod and herring stocks, and the ensuing changes in species composition and predators' diets between low–capelin and high–capelin years are the most typical biological fluctuations in the Barents Sea, and past capelin stock collapses in 1985-1989, 1993-1997, and 2003-2006 had differential effects on predators and prey availability (Gjøsæter et al. 2009). As reproduced by the model, capelin biomass generally shows an inverse relationship to krill abundance (Eriksen et al. 2017). Seabirds show a strong correlation to capelin abundance over the calibration period in the model, which has been empirically observed e.g. for black-legged kittiwakes (Barrett 2007).

The diet composition of Atlantic cod, the species with the most detailed empirical data available on changes in diet over time, provides further indication that the fluctuations reproduced by the model are connected to the correct changes in predator-prey interactions underlying these fluctuations in the real system. The fluctuations in capelin, krill and amphipods are adequately reflected in the cod diet, and lead to higher cannibalism in low-capelin years (Durant et al. 2008; Bogstad et al. 2015; Eriksen et al. 2017). Abundance of macrozooplanktonic amphipods *Themisto* spp. is usually controlled by capelin, while in low-capelin years, the consumption by cod, harp seals and seabirds increases (Dalpadado et al. 2001).

The typical fluctuations of capelin and adult herring in an interval of 10 years, and a cycle of 5-6 years for herring juveniles, are also produced under constant temperature forcing, as a result of internal Lotka–Volterra type predator-prey cycles (Supplemental **Figure 8**). Thus, while it has been hypothesized that the biomass fluctuations in the Barents Sea are a direct consequence of regular temperature oscillations e.g. connected to lunar cycles (Yndestad 2003; Klyashtorin et al. 2009; Yndestad 2009), our model shows that the basic patterns of these fluctuations can be reproduced without temperature forcing, only from predator-prey interactions. Yet, some typical features are only reproduced when temperature forcing is applied: in our stable (non temperature–driven) model, cod and herring fluctuate synchronously (cf. Supplemental Figure 8). Only when applying the variation of temperature-dependent growth via the organismal thermal window in the calibration and projection period, cod and herring enter the empirically observed anti-correlated fluctuations.

The model thus reproduces typical fluctuations and correlations from diet compositions, and demonstrates that the combination of feeding interactions and organismal thermal windows can explain empirically observed fluctuations among fish stocks in the Barents Sea food web. Some extreme fluctuations in capelin juveniles (1990–92) and herring juveniles (1993–95 and 2004–06) are not reproduced by the model, and some biomass peaks appear shifted or delayed. This may be due to the limited life stage resolution in the model, with predation effects on early life stages are not considered. For instance, when cod predation pressure is not too high, herring can prey extensively on cod eggs and larvae, leading to a negative feedback on cod recruitment (Pedersen et al. 2016).

Furthermore, we used survey-based estimates for model calibration, in order not to introduce additional assumptions of VPA (virtual population analysis) model-based estimates (such as stock-recruitment functions and natural mortalities). However, survey-based estimates can be subject to some bias, e.g. with regard to length selectivity of trawls and timing of settlement to deeper waters of demersal fish cod and haddock (Dingsør 2005). The high biomass of polar cod recorded in the years 2004–2010, which is not reproduced based only on temperature and food web conditions, may be explained by bias in the survey data with regard to the sea ice extent, as Norwegian-Russian ecosystem surveys are conducted further North in years with low sea ice extent, systematically catching more Polar cod (Eriksen 2015), while other authors find polar cod to have declined in abundance in the Barents Sea Region in recent years (Hop & Gjøsæter 2013).

In a whole-food web model of the Barents Sea, it has also been found that calibration of vulnerability parameters for species interactions succeeds in reproducing fluctuations of larger fish species, but variations in planktonic groups and fish with shorter life spans are improved when primary production forcing is included (Skaret & Pitcher 2016). To which degree fluctuations in mammals and seabirds reflect real changes in the calibration period is uncertain, as abundance estimates are more difficult for these low density, long-lived and highly mobile species, and not available on a yearly basis. In the model, biomass levels of these species are assumed to be determined by food abundance and are under strong density dependence, i.e. acting as a 'closure' of the energy flow in the model (Fulton et al. 2003), thus their stability may be overestimated for some species and their regional abundance highly influenced by changes in habitat availability and movement patterns not included in the model.

Projected shifts among species under continued ocean warming

The projected shifts among zooplankton groups are in agreement with observed correlations and trends in the Barents Sea: In the model, krill is increasing under warming conditions, while amphipods are decreasing, matching with observed temperature correlations and expectations for these groups under continuing warming conditions in the Barents Sea (Johannesen et al. 2012). These changes lead to impacts on planktivore fish biomass, as seen in capelin in our model, as capelin has an important position in the energy transfer in arctic/subarctic marine food webs (Wassmann et al. 2006; Yaragina & Dolgov 2009).

The projected declines in the pelagic fish capelin and polar cod are caused by the combination of a temperature–mediated decrease in growth, increasing predation pressure by herring and cod for capelin, and reduced prey availability (amphipods) for polar cod. With a similar planktonic diet and a preference for slightly higher temperatures, capelin is a direct competitor to polar cod (McNicholl et al. 2015), and is anticipated to partly replace polar cod in the more Northern, Arctic parts of the Barents Sea, when capelin and cod are shifting their distributions more northwards (Renaud et al. 2011; Hop & Gjøsæter 2013). The capelin decrease causes declines in harp seal biomass in our model, and is reflected in the minke whale diet, with increasing relative contribution of krill and copepods. This change in diet has been observed in years when the abundance of both capelin and herring is low (1995–96), with negative effects on body condition (Bogstad et al. 2015).

For the demersal piscivore predator cod, and to some extent for haddock, moderate reductions are projected in the second half of the century, with short-term gains changing to a downward trend for cod. Generally, a continuation of the high production and biomass of these species is expected under warming scenarios in the Barents Sea due to faster growth and maturation, but it is acknowledged that other processes, e.g. increased cannibalism and changes in prey availability, may act against this effect (ICES AFWG 2015). Other studies using population models with a temperature-corrected recruitment function show that the uncertainty in temperature impact on recruitment is too high to produce reliable forecasts of future Barents Sea cod stock levels under changing climate, using these classical models (Howell et al. 2013).

Harp seals and 'other seabirds' are decreasing in biomass especially in the second half of the projection, and their inter-annual variability decreases due to a reduced importance in capelin in their diet and a shift towards other food sources (e.g. krill). Sperm whales decrease slightly, and orcas are highly fluctuating with herring biomass, but remain relatively stable. Mammal responses to food availability may not necessarily result to changes in total abundance as projected by the model, but can be reflected in physical condition of individuals and cause changes in migration patterns, as abundance of cetaceans is strongly associated with food distribution patterns and search behavior (Nøttestad et al. 2015). Orcas and other tooth whales have been increasing in recent years near the Northern Norwegian coast, and the proportion of pelagic fish, mackerel and herring, in their diet has increased while amphipods and krill have decreased (Nøttestad et al. 2015). Under retreating sea ice, pelagic fish species such as capelin, and marine mammals such as minke whales and harp seals may be able to expand their habitat into the Arctic ocean, thus potentially compensating to some extent the losses in food availability

(Darnis et al. 2012; Haug et al. 2017). Furthermore, the immigration of other fish species may affect interactions in the Barents Sea–Lofoten system, such as Atlantic mackerel *Scomber scombrus*, which has been recently recorded in the Barents Sea area (Berge et al. 2015).

Potential impacts of ocean acidification on the food web

Projected effects of ocean acidification-mediated energy losses affect zooplankton species and most fish species negatively, and the strength of effects depend on the position in the food web. Capelin and polar cod, which are subject to a high degree of top-down control in the model, are not or even indirectly positively affected by acidification. The projected reductions in biomass of species under strong feeding pressure, i.e. the zooplankton groups copepods, krill and amphipods, as well as herring, do not significantly deviate from the warming scenario as quantified by sensitivity analysis. They also do not rely much on the assumption whether energy losses are compensated for by increased feeding, and impacts are indeed slightly higher under high (90%) feeding compensation, due to the increased consumption by their predators.

In contrast, most higher-level predators, such as Atlantic cod, baleen whales and orcas, are impacted more by ocean acidification under a scenario of lower (50%) feeding compensation, and more so on the ascending slope of their biomass fluctuations, when the impact of their consumption on their biomass is still higher than the feedback of predation and density-dependent natural mortalities. For harp seals, the response to acidification is aggravated with increasing ocean warming, when the warming-related decreases in capelin results in a shift towards krill and amphipods in the harp seal diet, which are both significantly impacts by ocean acidification.

The negative ocean acidification effects on cod, herring and haddock biomass affect the projected fisheries yields, with slight losses in catches under the 90% compensation scenario, which approximately double under only 50% compensation. These effects are increased under low states of the fluctuating biomasses, when environmental and prey availability is unfavorable, and may thus be ameliorated by temporal reductions in landings, providing justification to incorporate the progressing acidification as a factor into the fisheries management regime in the Barents Sea.

For acidification–related impacts on mortality and growth, recent investigations using end-to-end models of marine ecosystems have shown that indirect effects, e.g. on demersal fish species which prey on sensitive benthic species, may be equally or more relevant than direct impacts, while impacts can be compensated in highly productive groups such as copepods (Marshall et al. 2017; Fay et al. 2017). Our analysis adds further detail to this picture, demonstrating that metabolic energy loss by ocean acidification can affect also highly productive species, and is a result of the combination of the amount of feeding compensation and species' position in the food web.

This analysis, however, focuses on general anticipated effects of ocean acidification on organismal energy budgets, and does not include potential effects on specific organismal processes, e.g. in more sensitive early life stages of fish or on calcifying plankton groups (Kroeker et al. 2013), which may more selectively impact certain species and thus cause reductions in fish recruitment and further shifts in food web dynamics.

Implications for the resilience of marine ecosystems and living resources under climate change, and directions for further research

Our model reproduces food web behavior based on biological processes, enabling the investigation of emergent properties of marine food webs and the conditions for resilience or resistance to perturbation (Link et al. 2015), and can thus be applied to identify potential regime shifts and tipping points under changing environmental drivers, providing important long–term management advice for marine systems (Hannah et al. 2010; Plaganyi et al. 2012). Ecological resilience defines how variable ecosystems can uphold ecosystem functions under external perturbations (Oliver et al. 2015). Climatic fluctuations play a very prominent role in the perceptions of societal stakeholders of the marine ecosystems in Northern Norway, and apart from affecting the highly fluctuating fisheries for capelin, the projected changes in food availability for toothed whales and seabirds under ocean warming and acidification point to impacts on marine nature tourism stakeholders in the area, which rely on certain minimum levels (sighting probabilities) of these species for being able to provide tours (Koenigstein et al. 2016b; Tiller et al. 2016).

Impacts on trophic energy transfer are an important aspect of climate change effects on marine ecosystems, as changes in lower trophic levels can be amplified in the higher food web (Chust et al. 2014; Lefort et al. 2014; Stock et al. 2014). Climate impacts on organismal functions such as growth and survival are modulated by food availability (co-determined e.g. by competition with other fish species and spatio-temporal matching of larval stages with plankton production) and a lag in the propagation of population-level effects (Landa et al. 2014). For the most productive marine ecosystems, upwelling systems and high-latitude shelf seas, energy transfer from primary production to fisheries passes a small number of species on the trophic level of planktivores, which may thus represent 'wasp-waists' in the food web (Rice 1995; Jordán et al. 2005; Bakun 2006).

In our model, shifts among species are projected due to direct and indirect effects, but no total collapses of species are projected. Rather, species with projected declines stabilize at lower biomass levels towards the end of the simulation period. The decreasing predation with low prey biomass levels assumed in the Holling type II functional response formulation, the comparatively high diet diversity and the density-dependent mortality of predators, cause a certain degree of stability in the model, and prevent runaway dynamics and a total collapse of species when drivers change in the range of the applied scenarios (cf. Fulton et al. 2003). At the same time, the density-dependent formulations of mortalities and consumption are sufficient to produce trophic cascades (cf. Heath et al. 2014). These are a feature often observed in marine food webs and linked to long-term regime shifts under multiple environmental and anthropogenic drivers, and thus an important question for management of marine systems (deYoung et al. 2008; Levin & Möllmann 2015).

The Barents Sea is a marine region with a comparatively high degree of top-down control (Johannesen et al. 2012). The available multi-species models for the Barents Sea thus focus on top-down effects (predation mortalities by top predators), but the inclusion of bottom-up effects, i.e. varying food abundances for fish could improve understanding of the system (Bogstad et al. 2015). Other multi-species models for the Barents Sea have shown that a focus on marine mammals (high structural resolution in top-level predators) may overestimate resilience to disturbance (Yaragina & Dolgov 2009), and that food web resilience increases with increasing aggregation of groups (Pinnegar et al. 2005). More detailed comparison of model structure and assumptions is thus necessary to make more certain statements about the probability and conditions of possible regime shifts under future climate change in the Barents Sea.

Further factors not considered here are expected to impact lower trophic level productivity and potentially lead to repercussion in the higher food web of the Barents Sea. For instance, we have only considered energy influx into the system in terms of zooplankton advection and heat transport (temperature oscillations) from Atlantic waters, but not Arctic water zooplankton species (*Calanus glacialis* and ice-associated amphipods) entering from the North and East (Hunt et al. 2013). Changes in primary production by phytoplankton and ice algae, and changes in species composition of zooplankton groups, e.g. from Arctic copepods and amphipods to their boreal congeners, may further affect energy content of prey for fish. Under continuing warming and decreasing ice extent, the period of primary production will be extended, with increasing contribution of ice algae production due to decreasing ice thickness (Wassmann & Reigstad 2011). We assume here that total primary production will not be altered significantly, as stratification will likely increase nutrient limitation of phytoplankton, leading to reductions in the Southern Barents Sea, and ice algae production in the Northern part contributes only a small part of primary production, of which a high percentage is exported vertically (Slagstad et al. 2011; Sakshaug et al. 1994; Wassmann & Reigstad 2011). A concomitant increase in zooplankton production will be hindered by the seasonal light cycle which limits the phytoplankton spring bloom, unless arcto-boreal zooplankton such as *Calanus finnmarchicus* can adapt to the high temperatures, or temperate zooplankton species such as *Calanus helgolandicus* immigrating from the South can adapt their life cycles to resemble those of Arctic species, which overwinter at depth with energy stored in lipid reserves (Sundby et al. 2016).

