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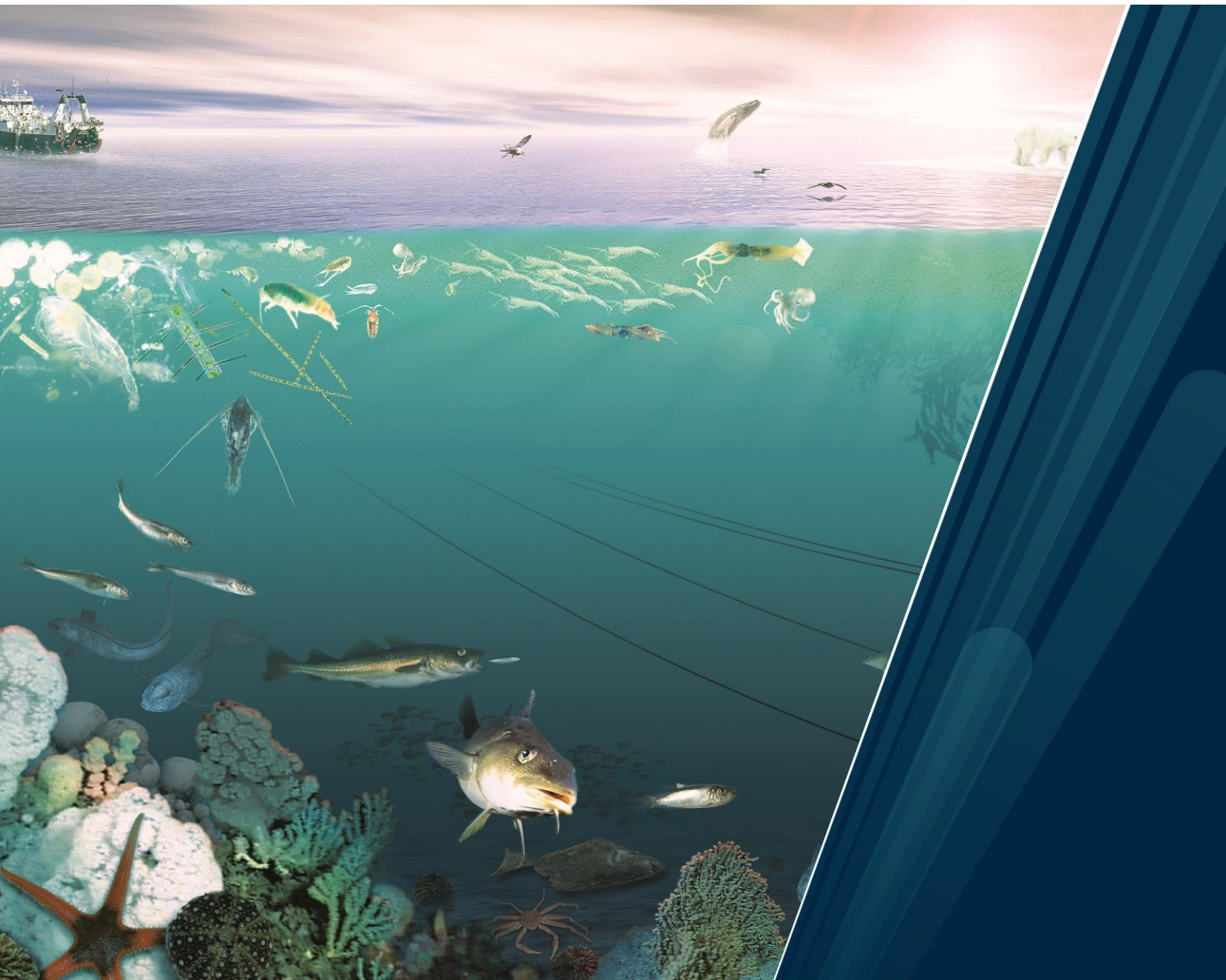
Faculty of Biosciences, Fisheries, and Economics

Department of Arctic and Marine Biology

## **Investigating the drivers of the Nordic Seas food-web dynamics using Chance and Necessity modelling**

Elliot Sivel

A dissertation for the degree of Philosophiae Doctor – April 2022





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The Arctic University of  
Norway



Institute of Marine  
Research



The Nansen Legacy



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## Summary

Marine ecosystems are complex entities with varying structure and functions. These variations can result from (1) impacts of anthropogenic stressors, (2) internal dynamics, and (3) stochastic events. Previous studies have focused on assessing effects of anthropogenic stressors on the variability of marine ecosystems to define management policies aiming at reducing stressors impacts on marine ecosystems. Historically, variability was studied using ecological time-series, but these often covered relatively short time periods and data were not available for some important groups. As an alternative to archaeological and paleontological data, one can also use numerical models to simulate ecosystem dynamics over periods longer than observational records permit. Chance and Necessity modelling (CaN) is a stochastic mass-balanced food-web modelling framework. Chance represents the indeterminacy of ecological processes, while Necessity corresponds to the physical and biological constraints of food-webs. Two CaN models have been developed: The Non-Deterministic Network Dynamic model (NDND) and the RCaN model.