In conclusion, our work highlights the relevance of both organismal temperature preferences and feeding interactions in shaping food web dynamics in the Barents Sea, pointing to the possibility of extrapolating future food web shifts under climate change from historical ecological fluctuations. Incorporating greater detail on community dynamics in lower trophic levels, and the potential for life–history adaptation with regard to spatial habitat availability and phenology into the model would provide a more comprehensive picture of the ecological shifts to be expected under climate change in the Barents Sea. The work emphasizes the importance of quantifying organismal environmental windows under realistic and variable feeding conditions and identifying the extent of feeding compensation under energy losses connected to ocean acidification, as important determinants of potential regime shifts under climate change. This demonstrates that more empirical research on environment–related feeding behavior is needed, linking planktonic and fish food webs, conducted e.g. in aquarium experiments under different food availability and environmental driver conditions.

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Supplement

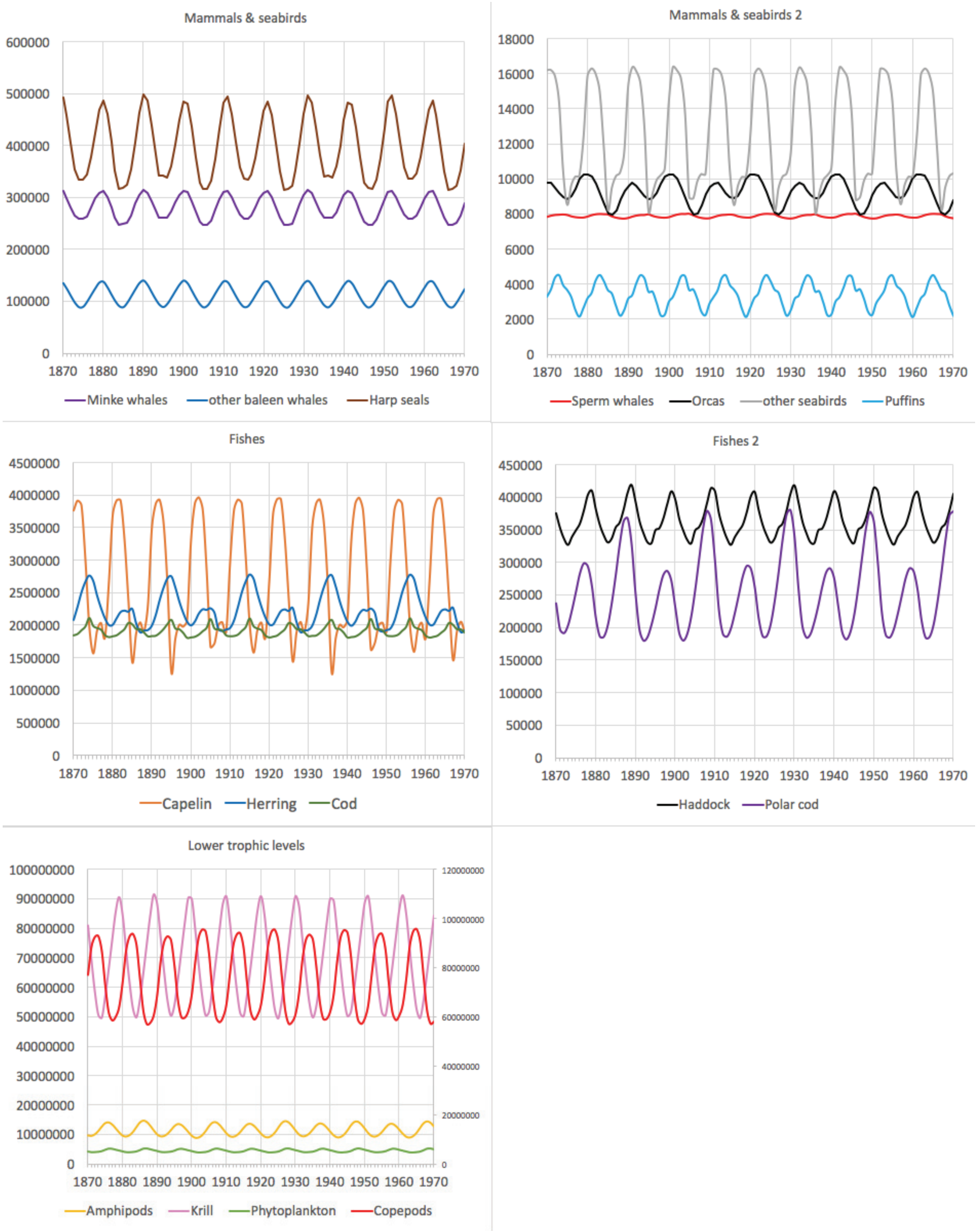

Figure 7: Internal oscillations of the model: Biomass fluctuations (tons) over a period of 100 years without application of temperature forcing

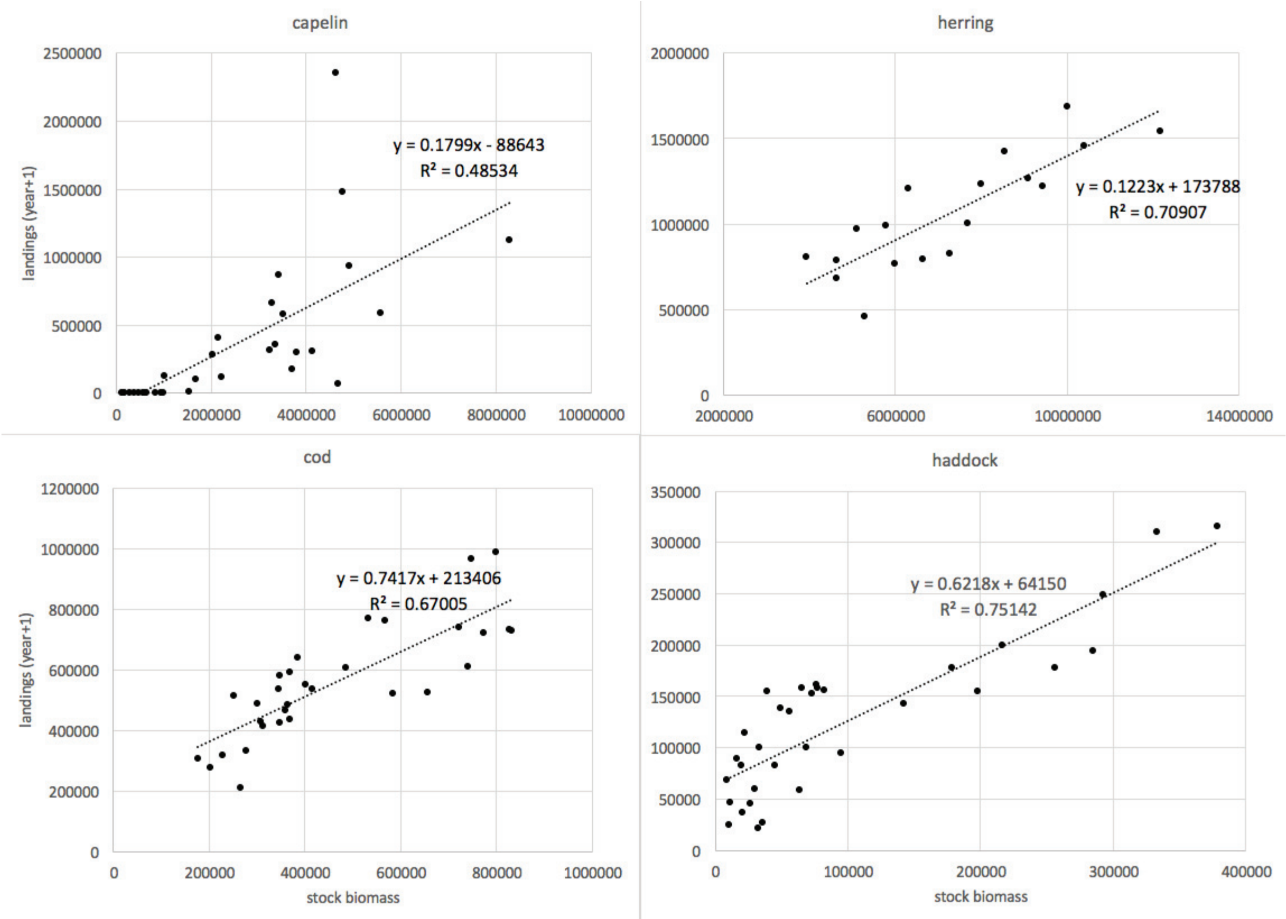

Figure 8: Relationship between fish stock biomass and quota in the following year for the fished stocks capelin, herring, Barents Sea cod and Northeast Arctic haddock, for the years 1983–2014 (1988–2014 for herring), with linear regression and R^2 value of the fit. The relations for herring, cod and haddock were applied in projections, while for capelin a survivorship rule was applied (see material & methods)

THESIS DISCUSSION AND CONCLUSIONS

Conclusions and context of the research papers

Analyzing the available approaches for modeling climate change impacts on marine ecosystems and fisheries (Paper 1)

In marine biology, computer models are important tools to investigate organismal and ecological mechanisms and set empirical results into the ecosystem context, and can thus serve to identify potential ecological impacts of and societal adaptation options to climate change effects in marine systems (Reuter & Koenigstein 2017, in German). The work in the present thesis was built upon a detailed analysis of the available modeling approaches for marine systems, and their strengths and weaknesses in representing biological processes (Paper 1).

At the current state of science, most models are focusing on specific hierarchical levels of biological organization, ignoring or aggregating relevant processes on other levels. The biological aspects that should be incorporated in more detail into ecological models to improve scientific understanding and, in the long term, projective capacity of models, include 1) organism-level trade-offs and thresholds in response to multiple environmental drivers, 2) life cycles and life stage–specific sensitivities which determine population responses, 3) food web structure and interactions which govern resilience of the ecosystem, 4) anthropogenic impacts which form societal feedbacks to changes in biological productivity.

It is a scientific challenge to improve the mechanistic incorporation of these processes into projections of climate change impacts in dynamic marine ecosystems, while avoiding the problems associated with parameterization, calibration and sensitivity analysis of highly complex 'end–to–end' models, which currently restricts the assessment of uncertainty and the usefulness of these models for policy and management advice (Rose 2012; Voinov & Shugart 2013; Morris et al. 2014). While first applications of end–to–end models to investigate the future impacts of ocean acidification and/or warming in marine ecosystems have emerged, they are thus far ‚black box’ models which directly transfer experimentally quantified survival (and sometimes growth) rates from meta–analyses to marine ecosystems, without considering interactions with other organismal processes or potential for organismal and population adaptation (e.g. Fay et al. 2017; Marshall et al. 2017).

To address the questions of this thesis, we chose to develop a model of the focus marine ecosystem, the Barents Sea–Lofoten system, that is deliberately simplified to incorporate the main drivers of its dynamics, whether environmental or anthropogenic, re–creating its characteristic behavior and investigating the conditions for substantial shifts (cf. Hannah et al. 2010; Plaganyi et al. 2012). Yet, the question to be investigated demands that the model structure should be biologically realistic and incorporate the processes which are of known importance and potentially altered under climate change, to enable quantitative integration of experimental results and basal ecological relationships. Model parameters and calibration factors should be biologically meaningful and quantifiable, in order to improve the utility of the model for scientific communication, and enable advancement towards an improved integrated understanding of climate impacts on a marine system.

Incorporation of stakeholder knowledge, affected user groups and adaptation options (Paper 2)

Apart from the current state of scientific knowledge, an important basis for the structure of the developed model of ocean warming and acidification effects in the Barents Sea have been the interests and concerns of potentially affected stakeholders in the region, to incorporate their field knowledge and experience, and ensure societal relevance of the modelling work (Paper 2).

Based on 35 personal interviews, two local workshops, and an online survey, we identified the ecosystem elements, processes and services of concern to societal stakeholders from Norway and Russia. Natural climatic and ecosystem fluctuations, and biological processes such as recruitment and feeding interactions among fish species and their prey, played a surprisingly important role in stakeholders' perceptions. As a consequence, we designed a multi-species model with the aim of reproducing the multi-annual fluctuations in the Barents Sea–Lofoten system, based on the biological processes underlying ecosystem dynamics under different temperature conditions. By this, while being scientifically sound, the model results would possess high relevance to the stakeholders, who see their perceptions of the system reproduced, improving the trustworthiness of projected long–term climate change impacts and the potential to communicate scientific uncertainties.

Our stakeholder group evaluated the projected changes of a preliminary model and discussed feasible personal and societal adaptation options, exemplifying a science–based decision process among the societal groups potentially affected by climate change. It was found that impacts of ocean warming can be both positive and negative for the different user groups, leading to compensation potential for some impacts, e.g. by switching fisheries target species. In contrast, effects that reduce productivity across the entire ecosystem, as is potentially the case with ocean acidification, can produce impacts which cannot be compensated, especially on user groups with a smaller range of adaptation options, such as coastal small–scale fishers and the marine tourism sector. The ecologically informed ecosystem service assessment and discourse–based evaluation performed in this work demonstrate that it is possible to investigate trade–offs in the governance of the regional marine–human system, and with a sufficiently large and representative stakeholder group, societal adaptation strategies to balance interests of the user groups under multiple system drivers (warming, acidification, and biomass extraction by fisheries) could be identified.

In the meantime, another stakeholder consultation study in our focus region has reported stakeholder observations from the fisheries sector that agree with our study, such as the prevalence of the topics of environmental variability on seasonal and multi–annual scales, the recently immigrated mackerel stock in the area, lower adaptive capacity of small-scale fishers to climate change–induced changes, and the significance of aquaculture as an adaptation option to uphold fish provision (Tiller et al. 2016). Nevertheless, in this study based on conceptual and probabilistic models, the topics ocean acidification, food web changes, and the biological carbon pump had to be excluded due to the high degree of scientific uncertainty. In contrast, the deterministic model constructed in our approach provides a quantitative link from ecosystem structure and dynamics to the provision of ecosystem services, and thus demonstrates a methodology for explaining trade–offs among services and providing in–depth understanding to inform sustainable management of natural systems (cf. Bennett et al. 2009; Fu et al. 2013).

The discussions among stakeholders at our workshops revealed that, while Norwegian fisheries management will likely enable adaptation to the projected changes among fish stocks, social aspects of quota distributions, with regard to small–scale fisheries and the cultural importance of the cod fishery in the high North of Norway, and ecological aspects not considered in current models, such as sensitive spawning habitat for fish and other areas relevant for biodiversity (e.g. cold-water coral reefs), need to be considered in management regimes. The deliberative approach applied in our work can integrate stakeholders' perceptions and different forms of knowledge into the derivation of adaptation options relevant for governance, and with an adequate representation of important system characteristics and scientific uncertainties, can potentially be employed to support social learning among different stakeholder groups and knowledge co–production with science (cf. Squires & Renn 2011; Waylen et al. 2014).

A specialized model for integrating experimental data and forecasting recruitment success of Atlantic cod (Paper 3)

An issue of considerable scientific uncertainty, and a prominent concern among the stakeholders participating in the work of this thesis, was the question whether changing environmental conditions, and ocean acidification in particular, will impact the future recruitment of fish populations. The existing recruitment functions used in fisheries assessment models assume a stable dependence of recruitment on the spawning stock, and thus fail to resolve the influences of environmental and biotic drivers on fish stock variability (Rice & Browman 2014; Pepin 2016), although it is well–established that temperature and other factors can have a considerable influence on recruitment (Pécuchet et al. 2015; Szuwalski et al. 2015). While statistical correlations among recruitment and environmental parameters have been identified for some fish stocks, they are not used in fisheries management, because it is impossible to assess and quantify their validity and uncertainty under changing environmental regimes (Howell et al. 2013; Skern-Mauritzen et al. 2015).

While the direct effects of environmental drivers on survival and development of fish early life stages can be quantified experimentally, it is unclear how these results can be integrated with the modulation by biotic factors in marine ecosystems (e.g. food availability and predation), and to which degree they can be compensated by evolutionary adaptation of fish populations. To address these issues, we developed a specialized early life stage model, incorporating experimental data gained from eggs and larvae of Atlantic cod from the Barents Sea under different temperature and pH conditions (Paper 3).

Experimental results on egg fertilization, egg and larval survival and development times were incorporated, and the model was calibrated using empirical time series of egg production, temperature and prey abundance, successfully reproducing Barents Sea cod age–0 recruitment over three decades. The projection of recruitment success under warming and acidification scenarios show severe reductions in average recruitment success of Barents Sea cod, and that considerable rates of evolutionary adaptation to acidification and shifts in organismal thermal windows would be needed to completely buffer future impacts on recruitment.

The developed model provides a proof–of–concept that experimental and observational data on multiple driver effects can be integrated among life stages into model–based projections, achieving a good explanation of empirical cod age–0 recruitment. This enables the identification of population bottlenecks resulting from life stages which are highly sensitive to multiple driver effects, and the estimation of uncertainty associated with inter–individual and ecological variation. It thus creates a basis for improved consideration of experimental and field observations in projections of future marine fish recruitment under climate change scenarios, as a complementing tool for informing management and policy, and as a module to be incorporated into higher–level population and ecosystem models. An evaluation of density–dependent mortality compensation in later life stages using these models, and more experimental research on possible maternal effects, genetic variability and adaptation potential, are needed to provide a conclusive assessment of the impacts that increased early life stage mortality under ocean acidification and warming will have on the recruitment of Barents Sea cod, and potentially other marine fish stocks.

Simulating marine food web dynamics in the Barents Sea and assessing the interacting effects of warming, acidification and fisheries (Paper 4)

To assess climate change impacts on marine species, it is necessary to incorporate food web interactions, as these can buffer changes on the species level, but can also trigger positive feedbacks, which may lead to sudden and unexpected regime shifts with strong ecological and socio–economic impacts (Mangel & Levin 2005; deYoung et al. 2008). The degree of exploitation by fisheries is another important co-determinant of the dynamic behavior of marine ecosystems (Fogarty et al. 2016) and affects their response to environmental drivers through impacts e.g. on productivity, age structure and evolution of fish stocks (Jorgensen et al. 2007; Perry, Cury, et al. 2010).

Building on the detailed analysis of capacities of different model assumptions (cf. Paper 1), and the stakeholder interests and concerns identified (cf. Paper 2), we constructed a novel model to assess the interacting impacts of ocean warming, ocean acidification and fisheries on the marine food-web of the Barents Sea (Paper 4). Based on organismal thermal performance curves and food-web interactions, the model reproduces the characteristic biomass fluctuations in the Barents Sea over three decades. Building on this, shifts among species in the food web under continuing ocean warming and acidification are projected, which lead to impacts on fisheries and top–level predators in the system.

Compared to existing approaches, the developed model can be described as a hybrid between a multi-species population model and a trophodynamic (food web) model (cf. Plaganyi 2007; Koenigstein et al. 2016). It is based on the carbon biomass fixed by primary production, which is then transferred to higher levels of the food–web (cf. Polovina 1984; Ulanowicz 1986). Estimates of diet composition are used to couple the stocks in the model via dynamic feeding interactions (Magnússon 1995; Rose & Sable 2009), and sensitivity settings are used to determine the functional responses of predators to increasing biomass, as integrative values which can describe ecological and behavioral aspects of foraging (Ahrens et al. 2012). Importantly, to be able to simulate natural environment–dependent fluctuations and assess the combined impacts of multiple climate change drivers on specific organismal processes, the model possesses a higher degree of biological detail than other existing modeling approaches on the level of food webs or ecosystems. Population dynamics are described based on the processes growth, aging, reproduction, predation and consumption, and organismal thermal windows incorporated to describe temperature–dependent growth performance.

The developed model focuses on the pelagic–demersal food web and the associated predators, neglecting interactions e.g. with benthic organisms, and other environmental drivers such as sea ice reduction, which may impact the habitat of e.g. polar cod and capelin. Yet, its process–based structure prepares the ground for incorporating greater detail on organismal life cycles, eco–

evolutionary strategies with regard to energy allocation and reproductive investment, and species' dependence on habitat availability, which would further improve fit to empirical fluctuations and increase mechanistic detail of environmental driver impacts and interactions (see section 'next steps'). More quantitative data on organismal energy allocation over the range of the thermal window and on the energetic cost associated with increased acid–base regulation under acidification for the species in the model, e.g. from aquarium experiments and energy budget models, would provide an improved empirical basis for projections of the changes in energy transfer in the food web than can be expected under future warming and acidification scenarios.

It is planned to incorporate the dynamic cod recruitment model (described in paper 3) as a module into the food web model, which would enable the assessment of the quantified early life stage mortality effects of temperature and acidification within the dynamic ecosystem context for cod, and potentially for capelin, herring and other stocks where sufficient data is available. Due to its design, the food web model offers insights on potentially impacted marine ecosystem services and prepares the grounds for exploring ecosystem–based management options, e.g. based on another assessment of the projections and associated uncertainties of the finalized model with the stakeholder group. Policy–relevant ecological trade–offs exist between fisheries yields and abundance of higher trophic level species (cf. Szuwalski et al. 2016), such as whales and seabirds relevant for marine nature tourism in our focus region, and also with regard to an increased biomass extraction from lower trophic levels (e.g. capelin and krill), as has been suggested to provide feed for the growing marine aquaculture sector as an adaptation to declining wild fish stocks (see 'socio–economic consequences and societal adaptation options').

Societal consequences, adaptation options and implications for marine governance in Norway

Societal impacts derived from the model

The model results point to impacts on the provision of ecosystem services to societal groups, and trade–offs among the exploitation of fish stocks by fisheries and the biomasses of higher trophic level predators, mammals and seabirds, which possess cultural, educational and recreational values. The projected decreases in tooth whales and seabirds are likely to have consequences for tourism business in the high north. Whale tours, which are dependent mostly on sperm whales, may be impacted, as the occurrence of orcas alone is too variable to serve as a mainstay for tourism businesses (cf. paper 3). As seabirds are projected to decline, alternatives for providing tours are further decreasing for tour operators.

Importantly, these are not only economic impacts, but distinct impacts on cultural and educational ecosystem services in the area. Atlantic cod has an exceptional cultural significance on the Lofoten islands and in the Northern Norwegian provinces. The associated small–scale fisheries vessels and harbors represent a unique cultural asset of the area that has touristic relevance. The top–level predators whales and seabirds are the most visible parts of the marine ecosystem for the biggest part of the population, and thus also possess high aesthetic and educational significance. For many coastal communities, economic activities are closely connected to marine environments, cod fishing in the fjords and coastal areas has a cultural and historical significance far beyond that, and climate change adaptation will have to happen under the challenges posed by demographic aging and the remoteness of these communities (West & Hovelsrud 2010; Dannevig & Hovelsrud 2015).

The combined stakeholder involvement and model design process has also yielded indications for sectors that cannot reasonably be integrated into ecosystem–based model projections and assessments. For instance, aquaculture is a topic of high relevance in the climate change context, as it is an important sector of the marine economy in Norway and also seen as a potential compensation for declining food provision by wild fish stocks (Tiller et al. 2016). The sector is however, largely disconnected from climate change impacts on the regional marine ecosystems. While tendencies to move facilities to locations in the North of Norway may increase with ocean warming, acidification represents a minor concern for the sector, as early life stages are reared in protected hatcheries, and for juvenile and adult fish, reductions in growth and behavioral impacts are not expected to be relevant under the high feeding levels and in artificial environments (Ellis et al. 2016). The interactions with components of the marine ecosystem are localized and extremely difficult to quantify, such as spread of parasites (e.g. 'salmon lice'), interbreeding of escaped fish on wild populations, impacts of nutrient discharges on the benthic ecosystems in the fjords, and spatial competition with fisheries and other marine sectors. These impacts should rather be addressed, and are being addressed in Norway within the legislative frameworks on industrial environmental impacts and spatial marine zone management, involving appropriate precautionary environmental regulations and regular monitoring. For climate change projections, it seems more adequate to include the role of aquaculture as an adaptation option as part of the framing scenarios (see 'Development of framing scenarios'; Table 1).

A further marine ecosystem service of high societal relevance is the climate regulation by sequestration and export of carbon from the atmosphere (Le Quéré & Metzl, 2004; Beaumont et al. 2009). First economic estimates for Norway have indicated that the costs associated with an acidification–mediated reduction in biological carbon uptake may be several orders of magnitude higher than effects on fisheries and aquaculture (Armstrong et al., 2012). The biological carbon pump takes up CO_2 via primary production and exports it to the depth mainly via sinking particles, and it is unclear whether reduced ice cover in the Arctic ocean may lead to increased biological CO_2 uptake in the Northern parts of the Barents Sea, or stratification will act against it (Wassmann et al., 2006; Wassmann and Reigstad, 2011). Because of the high uncertainties associated with the biogeochemical parameters and biological processes in lower trophic levels, we did not assess changes in the biological carbon pump with the developed food web model. However, the model is equipped to incorporate the results from biogeochemical models (Manizza et al., 2013; Skogen et al., 2014) into the context of higher trophic levels once reliable estimates are available, and/or make use of the results from mesocosm experiments (Riebesell et al., 2013; Spilling et al., 2016) when the sources of the high variability observed in these experiments have been better understood (Moreno de Castro et al., 2017).

The interactions among these ecosystem services exemplify the upcoming questions and conflict under progressing climate change in the area. These will be applicable for increasing parts of the Arctic, as under continuing ice melt, changes in habitat and biological processes for many Arctic and subarctic species will lead to movement of boreal species into the Arctic (Haug et al. 2017). Ensuing changes in biodiversity, habitat conditions and competition for polar fish species pose special challenges for future Arctic fisheries management, biodiversity conservation, and interdisciplinary science (Bluhm et al. 2011; Christiansen et al. 2014).

Adaptation options within the existing governance frameworks

The variety of the potential societal impacts of the ecological changes identified here, and the importance of interactions in the ecosystem and with the societal system illustrate that future changes in the fish stocks in the Barents Sea should not be addressed exclusively from a fisheries management perspective, but important trade–offs with other sectors and societal uses exist. For instance, reductions in fisheries exploitation may help to secure mammal and seabird populations and the cultural and recreational services provided by them. The identified impacts can thus form the basis for identifying adaptation options for the affected societal groups within the current marine governance system in Norway.

As fisheries are the second most important economic sector in Norway, fisheries management has a prominent political role and is coordinated on a national level by the Ministry of Fisheries and Coastal Affairs, advised by the Directorate of Fisheries. Catch quota are negotiated twice a year in a Management Council, based on agreements with other nations on co-used fish stocks and scientific information from the International Council for the Exploration of the Sea (ICES) and the Institute of Marine Research (Mikalsen & Jentoft 2001). The Norwegian Fishers Association and its regional organizations are the most powerful stakeholders in the Management Council, and fishers provide catch logs to inform stock management and are often surveyed by catch control systems (Johnsen 2013; Jentoft & Mikalsen 2014).

The Norwegian national fisheries management regime and international cooperation in the last decades are regarded as successful (FAO 2013), with high stock levels e.g. in the Barents Sea cod stock, albeit facilitated by favorable environmental conditions under ocean warming (Eide et al.

2013, Kjesbu et al. 2014). The Integrated Management plans for the Barents Sea and the area around Lofoten islands installed in 2007 prescribe a regular assessment of the state of the ecosystem, human uses and their ecological impacts, and put sensible areas such as cold water coral reefs under a special protection status (Hoel et al. 2009; Harsem & Hoel 2012). The results of the models developed in this thesis demonstrate that the currently positive trend in fish stocks can be suddenly reversed, when temperature optima for early life stage survival or for organismal growth performance of fish species are passed, as projected for capelin and cod, or through indirect impacts in the food web. The current temperature facilitation thus should not be assumed to continue in the coming decades, but governance mechanisms should be adaptive to recognize and respond also to adverse environmental regimes. The work also underscores the importance of protecting areas which are important for sensitive life stages of fish and zooplankton, such as spawning areas, from additional stressors e.g. through pollution.

The existing legal guidelines and their enforcement have succeeded to evoke a degree of self–governance among fishers (Johnsen 2013). Adaptation options for the fisheries sector with regard to ocean warming and acidification include the distribution of quota, gear regulations (e.g. type and mesh size of nets) and vessel size regulations. Furthermore, it has been suggested that marine living resources should be harvested on all trophic levels, according to productivity, instead on the current focus on the highest, most economically yielding species. This ‘balanced harvesting‘ approach may lead to more stable and increased biomass yields and conserve community composition (Garcia et al. 2011; Froese et al. 2015). Indeed, harvest in the Barents Sea seems to be more balanced than harvest in many other systems, but variability in fish stock biomass and recruitment pose significant challenges (Howell et al. 2016). From the projections of our model, it seems highly questionable that a harvest of krill or copepods, or an increased harvest of capelin for a regional production of fish meal for aquaculture feed, would be advisable options under future warming and acidification, as these species are projected to decrease and impacts on the higher trophic level species could be exacerbated.