Three questions were addressed in this thesis. First, what are the possible food-web configurations of the Barents Sea in terms of biomass and trophic flows. I simulated biomass and trophic flow trajectories to define a reference for the stochastic variability of the Barents Sea food-web. I also reconstructed past trajectories of the Barents Sea food-web using the RCaN model to identify if the past variability of the Barents Sea food-web is representative of its possible variability. I found that the Barents Sea food-web could be characterized by four food-web configurations and three trophic pathways corresponding to gradients of biomass and trophic flows, respectively. The results also showed that food-web configurations observed in recent decades corresponded only to a fraction of possible configurations.

Second, I explored trophic control in the Barents Sea food-web and the Norwegian pelagic food-web. Wasp-waist trophic control was previously described in the Barents Sea, where capelin plays an essential role in transferring energy from lower trophic levels to higher ones. A recent study suggested that trophic control in the Barents Sea is fluctuating on inter-decadal timescale. Thus, I aimed to identify whether trophic control was persistent in the Barents Sea food-web. As for the first question, I compared results from NDND simulations to results from RCaN model reconstructions. I found that fluctuating trophic control is to be expected in the Barents Sea food-web. Furthermore, trophic control in reconstructed dynamics also displayed fluctuating trophic control at inter-decadal timescale. In the Norwegian Sea, previous studies



investigating only a few species of the ecosystem suggested top-down control of zooplankton by herring. Using a RCaN model for the pelagic food-web of the Norwegian Sea, past dynamics for planktivorous fish species and zooplankton groups were reconstructed. The results are consistent with bottom-up trophic control of planktivorous fish species by zooplankton groups, but not with top-down control on copepods and krill. This suggest that previous conclusion may need to be reevaluated.

Third, I investigated possible combined effects of climate change and fisheries on the stability of the Barents Sea food-web. I used a scenario-based approach for four scenarios of climate change and fisheries (16 scenarios in total). Changes in stability displayed synergism between temperature and fisheries given that temperature affected only harvested species. Species biomass was significantly affected by changes in temperature and fisheries while stability was weakly affected. Weak changes in stability were explained by the positive relationship between mean biomass and biomass variance (Taylor's law). Given that the measure of stability corresponds to the inverse of the coefficient of variation, proportional increase of mean biomass and biomass variance resulted in constant stability values.

Dynamical models have a central role in my work and their performance needs to be evaluated in relation to the specific objectives of this thesis. Unfortunately, an evaluation protocol allowing model evaluation in a consistent and transparent manner did not exist when I started this study. Thus, I contributed to the development of a standardized protocol for reporting the evaluation of model applications. This protocol was applied to a series of ecosystem models used in the framework of the Nansen Legacy project, among which the NDND model. This protocol aims at increasing the transparency and the reproducibility of the model evaluation process by developing a culture of reporting and describing such process.

## List of papers

- I. **Sivel, E.**, Planque, B., Lindstrøm, U., & Yoccoz, N. G. (2021). Multiple configurations and fluctuating trophic control in the Barents Sea food-web. *PLOS ONE*, 16(7), e0254015. <https://doi.org/10.1371/journal.pone.0254015>
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- IV. Planque, B., Favreau, A., Husson, B., Mousing, E., Hansen, C., Broms, C., Lindstrøm, U., & Sivel, E. (2021). Quantification of trophic interactions in the Norwegian Sea pelagic food-web over multiple decades. *Zenodo*. <https://doi.org/10.5281/zenodo.5710848> -- Submitted to *ICES Journal of Marine Science*

# Table of Contents

1	Introduction .....	1
1.1	Drivers of ecosystem variability .....	1
1.2	Investigating natural variability for management.....	2
1.3	Available tools to investigate ecosystem variability .....	3
1.4	Chance and Necessity (CaN).....	4
1.5	Model evaluation .....	5
1.6	Nordic Seas.....	6
1.6.1	The Barents Sea ecosystem .....	6
1.6.2	The Norwegian Sea ecosystem .....	7
1.7	Climate change and fisheries effects on ecosystem variability .....	8
2	Objectives.....	10
3	Methodological considerations .....	12
3.1	Model principles .....	12
3.2	Non-trophic model components .....	13
3.2.1	Primary production.....	13
3.2.2	Harvesting in CaN models .....	14
3.3	Implementation of climate in CaN models.....	15
4	Summary of results.....	16
4.1	Paper I: Multiple configurations and fluctuating trophic control in the Barents Sea food-web.....	16
4.2	Paper II: Combined effects of temperature and fishing mortality on the Barents Sea ecosystem stability .....	18
4.3	Paper III: A standard protocol for describing the evaluation of models .....	22
4.4	Paper IV: Quantification of trophic interactions in the Norwegian Sea pelagic food-web over multiple decades .....	23
5	Discussion .....	26