The other user groups identified in this work, apart from fisheries, are involved in governance mainly via the Norwegian integrated coastal zone management procedures. Municipal governments have the legal duty to invite potentially affected stakeholders to participate in planning processes. This involves state representatives such as the County Governor and the Coast Directorate, and user groups such as fish farmers, tourism entrepreneurs, environmental and outdoor activity organizations, transportation and military sectors, land owners and indigenous Sami representatives (Buanes et al. 2004). The other user groups of marine ecosystem services which participated in this study, for instance tourism businesses linked to marine environments (e.g. whale, seal and seabird watching tours, sports fishing, sea kayaking, sailing and other nature-related activities), are not as well-organized as the fisheries sector, although the establishment of broader participation in the

Strategic Council for Tourism with yearly meetings is intended (NMTI 2012). Environmental organizations are mostly nationally organized and engage as quasi–stakeholders by cooperating with industry or governmental agencies or by lobbying, and other stakeholder groups such as indigenous peoples and seafood consumers do not regularly participate in decisions, while Sámi representatives do have a modest influence in the North (Mikalsen & Jentoft 2001; Buanes et al. 2004). Recently, fisheries associations and environmental NGOs have successfully joined forces to fight off oil and gas exploration plans around the Lofoten Islands because of concerns for the recruitment of Barents Sea cod (Jentoft & Mikalsen 2014), which stresses the high societal significance of the traditional fisheries in Norway. In the context of increasing oil and gas exploration efforts in the Barents Sea and the Arctic under retreating sea ice, a scientific knowledge gap relevant for ecosystem–based governance are the interactive effects of acidification and pollutants from oil spills, which have been found in some fish larvae and zooplankton species (e.g. Ingvarsdóttir et al. 2012).

It has been criticized that debated topics are in the end decided among the involved national ministries, and thus subject to the power balance among institutions and influenced by political agendas, e.g. a promotion of aquaculture (Hoel & Olsen 2012; Jentoft & Mikalsen 2014). This can promote distrust by stakeholders, and it has been argued that fisheries management is not very transparent, benefiting corporatism and industry interests (Mikalsen & Jentoft 2003). The Norwegian Fishermen's Association is criticised for democracy deficits and domination by the interests of larger offshore–vessel owners (Mikalsen & Jentoft 2001), and industrial sectors often having more influence than less well–organized civic groups in stakeholder participation processes (Buanes et al. 2004). National authorities have actively opposed attempts for local co-management of fish stocks, e.g. by indigenous Sámi people (Jentoft & Mikalsen 2014). While the coastal cod stocks in the fjords are different from the larger (‘Northeast Arctic’) Barents Sea cod stock, ecological interactions have been reported in our interview series, for instance that predation pressure by harp seals drives cod further into the fjords. The developed model can thus still be relevant for local conditions and user groups of these coastal stocks in Northern Norway.

As some of the identified user groups, such as small–scale fishers and local tourism entrepreneurs, have fewer adaptation options to potential ecological shifts under climate change and ocean acidification, they request better incorporation of environmental fluctuations, interactions among fish species and changes in primary and secondary productivity into scientific projections and management processes (Koenigstein & Goessling–Reisemann 2014). An improved participation of stakeholder groups other than the fishing industry, a more comprehensive assessment of future regional and local changes in marine ecosystem services, and better recognition of the cultural significance of marine species by incorporating public opinion, could further improve scientific anchorage and societal support for the Norwegian management of marine resources and areas.

Finally, it is important to consider that many of the adaptation options for stakeholder groups identified in this work depend on socio-economic and other background factors, e.g. vessel fuel costs for small–scale fishers and tour operators, or global fish market prices for the fisheries sector (paper 2; Koenigstein & Goessling-Reisemann 2014). Furthermore, in climate forecasts over multiple decades, the contribution of uncertainty in socio–economic background scenarios to total projection uncertainty becomes higher than that of internal system variability and model uncertainty (Hawkins & Sutton 2009). An assessment of robust and feasible governance strategies based on the societal adaptation options identified here thus will have to consider these factors by developing consistent framing scenarios, which can serve as a background for stakeholder valuations of the model projections (van Notten et al. 2003; Börjeson et al. 2006).

Next steps towards the quantitative integration of experimental and empirical data into regional analyses of marine ecosystems under climate change

This work provides first explorations of how experimentally quantified, temperature–dependent rates of organismal survival and performance can be incorporated into ecological models on the levels of populations and communities. We have incorporated experimentally quantified thermal survival curves for cod eggs and larvae into a recruitment model (Paper 3), and integrated organismal growth windows to determine energetic efficiency of fish species in the food web, describing competition and feeding interactions (Paper 4). The work thus exemplifies two possible approaches of applying organismal thermal windows and interacting physiological drivers to put organismal performance into the biological context on higher levels of description. In both cases, the interactive effects of acidification as an additional physiological stressor depend on the suitability of the current environmental temperature (position in the thermal window), and additionally, the degree of compensation by increased feeding in the food web model.

Presently, there remains insufficient clarity about how to advance beyond conceptual schemes and quantify relevant points of the organismal performance curve (Claireaux & Chabot 2016; Farrell 2016). The models developed in the presented thesis demonstrate two approaches for linking levels of description by quantifying thermal windows. In the recruitment model, the form of the thermal survival curves experimentally quantified for cod eggs resembles an individual performance curve. Yet, the combination in the model with a temperature effect on development times leads to a flattening of the right side of the curve, as additional time–dependent mortality is partially compensated by faster development times, an effect that coincides with field observations and results of individual–based models (cf. Paper 3). The population–level survival curve is shifted towards higher temperatures over the projection period to simulate an adaptation of the population to ocean warming.

In the food web model, the position (temperature optimum) and width of the thermal performance curve is used to describe ecological differences among species, i.e. cold–adapted vs. warm–adapted and stenothermal vs. eurythermal organisms, and their growth performance relative to each other at a certain temperature (cf. Pörtner & Farrell 2008; Pörtner et al. 2014). This approach enables a straightforward integration of organismal energy allocation with energy (biomass) flow through the food web, and sufficiently modulates the food web dynamics in the model to reproduce empirically observed correlations in the Barents Sea (cf. Paper 4). However, the heights at the optimal level of the realized temperature–dependent productivity curves in the biomass–based food web model diverge from the individual–level curves expected for organisms under different thermal regimes (e.g. polar, temperate and tropic; cf. Pörtner et al. 2014). The reason is that population–level consumption is highly dependent on the number of individuals, and per–biomass consumption applied in our model, as in other trophodynamic models, is thus higher in smaller species such as capelin, and in the juvenile stages (cf. paper 4).

Organismal metabolic processes such as feeding, respiration, growth and reproduction, linked to external parameters such as temperature and food availability, determine energy transfer in ecological communities (Brown et al. 2004). There is strong rationale that metabolic phenotypes can be linked to behavioral traits, which mediate the effects of environmental drivers on organismal performance (Metcalfe et al. 2015). Nevertheless, to derive fitness of an organism in its environment from quantified thermal performance curves, differences among specific organismal processes and among life stages of an organism have to be considered, and mediation by ecological interactions and anthropogenic drivers incorporated, using ecological models (Sinclair et al. 2016). The two models developed in this thesis thus represent examples how differences among life stages and levels of description and model assumptions have to be considered when incorporating organismal energetic properties and physiological principles into ecological projections.

While not yet providing a complete description, taken together, the two models exemplify how temperature influences on survival and growth performance can be integrated for different life stages and, considering availability of and competition for food resources, build a mechanistic basis for explaining how ecological community dynamics will be altered by climate change (Lancaster et al. 2017; Kordas et al. 2011). Differences in eco–evolutionary life history strategies among species can be integrated by adjusting reproductive investment and timing of spawning (Lowerre-Barbieri et al. 2016). To fill the remaining gaps in this understanding, more experimental work is needed to quantify aerobic scope and organismal strategies of energy allocation to organismal processes under different conditions.

The many interacting factors found in these two studies emphasize that caution should be exerted when attempting to use organismal temperature preference to determine future distributions and abundances of marine species. Marine species have evolved under the variability of spatio–temporally changing seascapes, and adapted their functional capacities and life cycles, enabling the co-existence of species in different niches (Kavanaugh et al. 2016). Spatial distribution of a fish stock can thus be more influenced by the size of the stock, via density-dependent biotic drivers, than by direct temperature preference. In the Barents Sea, the experienced ambient temperatures of two fish species, mackerel and haddock, have even actually decreased on average under recent warming conditions (Landa et al. 2014; Sundby et al. 2016), which violates the assumptions used in deriving the response functions for climate envelope models (cf. Woodin et al. 2013).

The developed model framework enables the incorporation of changes in energy content of planktonic prey for fish, mammals and seabirds, linked to changes in species composition in planktonic groups such as copepods, amphipods and krill. The productivity of these lower trophic level groups has to be informed by spatially resolved oceanographic models, and incorporate characterization of omnivores vs. specialist feeding strategies among the predators. The opportunistic feeding of many marine fish species, including the most important species in our study such as Atlantic cod, may buffer changes in plankton composition to some extent. On the other hand, our work exemplifies that even in this omnivore, the survival of early life stages in the regional system strongly relies on one single type of prey, i.e. copepods in the Lofoten spawning region. It has been postulated that early life stages of marine organisms are can form a ‘sensitivity bottleneck’ for marine populations under climate change story and in adaptation of fish to multiple environmental drivers (Rijnsdorp et al. 2009), and the case of Barents Sea cod illustrates that habitat and food availability are factors that can co–determine this bottleneck.

In conclusion, the study of the Barents Sea–Lofoten system demonstrates that biotic factors interact with environmental drivers in determining species responses, and the determinants of marine system responses to climate change can be highly region–specific. Identification of the ecological dynamics and physiological characteristics of organisms, as well as of the uses, responses and adaptive capacities of human user groups in the region can contribute much to an integrated analysis of marine systems. Thus, analyses of climate change impacts on marine–human systems on a regional scale will enable improved systemic understanding and identification of mitigation and adaptation options to climate change, advancing knowledge about how a sustainable provision of living marine resources and other ecosystem services can be achieved. On roughly the same scale as national and regional management boundaries, regional descriptions of marine–human systems, as in the present work, also offer the potential for finding improved governance options.

Outlook: Advancing integrated, interdisciplinary studies of marine–human systems

Models of marine ecosystems are still struggling with many problems, and some have called it an illusion that quantitative projections of these complex adaptive systems will ever be possible (Planque 2016). Others point out that knowledge about marine systems, available data and capabilities of models have finally arrived at the state where forecasting of marine system dynamics over decadal time-scales for fisheries and ecosystem-based management seems feasible, and first examples are emerging (Hobday et al. 2017).

Until recently, models could be divided into those aiming at robust short–term predictions for management and neglecting process detail, and those aiming at increasing systemic understanding (Rose & Allen 2013). Among modelers, elegantly simple model structures have often been valued higher than usefulness for applied questions of management and conservation, which has led to frustration in the communication between modelers and policymakers (Ruiz & Kuikka 2012). Under the increasing societal and political demand to understand and extrapolate complex questions such as the impacts of climate change, oversimplifications and trade–offs in the design of models currently used for management applications become increasingly obvious (Dickey-Collas et al. 2014), and scientists are put in the situation of having to provide simple answers to complex questions for which only vague information is available (Griffith & Fulton 2014). Better communication of model assumptions and uncertainties and an improved integration of social and economic systems can help to avoid blind belief in projections, and increase the utility of models as tools for policy-making and management of marine resources (Hyder et al. 2015).

Global climate change and the associated ecological changes are a considerable challenge for governance of marine–ecological systems, and an integrative systems perspective which links elements and describes their interactions across scales is necessary (Charles 2012; Perry, Barange, et al. 2010; Osterblom et al. 2013). Increased interdisciplinary integration of empirical data and models is necessary to improve understanding of exploited marine systems and the societal responses associated with specific changes (Essington et al. 2016). For instance, to achieve desired system states in the future, we have to address inertia in ecological and societal responses and the path dependence of management and policy regimes. In the past, delayed responses to changes in environmental conditions have led to overuse and collapses of living marine resources, e.g. in the Gulf of Maine cod and the Norwegian herring stock (Hannesson & Herrick 2006; Pershing et al. 2015).

Conceptual and probabilistic models can yield useful insights on system structure, and a comparison of system structures and historical responses among regions can help to identify characteristic links between societal dynamics and regional natural fluctuations and changes. Yet, an understanding of dynamic system behavior emerging from its components is necessary to identify future shifts, feedbacks and possible tipping points. Thus, system models have to be quantified based on natural and societal processes that can be empirically observed (Osterblom et al. 2016). While there are numerous challenges to quantitatively modeling social–ecological systems (Schlüter et al. 2012), first examples have shown that with an adequate set of submodels for the different aspects of the problem, specific real–world problems in the interaction between the natural and the human system in the sustainable use of marine ecosystems can be addressed (Fulton et al. 2015; Liquete et al. 2016). Both in ecosystems and in societies, processes of self-organization act. These can be used to build an improved understanding of system behavior and resilience, describing system properties as they emerge from component characteristics (Evans et al. 2013).

This knowledge can be used to identify suitable governance options and increase societal resilience towards climate change impacts (Ostrom 2007; Levin & Lubchenco 2008). Important open questions include the perceptions of actors, criteria for societal decisions, thus questions of environmental psychology (van Putten et al. 2015). Thus, more quantitative data for social processes needs to be gathered, by experiments with involved user groups, which can involve participatory modelling. In this process, stakeholders can act as representatives of societies to inform transdisciplinary research of marine social–ecological systems (Mackinson et al. 2011; Lang et al. 2012). Participatory research has high potential for explaining scientific knowledge and uncertainty, but it is necessary to involve social scientists and societal stakeholders into the conceptualization of natural science research programs at an early stage (Mobjörk 2010; Storch et al. 2015). Only by this will it be possible to link all available types of knowledge, quantitative data, expert opinions, stakeholder knowledge and experience, to support social learning (Squires & Renn 2011). The toolset for this endeavor will include models, maps and scenarios, to serve as boundary objects for communication and simplification.