5.1	Exploring the possible variability of the Barents Sea food-web. ....	26
5.2	Trophic control in the Nordic Seas.....	28
5.2.1	Fluctuating trophic control in the Barents Sea.....	28
5.2.2	Trophic control in the Norwegian Sea.....	29
5.3	The combined effects of climate and fisheries on ecosystem stability.....	29
5.3.1	Synergistic effect of temperature and fisheries.....	29
5.3.2	Taylor’s law.....	30
5.3.3	Compensatory vs. additive fisheries.....	31
5.4	Model evaluation.....	32
5.4.1	OPE protocol.....	32
5.4.2	Sensitivity analysis.....	33
6	Conclusion.....	34
7	References.....	35

# 1 Introduction

## 1.1 Drivers of ecosystem variability

Marine ecosystems are dynamic systems that constantly evolve through various structural and functional states (Calvo et al., 2011; Niiranen et al., 2013; Fossheim et al., 2015; Kortsch et al., 2015). The complexity of ecosystem dynamics results from a large diversity of species and habitats, but also from non-linear feedback mechanisms (Levin, 1998, 2005; Levin et al., 2013). Variations in ecosystem dynamics can result from three different drivers: (1) External pressures driven by human activities, such as climate change and fisheries (Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012; Lilly et al., 2013), (2) internal dynamics emerging from its functioning (D. Ø. Hjermann et al., 2010; Stige et al., 2014), and (3) stochasticity (Lande, 1993; Shoemaker et al., 2020). Understanding the causes of variability in space and time is crucial for management of resources.

Several studies have focused on how anthropogenic activities affect the occurrence of multiple ecosystem states in the same region at different time-periods (Poloczanska et al., 2016; Ortuño Crespo & Dunn, 2017). In marine ecosystems, human-induced climate change and fisheries are important drivers of ecosystem variability. Previous studies used sea surface temperature as an indicator of climate change and assessed its effects on ecosystems (e.g., Poloczanska et al., 2013; Seabra et al., 2015). Increased temperatures affected primary production in marine ecosystems. For instance, an increase of 30% of primary production was observed in the Arctic Seas based on satellite derived chlorophyll-a concentrations (Arrigo & van Dijken, 2015). Yet, this increase is closely related to the retreat of the sea ice in the Arctic (Dalpadado et al., 2020) and model outputs do not support this trend in ice-free ecosystems (Holt et al., 2016). Increased temperatures also have triggered poleward migrations of marine species in many ecosystems (e.g., Fossheim et al., 2015; Kleisner et al., 2017). These poleward migrations have affected species abundances (R. A. Hastings et al., 2020), but it also triggered structural changes in the food-web due to replacement of northern species by southern species (Kortsch et al., 2015; Fraier et al., 2017).

The direct effect of fisheries is the reduction in biomass of harvested species (Ortuño Crespo & Dunn, 2017). Top-predators biomass can particularly be affected by intensive fisheries (e.g., Cardinale et al., 2012; Dulvy et al., 2021). Studies focusing on the effects of top-predators removal by fisheries pointed out the establishment of trophic cascades in marine ecosystems (e.g., Frank, 2005; Donadi et al., 2017; Hernvann & Gascuel, 2020). For instance, removal of

benthic fish in the eastern Scotian Shelf resulted in increased biomass of their primary prey (Frank, 2005). A recent study also suggested that trophic cascades can occur in terms of biomass variation rather than in abundances (Uusi-Heikkilä et al., 2021).

Ecological processes affecting ecosystem dynamics are often uncertain because the underlying mechanisms are not well understood and difficult to measure. For instance, single species recruitment (i.e., proportion of juvenile fish entering the adult population) can affect ecosystem dynamics. The Norwegian spring-spawning herring (NSSH) is an essential species in the Norwegian Sea to transfer energy from zooplankton to marine mammals. Low recruitment success of NSSH since 2009 resulted in a decline of the NSSH stock (ICES, 2021a). There are many possible factors affecting recruitment (Trenkel et al., 2014). A recent study focusing on the NSSH recruitment identified that only predation by mackerel and temperature could affect the dynamics of NSSH recruitment (Garcia et al., 2021), but observations fitted poorly to model estimates. Other existing models to predict recruitment are often not able to reproduce the variability of observed recruitment (Szuwalski et al., 2015).