Interfaces, boundary objects and strategies for these inter– and transdisciplinary projects should be advanced systematically, enabling exchange and complementary testing of results and assumptions, and establishing a marine sustainability science (Kates 2001; Bai et al. 2015). The unique characteristics of marine ecosystems and their human uses seem to justify to establish a field of marine social–ecological systems research, as illustrated by e.g. a recent symposium held under this title by the International Council for the Exploration of the Sea (ICES) in Brest, France in June 2016 (ICES 2016). To incorporate quantitative research of marine–human systems behavior under this field, we will need to establish common methods that unite a variety of projects with similar goals that are currently being developed in parallel, e.g. Integrated Ecosystem Assessments and Ecosystem-Based Management (Levin et al. 2009; Long et al. 2015), Integrated Coastal Zone Management and Marine Ecosystem Service Assessments (Nobre et al. 2010; Lester et al. 2013; Villasante et al. 2016) and Marine Environmental Impact and Life Cycle Assessment (Woods et al.

2016). More than common methods, a common language will have to be established and common frameworks found.

Of course, a practical model simplification, i.e. the point at which a system is adequately represented in the model, is highly subjective and will be perceived differently by different stakeholder groups and communities (Rice et al. 2014). As has been the case with other inter– and transdisciplinary pursuits, e.g. the technosciences and transformation research, claims will be made that science is trespassing into the policy sector and makes normative statements (Jahn et al. 2012). The work of the Intergovernmental Panel for Climate Change has exemplified in the climate change context how expert knowledge can be compiled to provide policy advice, in a semi-quantitative, stepwise distillation of scientific knowledge. Key will be the open communication of assumptions and uncertainties of the underlying science, among scientists of different disciplines and with the public, policymakers and media.

We have to be bold, in trying to quantify social-ecological systems and their behavior. At the same time, we have to resist the temptation of claiming that we could already reliably project future marine system responses. Assumptions, limitations and uncertainties of the present models have to be acknowledged, and different research approaches linked and embedded into scenario–based analyses. Only if we dare to progress into quantification of marine–human system behavior, making prudent use of models and other boundary objects, will we learn from successful and failed predictions, advance our understanding and enable anticipation of future changes in marine–human systems.

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Ocean acidification and warming in the Norwegian and Barents Seas: impacts on marine ecosystems and human uses

stakeholder consultation report

Stefan Koenigstein & Stefan Goessling-Reisemann
University of Bremen/Germany, Sustainability Research Center (artec)

artec
Sustainability
Research Center

Universität Bremen

BIOACID
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Preface

Climate change and ocean acidification are predicted to impact marine ecosystems and influence food webs, biodiversity and living marine resources, and therefore affect human societies. Within the research project BIOACID (Biological Impacts of Ocean Acidification, phase 2, www.bioacid.de), we brought together people with an interest in the marine ecosystems of the Norwegian Sea and Barents Sea, a region where ocean physics models project an early impact of ocean acidification and warming.

This report synthesizes the results from personal interviews with science experts and stakeholders conducted in Norway in the course of 2013, and from a stakeholder workshop in Bergen/Norway in October 2013. Participants included fishermen and representatives from fishing associations and aquaculture companies, environmental organisations, tourism businesses (hotels/camps, sport fishing, whale watching) and governmental agencies. We asked them about their knowledge about climate change in the ocean, presented the current state of scientific knowledge about possible ecological effects and economic consequences of ocean acidification and warming (OAW), and explained possible research approaches.

In our work, we strive to identify the ecosystem services relevant to society and integrate stakeholders into socio-economic projections and the search for adaptation strategies. A participatory modelling approach is used: communicating with stakeholders and experts and presenting integrated data in a simplified form, visualizing the connections in the ecosystem and to society, and communicating and discussing impacts of climate change and ocean acidification to stakeholders and the public.

The objective of this first phase of stakeholder integration was to identify questions and concerns of stakeholders, determine the relevant ecosystem services potentially affected by ocean acidification and warming in dialogue with them, and to construct a model structure to explain the linkages between OAW and identified ecosystem services based on the stakeholders' input.

The target questions were:

- How might the marine ecosystems of the Norwegian Sea and the Barents Sea be impacted by warming, acidification and other climate change phenomena?
- How do these impacts interact with the pressure from human use and the extraction of resources?
- How will human societies and economies be affected by these changes in the ecosystems? Whose interests will be touched?
- Which topics are stakeholders interested in? How much does science know? Which questions should be addressed, what factors should be included in research programs?

1. Introduction: climate change, ocean acidification and impacts on marine ecosystems

Human societies depend on the oceans in many ways, but our understanding of their internal processes and their susceptibility to global change are incomplete. The oceans are substantial drivers of our climate but are also affected by climate change. Increasing levels of CO_2 and other greenhouse gases in the atmosphere are changing the earth's climate system, leading to a global warming that will also impact the oceans (IPCC, 2013).

Observations and models agree in a general increase of temperatures in all oceanic regions, but with strong variability between regions (Stocker et al., 2013). Driven by the rise in temperatures, the global ocean system will undergo complex changes in a variety of factors. Increasing temperatures lead to changes in evaporation and sea level rise, melting of sea ice, deoxygenation, and changes in salinity, global ocean currents and the vertical temperature profile. These changes will have profound impacts on the productivity and distribution of marine life (Brander, 2012). Thus, to achieve a sustainable management and use of the oceans under the conditions of climate change is one of the great challenges of our time (European Marine Board, 2013).

Increased atmospheric CO_2 levels also cause a direct chemical interaction with the surface ocean, which is named ocean acidification (OA). First widely discussed after a comprehensive study of the Royal Society in 2005 (The Royal Society, 2005), the problem has been increasingly recognized in the last years and is more and more incorporated into the global climate change debate (CBD Secretariat, 2009, IPCC, 2013). The United Nations Environmental Programme sees ocean acidification as a serious threat to marine biodiversity. In June 2012, the UN Conference on Sustainable Development (Rio+20) recognized ocean acidification as a threat to economically and ecologically important ecosystems and human wellbeing.

Ocean acidification is caused when an increased amount of atmospheric CO_2 dissolves into the ocean and lowers the pH value, making the water more acidic. As a direct chemical interaction of the atmosphere with the marine environment, it is simpler to predict than climate change effects in general. Since the beginning of the industrial revolution, the increase in atmospheric CO_2 from 280 to 400ppm has led to a drop of the average pH of ocean surface waters by about 0.1 units, from 8.2 to 8.1 (IPCC, 2013). This corresponds to a 26% increase in acidity, an acidification at a faster rate than at any time in the last 300 million years of earth history (IGBP et al., 2013).

The further progression of ocean acidification in the next decades will depend on the amount of CO_2 emissions. In a business-as-usual scenario, oceans are projected to reach an average CO_2 of 7.75 until the end of the century (Bopp et al., 2013). Even if emissions are strongly reduced as in the most optimistic IPCC scenario, oceans will reach an average pH of 8.05. In any case, these values will be subject to strong regional variation, and will be influenced by factors like changes in ocean currents, vertical layering and ice melting.

The impacts of ocean acidification are expected to be different depending on oceanic region and characteristics of the ecosystems. Colder surface waters in high latitudes are expected to be the first impacted areas, because cold water takes up more CO_2 and ice melting increases the problem, causing changes in currents and stratification (CBD Secretariat, 2009; IGBP et al., 2013). For the Arctic ocean, acidification is a major concern, with the highest pH changes expected until the end of the century and Arctic waters to become corrosive to some shell-producing organisms in the near future (AMAP, 2013). Economically important impacts are also expected to appear in upwelling regions, where a combination of acidification, temperature and hypoxia will act (IGBP et al., 2013). The Norwegian and Barents Seas share characteristics with both aforementioned regions, and can be expected to be impacted by a combination of the influences of continental upwelling along the Norwegian coast, and the influence of changes in arctic and subarctic waters.

Various impacts of ocean acidification on marine organisms and ecosystems have been found, but there are still many scientific uncertainties (Gattuso & Hansson, 2011). Known possible impacts include problems for shell-building organisms, probably leading to negative impacts on mollusks (snails, shellfish), starfish and sea urchins, in corals, and in calcifying microalgae (coccolithophores). Furthermore, early life stages of fish, squid and other animals may be impacted, as changes in larval development and fertilization, behavioral and perception changes are documented. The general impact on phytoplankton, and thus primary production in the ocean is still largely unclear (Wittmann & Pörtner, 2013, Gattuso & Hansson, 2011).

Over the last ten years, these questions have attracted considerable attention from the scientific community and have been the focus of collaborative and multidisciplinary research programs in Europe (e.g. EPOCA, BIOACID, UKOA, MedSeA). The effects of ocean acidification are being researched with a variety of approaches, including controlled aquarium experiments under increased CO_2 levels with individual organisms, where physiological parameters like survival, growth, calcification, respiration, photosynthesis or metabolic activities are measured. Analyses of chemical composition and molecular genetic analyses provide more detailed data, ‚mesocosm' experiments host whole ecological communities under near-natural conditions, and CO_2-rich ocean sites serve as natural laboratories (CBD Secretariat, 2009; Hilmi et al., 2012). Computer models serve to integrate data from this variety of approaches.

It is thus a scientific priority to improve the understanding of the impacts of ocean acidification on marine taxa and underlying processes, and to investigate the roles of adaptation and variability (European Marine Board, 2013). It is important to keep in mind that ocean acidification will occur together with other stressors (warming, increased UV radiation, hypoxia, pollution). Therefore, the effects should be considered in relation to other environmental changes in marine ecosystems and biological and chemical feedbacks (The Royal Society, 2005). The health, behaviour and function of individual organisms depends on environmental factors, but also on interactions with other organisms - including humans. Dramatic and unexpected regime shifts in marine systems can be triggered by minor fluctuations. On the other hand, effects are buffered by stress tolerance and adaptation of marine populations, and can also be mitigated by socio-technical adaptation of human societies in the use of marine ecosystems.

2. Ecosystem services & potential impacts

While substantial changes in marine ecosystems in response to rising CO_2 levels are expected within our lifetimes, it remains challenging to predict just how these changes will affect human societies. More work has to be done to achieve reliable, quantitative predictions of the impacts on ecosystem services that are relevant for human societies. Significant knowledge gaps are preventing economists from estimating the potential socio-economic impacts of ocean acidification (Hilmi et al., 2012), and only some partial analyses are available, which carry large uncertainties (Armstrong et al., 2012). Nevertheless, to achieve sustainable management and use of the oceans under the negative impacts of warming, acidification, and other consequences of human activity (e.g. over-fishing, habitat destruction, pollution, etc.) is one of the great challenges of our time (European Marine Board, 2013).

The concept of ‚ecosystem services' can be used to investigate the interactions between the marine ecosystems and human societies. Ecosystem services are "the benefits people obtain from ecosystems" (Millenium Ecosystem Assessment, 2005) and can be more exactly defined as "the ecological components directly consumed or enjoyed to produce human well-being" (Boyd & Banzhaf, 2007). Ecosystem services can be divided into four categories: supporting, provisioning, regulating and cultural services (Millenium Ecosystem Assessment, 2005). This concept can provide a theoretical basis for the economic quantification of services of nature used by mankind (TEEB 2010). But as benefits are subjective properties, the first step is to ask which ecosystem services are relevant to the stakeholders in the investigated region.

In the following paragraphs, we will discuss the relevant marine ecosystem services in our focus region, as identified by the stakeholders and by the scientific literature, and how they are potentially affected by ocean acidification and climate change in general. We will give an introduction about the current state of scientific knowledge on each service or aspect and present the views and opinions of the stakeholders that participated in our project.

2.1 Fisheries

Background: Fisheries are an important provisioning service of marine ecosystems, as they provide food to humanity and employment for coastal regions (World Ocean Review, 2013). In 2010, fisheries reached an economic value of USD 217.5 billion and provided livelihoods to 10–12% of the world's population, whereby 90% of fishers work in small-scale fisheries (FAO, 2012). While world fisheries yields have been stagnating since 1988, this is compensated for by the growth in aquaculture, which has reached half of the total production. Today, 30% of world fish stocks are over-exploited and a further 57% are fully exploited (FAO, 2012). Recognizing this problem and aiming to make fisheries management more sustainable, the European Union has recently reformed its Common Fisheries Policy towards a more ecosystem-based and precautionary approach (European Commission, 2013).

Climate change puts additional pressure on fisheries management (FAO, 2012). The impacts of climate change and ocean acidification on fish species and their prey organisms affect the stability of commercial fish stocks and are among the key research questions for the future of fisheries (European Marine Board, 2013). Impacts of ocean warming on fish stocks are visible already, as many stocks have shifted range visibly in the last decades, especially those at the edges of their species distribution range (Poloczanska et al., 2013). As species are moving towards the poles, temperate areas will continue to receive new species, tropical areas will have less species, and some polar species might disappear altogether. Fish body size decreases with increasing temperature, so average fish size is expected to decrease by 14-24% (Cheung et al., 2012).

The impact of ocean acidification on fish stocks is still unclear, since comprehensive research programs do not exist yet (AMAP, 2013), but it is expected to differ between world ocean regions. Shellfish and crustaceans represent a significant part of world aquaculture and fisheries yields and may be severely impacted, e.g. by acidification in coastal waters. An early estimate of the impact of ocean acidification on marine fisheries values it at US$ 10 billion per year (Kite-Powell, 2009). Fish stocks in Arctic regions with simpler food webs and influenced by ice melt, as well as shallower continental shelf fish stocks are speculated to be impacted more or earlier than other regions (AMAP 2013). Fisheries in the North Atlantic are expected to be impacted by more-than-average ocean warming and acidification, causing issues of fishing industry adaptation and relocation (Hilmi et al., 2013). While some studies have hypothesized an overall slightly positive effect for Norway (Armstrong et al., 2012), others predict a significant reduction for the whole Northeast Atlantic (Cheung et al., 2011).

In Norway, the fisheries sector plays a key economic and social role with a production of 2.3 million tons and 12.800 employees in 2011. The country is the world's second-largest seafood exporter by value of almost 1 billion USD, with the European Union as the largest market (FAO, 2013). The capture fishery can be divided between industrial offshore vessels and small-scale coastal fishery. Main capture species are cod, herring, capelin, mackerel, saithe and other whitefish. Fisheries are highly regulated and well-managed, and management agreements are reached between politics, fishing associations and scientific advisors (FAO, 2013). Most stocks are managed sustainably and Norway has stock management agreements with Russia for the Barents Sea and with the European Union, and has been active against illegal, unreported and unregulated fishing (FAO, 2012).

Statements on fisheries management

Overall, stakeholders from the fisheries sector were content with the state of the fish stocks and their economic situation. The interchange of information in fisheries management between fishers, scientists, administration and policymakers was generally regarded as good. Nevertheless, more multispecies and ecosystem-based management of fisheries were wished by participants from the fisheries sector, and more reliable forecasts of catch quota over a period of several years would be highly valuable to increase planning efficiency in vessel and processing capacities.

From a management perspective, range shifts of economically important stocks were seen as a challenge, leading to higher fuel costs and other technical as well as quota distribution problems. Range shifts across legal borders would create additional challenges because they might lead to international disputes. The recent cases of mackerel and herring were given as an example, where shifts of the stocks in the North Atlantic have led to unsolved disputes about the allocation of catch quota between the EU and Norway on one side and Iceland and the Faroe Islands on the other.

As possible adaptations to environmental change from the management side were mentioned a) quota adjustments, b) fishing gear improvements, and c) areas closed for certain types of fishing, e.g. bottom trawling. Fishing gear and method would have to be adapted to size of the target fish and stock occurrence. It was also pointed out that evaluation of management options should not be political and should leave choices open to decision makers. In the past, fisheries productivity had been increased by reducing the number of fishers. It was noted that fishing effort was determined by target species demand, which was also influenced by the amount used as feed for aquaculture. General fisheries moratoria were perceived as a danger for fish markets.

Statements on stock range shifts

Many stakeholders reported the observation of northwards stock range shifts in recent years, especially for cod and mackerel stocks. These stocks seemed to be shifting further to the Northeast into Finnmark and were becoming available to the local fishers there. It was pointed out that the appearance in new areas might also be caused by a range expansion caused by a large stock, which was suspected for mackerel. Sardines were reported as newly immigrated species into Norwegian waters.

Changes of timing and location of spawning of important commercial fish stocks were reported for the last years, e.g. a later spawning of capelin. The Northeast Arctic cod stock was reported to spawn increasingly further north of the area off Lofoten. One prominent concern was the consequence of the cod spawning area moving even further northeast, which would influence the stock and its potential for exploitation. It was detailed that in the Northeast Arctic cod stock, smaller juvenile cods presently dominated the East Barents Sea and were fished by Russian vessels, while bigger adult cods lived in the Western part and were fished by Norwegian vessels. Thus, a moving cod stock might lead to problems for Russian vessels if these were not prepared for the increase in size. From the Russian side, a range shift into the eastern Barents Sea and the Russian territory was also seen as a potentially new situation for management.

Spawning grounds of highly migratory stocks, e.g. herring, were described as very inconsistent, and therefore the attempt to predict herring migrations or distribution shifts was seen as useless. In herring stocks, fishers in Norway had historically experienced strong stock fluctuations, abrupt collapse and recovery, which had also contributed to the development of the management agreements established today.

A prediction of stock range shifts was generally valued as very helpful for planning in the fisheries sector. Fishers were interested if future changes could be expected to be abrupt, like in the past for herring stocks, or if there would be time to adapt to changes. Although most stocks were regarded as being in a good state, for some this was realized as a problem, as market prices of some commercial species, e.g. cod were very low due to high supply.

Statements on ecological interactions and model detail

From a management perspective, the two main factors of interest to be represented in ecosystem-based models were recruitment stability and distribution of stocks. Also, change of spawning areas, possible abrupt changes or collapses in stocks, as well as capacity for adaptation to climate change were seen as relevant. Furthermore, changes in growth rate and size distribution of fish individuals would be interesting parameters from a management perspective.

Implications of food web interactions were a regular concern for fishers. Connections between the states of mackerel, capelin, herring and cod stocks were mentioned. The large mackerel stocks along the Norwegian coast were also a reason for concern, because of food competition and juvenile predation of more valuable species. Workshop participants advised to make use of the high amount of information available about food web connections in the Norwegian and Barents Seas, to improve models and increase the knowledge about changes in the system. Models would be more credible if more of these food web interactions were incorporated. On the other hand, management representatives pointed out that complexity should not be overdone, projections should be sufficiently reliable for commercially relevant species but many other food web elements could probably be left out. In this context, the impact on the food web from high amounts of small fish being fished out for aquaculture feed was an additional interest.

A major concern about ocean acidification was the impact on fish recruitment. It was pointed out that present models only consider adult stock dynamics and earlier life stages are described by recruitment, but potential effects on larval growth and mortality would be a topic of high interest. Another topic of concern was primary production and whether it will remain sufficient to support fish stocks under climate change. Change of productivity and pelagic fish stocks in the Arctic Ocean under increasing ice melt was a further concern. There was interest in the effect of ocean acidification on the food of commercial fish species, e.g. copepods and pteropods, and possible changes in the ecological coupling to plankton production in spawning grounds.

Statements on socio-economic factors

A number of socio-economic connections became apparent in the fisheries sector. It was pointed out that social factors influence the adaptive capacity of fisheries towards changes in fish stocks. Historically, there had been a drastic reduction in workers from 120,000 in the 1940's down to 12,000 today. If harvests cannot be increased further, productivity will have to be increased further to keep the income stable. The impacts on employment could be mitigated only as long as there are other economic sectors that absorb the work force.

It was noted that the fuel use of trawl fisheries is considerable and that the fishing fleet accounts for 5-7% of Norwegian CO_2 emissions. There was seen potential for improving the carbon footprint of the fishing fleet.

Differences in estimation of adaptive capacity exist among groups of fishers: while the big offshore vessels based in West and South Norway can follow their target stocks by longer distances, coastal fishermen in Northern Norway might be left behind, because their smaller boats are not able to follow stocks from the fjords out to the open sea. Yet especially in these regions, fishery is of social importance, since it attenuates socio-economic pressure on the communities and plays an important role for the cultural heritage of traditional Sami culture. External pull for educated workers from the oil industry, livelihoods of fishers, employment alternatives and social structures were mentioned as relevant factors for the stability of Northern communities. Thus, changes in fish stocks could have locally and regionally dramatic impacts on communities, even when overall economic cost was limited.

Stakeholders noted that market demand, multi-species fisheries, by-catches and processing costs were further socio-economic factors which influence the connection between fish stocks and the fisheries sector, and which should be included in a comprehensive model. Also, various connections to aquaculture were mentioned, e.g. smaller capture fish were increasingly used as aquaculture feed, increasing demand and influencing market prices. Although an influence of ocean warming on the placement of aquaculture installations along the Norwegian coast was observed, stakeholders voted for not including aquaculture at this point of the model building process because no detailed information was currently available. The industry might be considered in the future of the project for its socio-economic relevance and connection with other fisheries.

Fishery is considered to play an important role for the food provision for humanity, i.e. it is considered essential for coping with population growth under limited resources. Prices were generally expected to increase in the future, with climate change possibly aggravating the situation. The marine sector would have to deliver a growing share of the world food production, maximize long-term fisheries yield and increase the aquaculture share. The economic importance of fisheries was expected to increase further in the future after the Norwegian oil peak, and a transition back to a fisheries-based economy would be possible if stocks continued to be managed sustainably.

A topic of pronounced interest for stakeholders from the fisheries sector was the oil exploration around Lofoten islands, which is feared to lead to pollution of cod spawning areas. A similar concern was the increased granting of mining licenses in the north of Norway. The impacts of pollutants and sediment discharges on fjord ecosystems were regarded as potentially dramatic and the rate of transport out into the open sea as unclear.

2.2 Tourism & recreation (cultural services)

Background: Marine ecosystems provide an array of cultural services that are used either by locals or by domestic and international tourists. Total worldwide revenue from international tourism amounts to USD 1,075 billion and keeps growing in spite of recent economic crises (World Tourism Organization, 2013). Tourism can support sustainable development, but is also one of the most highly climate-sensitive economic sectors (Simpson et al., 2008). It may be indirectly impacted by climate change through changes in water availability, biodiversity loss, reduced aesthetic value of landscapes, sea level rise causing coastal erosion, inundation and damage to infrastructure, and a rise in vector-borne diseases. On the other hand, tourism contributes about 5% of world carbon emissions (Simpson et al., 2008).

The oceans play a substantial role in tourism and recreation. In Europe, recreational saltwater fishing has approximately 8–10 million practitioners and is a considerable industry with socio-economic relevance (FAO, 2012). Recreational fisheries and associated tourism can provide alternative livelihoods for small-scale fishers, but tourism activities are also competing for space with professional fishery in some coastal areas (FAO, 2013).

In Norway, tourism is strongly connected to the coastal regions and the fjords, and fishing is the most well known activity (NMTI, 2012). The tourism industry, including transport, accommodation and gastronomy services, travel and tour companies, is an important employer especially in Northern Norway, where it provides 18,000 jobs and 6% of total added value (Klima- og Miljødepartementet, 2011). Sea fishing contributes significantly to added value and development in Norwegian coastal communities, creating a value of about € 26 million, with € 12 million just in the North (Klima- og Miljødepartementet, 2011). Apart from sea fishing, activities include whale and seal watching, bird-watching, kayaking, hiking, camping and other nature-related recreation activities. Whale watching revenue in Norway amounts to €12 million per year and has risen by 18% since 1994 (Greenpeace, n.d.).

While tourism economy can serve as an indirect indicator for recreation value, value for local recreation is more difficult to quantify. Apart from recreation, the coastal marine ecosystems provide aesthetic services, religious and spiritual services, cultural identity, as well as options for education and research. Most of these services are difficult to quantify on a monetary basis, but nevertheless have economic and societal value.

Statements on recreational fishing and other coastal tourism

Stakeholders reported that tourism in Norway was strongly connected to nature experience, and to the sea and maritime activities as cultural heritages of the Norwegian people. It was stated that a decrease in the experience of ‚intact nature‘ would have a severely negative impact on tourism.

Seabirds, seals and sea lions, and fish were mentioned as elements of the marine ecosystems that play a role in coastal tourism. Drastic drops in many seabird populations in recent years were reported for Northern Norway and Svalbard, which was suspected to be linked to declines in prey fish. The white-tailed eagle was mentioned as an exception and was reported to increasingly hunt for puffins instead of fish.

Stakeholders from the tourism sector confirmed recreational fishing as one of the most popular nature-related activities and an important pillar of Norwegian tourism, practiced from the shore and from small boats in fjords and the coastal areas up to 20-30km from the coast. It was pointed out that non-professional fishing is also officially controlled and monitored in Norway and fish exports are restricted. Among the most popular game fish were halibut, spawning Atlantic cod (skrei), catfish, plaice and saithe. Tourism linked to sports fishing was seen as especially relevant on the Lofoten and Vesterålen islands in Northern Norway, where occurrence of some of the game fish species was reportedly linked to the annual cod spawning migrations in spring, and sport fishing in this area had recently profited from increased numbers of spawning cod along the coast.

It was stated that tourism in Northern Norway was strongly linked to small-scale fishing, as boats, harbors and the connected activities (e.g. production of stockfish) were culturally unique and a strong pull-factor for tourists. Many ship owners used their vessels seasonally for professional fishing as well as for sport fishing or other recreational activities linked to tourism. Thus, it was pointed out that tourism could not simply serve as a substitute for fishing, and the socio-economic connections especially in the northern regions had to be considered. Boat ownership was also regarded as having a strong cultural significance for people from small coastal communities in the North, many of which were under pressure from modernization, urbanization and demographic ageing.

In Troms and Finnmark, many coastal cod stocks in the fjords were considered to be declining or to have collapsed, leading to dramatic consequences for local communities. There were concerns that high mackerel numbers coming into fjords might have negative impacts on cod because of food competition and direct feeding on cod larvae. Seals were also speculated to have an impact on cod populations in the fjords, driving them further into the fjords, but seal hunting was now prohibited.

Concerns were expressed about the fjords in the North being increasingly explored for construction of mineral mines, with new licenses progressively being granted. The pollution from mining waste was a substantial concern for stakeholders from environmental conservation groups. An increasing use of fjords for aquaculture was also reported, causing concerns about influences on fish spawning in fjords through space competition and emissions.

Statements on whale watching

Whale watching was seen as an important tourism and recreation activity in Lofoten, Vesterålen and the Tromsø region. According to stakeholders from the whale watching sector, the patterns of whale migration are variable, but the occurrence of most whale species was linked to the occurrence of their prey. While humpback whales were the most regular sighting, tooth whales like orcas and sperm whales followed the highly migratory herring stocks in their overwintering areas, which varied from year to year. It was added that many whale stocks had a social structure with dominant specimens, which could influence sightings. While minke whales were regarded as uninteresting for whale watching tours, they are commercially fished in Northern Norway and it was pointed out that the minke population is stable and being sustainably exploited as a resource.

Tour operators described the number of whale sightings as the defining variable for their business, and asked to consider that whales moving out to far from the coast would make it impossible to provide tourist trips. A lack of ecological information about stocks was diagnosed, as only minke whales and to a certain degree sperm and orcas were researched and information about possible impacts of climate change on whale stocks was scarce. Nevertheless, changes in prey abundance were expected to have drastic impacts. Whales were also mentioned as a generally important part of the marine food webs through their feeding interactions with lower trophic levels and also through the release of nutrients in the surface water layers. Winter whale watching was said to be closely connected to the overwintering location of herring stocks, but to provide only a small part of the revenue. Summer sightings might be more connected to other factors, for example deep zooplankton distribution. Other ecosystem links to fisheries were mentioned, e.g. sperm whales being increasingly observed to feed on cod, because squid seemed to have declined in the Norwegian Sea.

Concerns about negative impacts on whale stocks and whale watching activities by other human activities were expressed, e.g. by seismic exploration and noise produced by fishing and transport shipping, which is expected to increase under climate change due to the reduction of the Arctic ice cover.

2.3 Carbon uptake & primary production

Background: Carbon absorption is a regulating service of the oceans with great importance for the planet's climate. Atmospheric CO_2 is taken up by the ocean surface, primarily by chemical solution, which depends on temperature. In high latitudes, a high amount of CO_2 is taken up because of low water temperatures, forming water masses that are cold and carbon-rich, which sink to the deep and drive the worldwide ocean circulations. In contrast, the additional CO_2 released by anthropogenic emissions enters the oceans uniformly at the surface and leads to a higher concentration in surface waters. All carbon is temporarily stored for up to 1000 years in the ocean, until it flows back up to the surface in upwelling regions (CBD Secretariat, 2009; IPCC, 2013). More than one quarter of all human CO_2 emissions are taken up by the oceans in this way. Therefore, the oceans represent a huge carbon reservoir and an important buffer against climate change. As ocean acidity increases, its capacity to chemically absorb CO_2 from the atmosphere decreases, reducing the capacity of the oceans to moderate climate change (IGBP et al. 2013).

In the future, warming of the North Atlantic, changes of the overturning circulations and an increased stratification will reduce the solubility of CO_2 and is expected to lead to a reduction in carbon uptake (Pérez et al., 2013).

The solubility pump is complemented by the so-called ‚biological pump', which converts some of the CO_2 taken up by the ocean into organic matter. By this process, the dissolved inorganic carbon in the water is taken up through photosynthesis by marine microalgae (phytoplankton), transformed into phytoplankton biomass and then further transported into the food web. A part of the plankton biomass sinks down into the deep layers of the ocean, where it is recycled by bacteria or, to a small fraction, buried forever in the marine sediments.

Rising water temperatures under climate change may decrease chemical solution of CO_2 in many areas, although reduced ice cover in the Arctic ocean may lead to higher primary production and biological CO_2 uptake (Manizza et al., 2013). The impact of ocean acidification on primary production is still unclear: While it has been speculated that photosynthesis will be generally positively impacted by a higher amount of CO_2 available, increased stability of depth layers might decrease nutrient input into the light zone at the surface and act negatively on primary production. It is unclear to what extent the different groups of phytoplankton will be negatively affected by increasingly stressful conditions caused by warming and acidification. As two important phytoplankton groups (coccolithophores and foraminiferans) and some of the zooplankton (e.g. pteropods, or sea butterflies) have calcareous shells or structures, it seems probable that they will be negatively impacted by ocean acidification (Kroeker et al., 2013). Total export capacity of organic matter could be reduced (Le Quéré & Metzl, 2004).

For Norway, first economic assessments have estimated that negative impacts of ocean acidification on carbon storage may be several orders of magnitude higher than effects on fisheries and aquaculture (Armstrong et al., 2012).

Statements on carbon cycle and emissions

Stakeholders with an environmental conservation background noted that Norway is internationally known to be an environmentally friendly country. Nevertheless, it was stated that Norway exported CO_2 emissions by the export of oil and by the import of goods produced from other countries, distorting the actual carbon budget. Additional compensation came from buying up CO_2 emission certificates. Most stakeholders regarded personal willingness in Norway's society to change behavior and cut CO_2 emissions as rather low. It was stated that due to the very good economic situation in Norway, people tended to be satisfied with the situation, but were ready to accept some additional cost for emission compensation.

Participants from the fisheries sector suggested that reduction of CO_2 emissions from fishing vessels was also a means of reducing impacts of a high CO_2 atmosphere.

Statements on primary production and biological carbon

Stakeholders from the fisheries and conservation fields repeatedly mentioned primary production as an important factor, as its potential changes under climate change would have impacts on the marine food webs and finally change the productivity of fish stocks. It was therefore a prominent concern that primary production would not suffice to support productive fish stocks under climate change and ocean acidification.

It was also suggested that the general structure of marine food webs, and the total biomass held in all trophic levels, further determined the amount of carbon stored in biological organisms. The net carbon effect of climate change on food webs under extraction of biomass by fishing was therefore an interest. Whales, big fish and squid also were noted for their role in carbon cycling, releasing organic matter and nutrients at the surface and in the deep.

2.4 Biodiversity

Background: Biodiversity is not an ecosystem service by itself, but a basic property of all ecosystems. Through the provision of ecosystem services, biodiversity affects human well-being and forms the basis of human economies (Millenium Ecosystem Assessment, 2005; TEEB, 2010). Loss of biodiversity can be seen as one of the most pressing economic problems of our time, but the lack of appropriate methods for economic valuation of biodiversity has contributed to the degradation of ecosystems and prevented the successful introduction of protective tools (Jones-Walters & Mulder, 2009). Worldwide, biodiversity is threatened by human activities, and marine biodiversity has been declining by 22% since the 1970s (Leadley et al., 2010; WWF, 2012).

Biodiversity is a central attribute for ecosystem resilience and contributes to a variety of services of the marine ecosystem, e.g. food provision, raw materials, climate regulation and biological habitat (Beaumont et al., 2008). Nevertheless, it is difficult to exactly define biodiversity, as it embraces variability of living organisms of any origin, on several biological levels of description, and includes species diversity, genetic diversity and ecosystem diversity (United Nations, 1992; Pearce & Moran, 1994; TEEB, 2010). It is thus extremely difficult to quantify the economic impacts of a loss of biodiversity. Representative data and indicators have to be found for each aspect, which can then form the basis of an objective and quantifiable evaluation. Nevertheless, it is an important concept in addressing the public and describes general properties of changing ecosystems.

Norwegian coastal waters have an overall good state of biodiversity, as measured by the Nature Index of the Norwegian Directorate for Nature Management, but ocean acidification is seen as one of a number of human-caused threats to biological diversity in Norwegian waters (Nybø et al., 2011). Changes in Arctic Ocean chemistry, influenced by climate change and sea ice melt, are expected to affect populations of calcifying species and impact biodiversity and trophic pathways (CAFF, 2013). Additionally, many polar organisms are highly adapted to their niches and may be highly threatened by change. Shifts in marine plankton community structure in the Arctic Ocean due to ocean warming and acidification are among the major tipping points in the earth system, where biodiversity loss can potentially pass an irreversible threshold (Leadley et al., 2010).

Sensitivity to ocean acidification differs among groups of animals, but in many species, reduced growth, increased mortality or impaired reproduction have been reported (Gattuso & Hansson, 2011). Shell-building molluscs (e.g. mussels, scallops, clams, oysters) will be impacted by ocean acidification with very high probability, since their calcium carbonate shells dissolve under a decreased pH. The same seems to be true for echinoderms (starfish, sea urchins, sea cucumbers), which have calcareous skeletons. Both groups play important ecological roles in benthic coastal ecosystems, as food for fish, and some species have a high economic significance for coastal communities in many world regions. Negative impacts on different groups of calcifying plankton organisms, as coccolithophores and foraminifera (phytoplankton) and pteropods (zooplankton) are expected under ocean acidification. The sensitivity of small crustaceans, copepods and krill, which form part of the zooplankton and play an important role in food webs in the Norwegian and Barents Sea, is still unclear, but these groups may be more influenced by temperature than acidification (IGBP et al., 2013; Kroeker et al., 2013; Kroeker et al., 2010; Wittmann & Pörtner, 2013).

Statements on biodiversity and ecosystem resilience

For interview and workshop participants, biodiversity was an important issue; therefore it is included as a separate topic in this report. Although most of the impacted organisms groups are not regularly visible to stakeholders, biodiversity was seen as a ‚buffer‘ for species loss, providing adaptation capacity in marine ecosystems under climate change. In this sense, biodiversity might be treated as an aspect in marine ecosystems that is not directly economically valuable, but informs about the resilience of ecosystems. Also, the cultural significance of biodiversity was noted. The stakeholders regarded the value of biodiversity as very difficult to quantify, but welcomed attempts to find indicators for this important property.

Some changes in distribution of species are directly visible for stakeholders and a connection to global change was mentioned frequently. Reported examples include brown seaweed (***Fucus***) along the Northern coasts, birch trees in Finnmark, newly introduced species as Sea bass and Pacific oyster in Oslofjord and Skagerrak. Changes in marine food webs were also suspected to play a role in the declines in seabird populations in Northern Norway and Svalbard.

Biodiversity was seen as important for ecosystem-based management of living resources. Stakeholders from different sectors noted that potential thresholds in the ecosystems have to be observed because they might be indicative of upcoming regime shifts or collapses. In the Arctic Ocean, the impact of a melting ice cover was perceived as likely having drastic impacts on biodiversity. Primary productivity was expected to change, and some species that live in close association with the sea ice might be threatened. For example, the ecological effects of a disappearance of polar cod in the high northern latitudes might be severe, therefore stakeholders wished to include this question in the investigation.

According to many stakeholders, conservation of biological diversity should be given political priority and has a value that should be included in studies and models. If some groups or species were severely impacted and went extinct, biodiversity would decline. Because of the complexity of marine food webs, questions were posed on how interactions between species would change, what would happen when key species were impacted, and what chain reactions might happen. On the other hand, stakeholders speculated that some impacts might also be buffered in the ecosystem.

2.5 Coral reefs

Background: Ocean acidification is expected to impact tropical coral reefs, which are already under high stress from increasing temperatures and acidification and may be severely impacted within the next decades (IGBP, 2013). Tropical coral reefs provide significant regulating services for coastal protection, cultural services for tourism and recreation, and supporting services as nursery ground for many fish species. In addition to acidification, warming, pollution, sedimentation and destructive fishing practices impact tropical coral reefs. Potential impacts are similar, but less well-investigated for cold-water coral reefs.

In Norway, the largest cold-water coral reefs in the world exist. It is estimated that 70% of cold-water corals will be exposed to corrosive acidic waters by 2100, and some populations will experience corrosive conditions as early as 2020 (CBD Secretariat, 2009). This leads to reduced calcification and increased dissolution rate of the dead skeletons which form the base of reefs (Maier et al., 2009; Roberts, 2006).

Overall, the ecological significance of cold-water coral environments is not well understood yet, but ocean acidification is threatening these sensitive ecosystems before their biological diversity and significance has been fully explored (The Royal Society, 2005). Ocean acidification is expected to have potentially catastrophic consequences in these deep sea ecosystems, acting together with deep-water warming and deoxygenation (European Marine Board, 2013).

Deep sea ecosystems provide a variety of supporting ecosystem services, but many gaps exist in their monetary and non-monetary valuation (Armstrong et al., 2012). They serve as a habitat for some demersal fish species and as spawning and feeding ground for others, so their loss is expected to have consequences for food webs (Turley et al., 2007; IGBP et al., 2013). They also play a significant role for local biodiversity and coastal carbon cycling (The Hermione project, 2012). Furthermore, they have an existence value and provide cultural services for education and research.

Statements on deep-water coral reefs

Workshop participants stated that ecological connections of deep-water coral reefs with other marine ecosystems are still unclear and seem to be only remotely connected to the priority issues in the present study. Their cultural significance was estimated as limited, and they lacked relevance for tourism. The significance of deep-water coral reefs as a protection against erosion of the continental slope was also seen as unclear.

Participants therefore voted not to consider the impacts of ocean acidification on deep-water coral reefs at this stage. Instead, they pointed out that deep-water coral reefs along the Norwegian coast had been closed areas for bottom trawling fishery since 1988, and suggested that the reefs should remain under a special protection status, adopting a precautionary approach because of their rarity. Therefore, deep-water coral reefs will not be further considered in this study at this point, which may change when indications for important ecological connections to model elements become substantiated.

3. Outlook

3.1 Developing a social-ecological model with stakeholder participation

To investigate how marine ecosystems and coastal communities will be affected by climate change, multi-disciplinary research is needed that takes into account environmental, economic and social factors (European Marine Board, 2013). Ecosystem-based marine resource management can benefit from stakeholder participation, considering both scientific and traditional knowledge, and taking a systemic approach that considers all relevant ecological, social, economic and governance elements (FAO 2012). It appears necessary to assess the biological and socio-economic risks from ocean acidification, but it remains challenging to quantify how marine ecosystems and fisheries will change and how societies will adapt to changes brought by ocean acidification (Hilmi et al., 2012; IGBP, 2013).

In recent years, the Norwegian Ministry for the Environment has developed integrated ecosystem-based management plans, covering the Norwegian Sea as well as the Barents Sea and the marine area off Lofoten (Klima- og Miljødepartementet, 2007; 2009; 2011). These plans aim to manage activities in those areas within a single context and use ecological principles to assess the various activities and the potential for future development. To understand the behavior of these marine systems and enable long-term management, it will be essential to adequately integrate climate change effects (Hoel & Olsen, 2012). The concept of ecological resilience under climate change for the Norwegian and Barents Seas is also being integrated into the work of environmental organizations, e.g. WWF Norway (Boisen & Jensen, 2013).

The links between elements of the ecosystem and the socio-economic system identified by our stakeholder consultation are being incorporated into a model of the combined social-ecological system that aims to explain mechanisms and uncertainties, identify critical parameters and investigate the system's resilience towards ocean acidification and warming.

General remarks on the model

General remarks from stakeholders for the project's modeling activities included that although management plans for the areas in question have been developed, no valid indicators for the vulnerability of species under climate change are included. Also, stakeholders demanded that the model should have a clear regional scope and a clear temporal horizon. The model should consider the background of natural variability, of seasonal and interannual fluctuations, and enable comparisons with the situation in historical warm periods. It should carefully consider natural causes apart from human-induced changes. The validity range of the model and the uncertainty would be of the highest interest in the end.

Stakeholders demanded that model complexity should not be too high and the representation of the marine food web should be limited to species absolutely necessary. On the other hand, elements that are left out should be named and reasons given for their exclusion. Of high interest to the participants was to what degree the structure of the ecosystem would be able to buffer impacts on its services. Natural variability and long-term adaptation of populations should be investigated experimentally and these factors should be considered in projections. Economic connections between fisheries sectors could remain simple at this point and be based on information about fish stocks and yields, i.e. stakeholders did not see the need to incorporate market mechanisms.

3.2 Conclusions

Our stakeholder consultation has produced a multifaceted overview and yielded detailed insights on the connections and interactions in the investigated social-ecological system. All stakeholder commentaries towards the model structure and components will be taken seriously in the currently ensuing modeling process. However, it will probably not be possible to incorporate all elements that were mentioned.

Statements from the stakeholders have also helped to identify relevant and potentially affected ecosystem services as well as possibilities for adaptation. These results will be used to investigate system resilience and explore possible futures and adaptation strategies. Into the model structure, indicators for the selected ecosystem services will be incorporated. Focusing on physical components and structures of the ecosystem allows a direct measurement, ideally in standardized biophysical units, and avoids double counting.

Nevertheless, many ecosystem services are difficult to quantify. Not all benefits may be captured, e.g. potential benefits from biodiversity. Furthermore, not all ecosystem services can be evaluated on a monetary basis. For an economic assessment, also non-market valuation methods will be used. Stakeholders as the beneficiaries of ecosystem services will form the basis for this valuation.

Appendix

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List of contributors

Note: Statements of participants represent their personal opinions and not necessarily their institution's official view. Names of participants are not given for privacy reasons.

#	Institution/company	City/county	Participant's background or focus area	Field
1	-	Bergen	Journalist	fisheries
2	-	Tromsø	Fisherman	fisheries
3	Abornes sea fishing	Troms	Sport fishing tours, fishery	tourism, fisheries
4	Akvaplan NIVA	Tromsø	Aquaculture and innovation	aquaculture, research
5	Aqua Lofoten Coast Adventure	Nordland	Tours, fishing, diving	tourism
6	Arctic Management and Assessment Programme (AMAP)	Oslo	Env. monitoring and assessment	intergov. agency
7	Association of Arctic Expedition Cruise Operators (AECO)	Netherlands	Arctic tourism	tourism
8	Bivdi - Sami Fishers' and Hunters' Association	Finnmark	Environmental conservation	env. NGO
9	CICERO (Center for International Climate and Environmental Research)	Nordland	Socio-economic impacts of climate change	research
10	Coastal Sami Resource Centre (Sjøsamisk kompetansesenter)	Finnmark	environmental and cultural conservation	env. NGO
11	Fiskarlaget Nord	Tromsø	Fisheries Management	fisheries
12	Fiskeridirektoratet (Directorate of Fisheries)	Bergen	Fisheries Management	governm. agency
13	Fram Centre	Tromsø	Fish research, aquaculture	research
14	Hvalsafari Andenes	Nordland	Whale watching	tourism
15	Ice Fish AS	Tromsø	Fish trade	fisheries
16	Institute of Marine Research (IMR), Bergen	Bergen	Oceanography and climate	research
17	Institute of Marine Research (IMR), Tromsø	Tromsø	Fisheries, food webs	research
18	KARAT Fisheries Holding, Russia	Murmansk	International affairs	fisheries
19	Lofoten Fishing AS	Nordland	Fishing	tourism
20	MAREFA (Marine Research and Education Fund of Andenes)	Nordland	Whale research	research, tourism
21	Maribell Sjøbuer AS	Troms	Sport fishing, tourism	tourism

22	Miljødirektoratet (Norwegian Environment Agency)	Trondheim	Natural resource use and conservation	governm. agency
23	NCE Tourism Fjord Norway	Bergen	Tourism association	tourism
24	Nergård AS	Tromsø	Fishery and fish processing	fisheries
25	NIVA (Norwegian Institute of Water Research)	Oslo	Marine chemistry and monitoring	research
26	Norges Fiskarlag (The Norwegian Fishermen's Association)	Trondheim	Fishery	fisheries
27	Norges Naturvernforbund (Friends of the Earth Norway)	Oslo	Marine Ecosystems	env. NGO
28	Norsk Institut for kulturminneforskning (NiKU)	Tromsø	Sami cultural studies	research
29	Norsk Sildesalgslag (Norwegian Fishermen's Sales Organisation for Pelagic Fish)	Bergen	Sales Director	fisheries
30	Norwegian Seafood Federation (FHL)	Bergen	Marine environmental issues	aquaculture
31	Rådgivende Biologer AS	Bergen	Environmental assessment	env. counselling
32	University of Bergen	Bergen	Fish stock dynamics	research
33	WWF Norway	Oslo	Fisheries and Marine Conservation, Socio-Economy	env. NGO

Stakeholder interview questionnaire

Note: The questionnaire was adjusted to stakeholder backgrounds and not all questions were posed to every stakeholder. Interviews were qualitative and flexible follow-up questions were used to further investigate topics of interest.

I. General situation

1. Are you satisfied with how your yields or gains have developed in the last years? Why / why not?
2. What are your biggest concerns about the future development of your business?
3. Which parts of the marine ecosystems are important for you? Which parts do you use?
4. Have you observed changes in the ecosystem in the last years/decades? Which changes?
5. What are your biggest concerns about the future development of the ecosystems?
6. Are you concerned about the effects of climate change on marine ecosystems? Do you think the observed changes may be connected to climate?

II. Climate change & ocean acidification

1. What impacts of climate change are you most concerned about?
2. Which society groups or users of ecosystems do you expect to be first or most strongly impacted?
3. Have you heard about ocean acidification? What?
4. How do you think climate change and ocean acidification could impact marine ecosystems?
5. What consequences might that have for you or your work?
6. How could you / your company react in order to mitigate consequences?

III. Science communication

1. Do science and politics support you / cooperate with you sufficiently?
2. What information do you need from science to plan ahead in the face of possible changes?
3. How should uncertainty of scientific statements be communicated?

IV. Climate change & society

1. What might be the main impacts of climate change on Norwegian societies? Which economic consequences have to be considered?
2. Which might be options for the society to adapt to climate change?
3. What obstacles exist for adaptation strategies?
4. How is the public perception of threat from climate change?
5. How high is the willingness to change one’s behavior or pay costs for the prevention of climate change consequences?

V. Management options

1. Which adaptation strategies / regulation measures (examples) decided by politics would you accept? Which not?
2. What factors and whose interests are relevant in decisions about adaptation strategies?
3. Which social or cultural backgrounds influence the acceptance of adaptation strategies?
4. Which other (national/international) dependencies have to be considered when developing strategies or making decisions?

Workshop agenda

Impacts of ocean warming and acidification on the marine ecosystems and their human uses: Stakeholder workshop within the Bioacid 2 project

17th October 2013, Institute of Marine Research (IMR), Bergen/Norway
Hosts: Stefan Koenigstein, Stefan Goessling-Reisemann (University of Bremen)

Part 1: State of scientific knowledge about potential impacts of ocean warming and acidification

- Welcome, BIOACID project concept, and introduction of participants
- scientific background and project presentation
  - state of scientific knowledge about ocean warming and acidification, connection to climate change, discussion
  - socio-economic impacts, modeling approaches, discussion
- Guided discussion of important ecosystem services and relevant impacts of climate change
  - concept of ecosystem services, selected services, discussion

Part 2: Discussion of stakeholder opinions and model structure

- Presentation of the basic model structure
  - discussion of model structure, 1) ecological, 2) socio-economical
- Final discussion (summary and discussion of results)
- other missing elements, general concerns
- conclusion, outlook and farewell (invitation to further participation)

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Statements about probabilities of future changes are not standardized in this report, and may reflect the personal views of the authors of the cited references, the interviewed experts or the report’s authors.

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Annex: Conference talks, awards, PhD courses and other related activities

Awards

Hochschulwettbewerb Wissenschaftsjahr 2016/17 Meere und Ozeane: Zeigt Eure Forschung! Gewinnerkonzept "Die Ozean GmbH - Das Spiel um die Meere". Projektförderung EUR 10.000,-. 09/2016–08/2017. http://www.hochschulwettbewerb.net/ozean-gmbh/

IMBER IMBIZO VI: Marine and human systems: Adressing multiple scales and mutliple stressors, Trieste (IT) 10/2015. 'Best Student Presentation'

Stiftung der Universität Bremen. Internetgestützte Öffentlichkeitsarbeit zu Effekten des Klimawandels auf marine Ökosysteme und deren menschliche Nutzung 07–12/2014. Projektförderung EUR 2500,-

Review of manuscripts for scientific journals

Marine Ecology Progress Series (INT–RES): "Trophodynamic effects of climate change-induced alterations to primary production along the Western Antarctic Peninsula"

Aquaculture Research (Wiley): "Comparative Growth and Mortality of cultured Lion's Paw scallops (*Nodipecten subnodosus*) from Gulf of California and Pacific populations and their reciprocal transplants"

Supervised students

Carla Espinosa (MSc Marine Geosciences, Universität Bremen). Geoscientifc project: Integrative modelling of oceanic climate change scenarios for the Barents Sea. 01–05/2017

Miriam Alonso (MSc Global Change: Ecosystem Science and Policy, University College of Dublin). Practical placement: Construction of socio-economic framing scenarios for climate change impacts in the Barents Sea. 01–03/2016

Research proposals prepared

'Climate–driven ecological variations and societal consequences in the Northern Humboldt ecosystem (CevicHe)'. Proposal submitted to the German Federal Ministry of Education and Research (BMBF) call: ‚Impacts of climate changes in coastal upwelling systems'. 11/2016 (pending)

'Climate change impacts on marine ecosystem services in a highly variable marine-human system: Participatory and integrative modelling of tipping points across levels of description (ClimTip)'. Proposal submitted to the BMBF call: 'Tipping points, dynamics and interactions of social and ecological systems (BioTip)‘. 01/2016 (not funded)

Conference talks and posters

Koenigstein, Stefan; Reuter, Hauke; Pörtner, Hans-Otto; Gößling-Reisemann, Stefan: Integrative modelling of environmental and anthropogenic driver effects on marine food web dynamics in the Barents Sea (Talk). **Session VII: Marine species interactions and ecosystem dynamics: Implications for management and conservation. YOUMARES 7: People and the 7 Seas.** Hamburg, 09/2016

Koenigstein, Stefan; Reuter, Hauke; Pörtner, Hans-Otto; Gößling-Reisemann, Stefan: Integrated modelling of ocean acidification and warming impacts on fish species and the marine food web in the Barents Sea (Talk). **4th International Symposium On The Ocean In A High-Co2 World.** Hobart, Tasmania (AUS), 05/2016 (participation funded by DAAD)

Koenigstein, Stefan; Ruth, Matthias; Gößling-Reisemann, Stefan: Participatory modelling of ocean warming and acidification impacts on a subarctic marine system (Talk)**. ICES MSEAS Symposium 2016 "Understanding marine socio-ecological systems: Including the human dimension in integrated ecosystem assessment“**. Brest (F) 6/2016.

Königstein, Stefan: Participatory modelling of ocean acidification and warming impacts on a subpolar marine system to identify adaptation options (Talk). **IMBER IMBIZO VI: Marine and human systems: Adressing multiple scales and multiple stressors.** Trieste (IT) 10/2015.

Koenigstein, S.: Model-based integration of experimental results and human uses to identify management options for marine ecosystems under climate change (Talk). **PICES/ICES 3rd Intern. Symposium on the Effects of Climate Change on the World's Oceans**. Santos (Brazil), 03/2015

Koenigstein, S. & Goessling-Reisemann, S.: Participatory modeling of climate change impacts on marine ecosystem services (Talk). *No living without the oceans: Marine Social-Ecological Systems*. **YOUMARES conference 2015.** Bremen 09/2015

Koenigstein, S.: Modelling ocean acidification impacts on marine ecosystems and societies: Integrating experimental results and ecosystem service uses (Poster + pitch talk). **UN IOC 2nd International Ocean Research Conference.** Barcelona (ES) 11/2014.

Koenigstein & Goessling-Reisemann, S.: A social-ecological model of climate change impacts on marine ecosystems: Integrating experimental results and ecosystem service uses (Poster). **IMBER Open Science Conference: Future Oceans - Research for marine sustainability: multiple stressors, drivers, challenges and solutions**. Bergen (NOR), 06/2014.

Koenigstein, S. & Goessling-Reisemann, S.: Advancing towards an end-to-end model of the impacts of ocean acidification and warming on Arctic Ocean ecosystem services: from effects on individual organisms to stakeholder integration (Poster + pitch talk). **Arctic Ocean Acidification conference.** Bergen (NOR) 05/2013.

External PhD training courses and summer schools

- Interdisciplinary PhD course in Marine Sustainability. Future Earth Norway, Bodø/Tromsø (NOR), 02/2017
- VECTORS Ecosystem Services Summer School. Plymouth Marine Laboratory, Plymouth (UK), 09/2014
- Ecopath with Ecosim Advanced courses: Ecosim / Ecospace / Fisheries Management with EwE. Instituto de Ciencias Marinas (ICM), Barcelona (ES), 11/2014.
- Quantitative Ecosystem Approach to Fisheries (Q-EAF) training course. Ifremer, Sète (F), 04/2014
- Innovative Approaches in Marine Environmental Modelling summer school. LabExMer/IUEM Brest (F), 08/2013
- European Campus of Excellence: Summer School on Climate Change in the Marine Realm, Sylt/Bremen, 08/2012

Other events

Project workshop within BIOACID phase II, Consortium 4: Integration von experimentellen Daten in sozial-ökologische und sozio-ökonomische Modelle. 10.3.2015, artec / Uni Bremen.

Other reports & studies

Koenigstein, S. (2015). Eisendüngung im Ozean. In: Gleich, A. von, Giese, B., Jensen, S. & Koenigstein, S. (2015). Umgang mit Nichtwissen bei explorativen Experimenten. Gutachten im Auftrag des Büros für Technikfolgenabschätzung am Deutschen Bundestag (TAB) (in German, unpublished)

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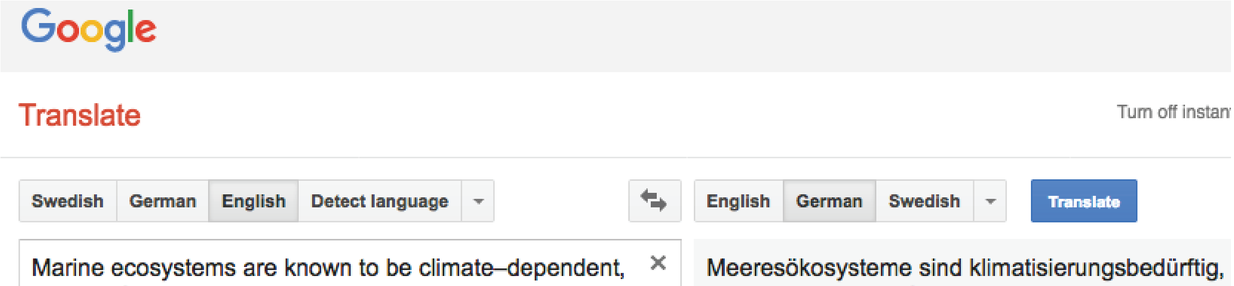
Ach ja, und danke an June für das Einfügen wirrer Zeichenkombinationen in den Text, wenn sie sich mal wieder auf meine Tastatur gelegt hat.



Marine ecosystems are known to be climate–dependent,

Meeresökosysteme sind klimatisierungsbedürftig,