Stochasticity, i.e., the randomness in ecosystem dynamics changes (Vellend et al., 2014), is often considered as a hurdle for understanding the functioning of natural systems (Boettiger, 2018). In management strategies, stochasticity is implemented as a source of uncertainty in models (Regan et al., 2002; Link et al., 2012). Yet, stochasticity can have an essential role in ecosystem dynamics and functioning. For instance, the duration of transient dynamics, i.e., ecosystem dynamics while not at equilibrium, can be extended due to stochasticity (Hastings et al., 2021). It is also an essential component of key ecological processes, such a prey encounter (Okamoto et al., 2016). A theoretical study showed that considering individual effects of environmental stochasticity (i.e., inherent stochasticity of environmental conditions) and demographic stochasticity (i.e., variability of demographic processes such as death or birth) makes it possible to predict the effect of stochasticity on ecosystem dynamics (Shoemaker et al., 2020). These authors advocated for the need to explore the role of stochasticity on ecosystem dynamics.

## **1.2 Investigating natural variability for management**

Defining a reference state of the natural variability of marine ecosystem dynamics against which status and change can be measured is essential for understanding the present and possible future changes in ecosystem dynamics (Landres et al., 1999). Landres et al, (1999) defines natural variability as the ecosystem variability given a set of environmental conditions, that are

relatively unaffected by human activities. Historical natural variability informs researchers on the ecological processes which affected past ecosystem dynamics and is used to predict present and future dynamics of natural systems. In terms of ecosystem management, historical natural variability is used to define management goals (often to return to past states of the ecosystem) or to assess the effect of disturbances on ecosystem dynamics (Landres et al., 1999; Szabó, 2010). Yet, natural disturbances represent a challenge for defining successful management policies.

### **1.3 Available tools to investigate ecosystem variability**

Traditionally, ecological studies have estimated natural variability from ecological time-series (Poulsen, 2010; McClenachan et al., 2012; Gatti et al., 2015). Unfortunately, ecological time-series are relatively short, typically less than 50 years (Lotze & Worm, 2009; K. Evans et al., 2015), while important shifts in ecosystem dynamics occur at inter-decadal timescales. Relatively short time-series are also problematic given that the lifespan of some species, such as whales, is 50-100 years (Sears & Perrin, 2018). Additionally, ecological time-series are often only available for few commercial species whereas the data coverage of non-commercial fish species and benthos is relatively poor. Consequently, making inference about past or future ecosystem dynamics requires to make assumptions about the ecological processes that can result in large uncertainties (Longhurst, 2010). Considering that variability is expected to increase with the length of the considered time-period (Lawton, 1988; Pimm & Redfearn, 1988), it is worth understanding ecosystem variability on longer timespan than 50 years.

Ecosystem dynamics can be reconstructed using archeological or paleontological data (Lotze & Worm, 2009). These methods enable to identify the effects of drivers on the past ecosystem dynamics over hundreds or thousands of years. For instance, climate variability have triggered multiple shifts in fish abundances that occurred over centennial or millennial timescales (Finney et al., 2010). Also, the Pacific herring stock mean abundance was significantly higher and more stable during time-periods prior to industrial fisheries (McKechnie et al., 2014). It pointed out that unknown biological processes, such as diseases, migration, and predation, may have confounded climate or anthropogenic effects. An alternative approach to historical time-series and paleontological data to investigate ecosystem variability is to simulate ecosystem dynamics using numerical models over multiple decades.

Food-web models simulate species dynamics based on transfer of biomass from a prey to its predator (Christensen & Walters, 2004). The most common food-web model is the Ecopath

with Ecosim (EwE) model (Polovina, 1984; Walters et al., 1997, 1999). The EwE is a deterministic mass-balanced food-web model which aims at assessing the effect of environmental changes and fisheries on marine ecosystem dynamics and test management strategies (policies and marine protected areas, Christensen et al., 2005). It includes a number of ecological processes (e.g., production, density-dependence...) to simulate species biomass dynamics. As knowledge about ecosystems increased, food-web models have constantly become more complex by adding more parameters and variables. However, deterministic food-web models are often not able to reproduce the species biomass variability emerging from ecological processes that are independent from trophic interactions, such as recruitment (Christensen & Walters, 2004). Recently, Pedersen et al. (2021) pointed out that EwE simulations for the Barents Sea ecosystem could not reproduce the variability of unexploited lower trophic levels. Additionally, regime shifts are manifestations of ecosystem dynamics but the lack of global understanding of their underlying mechanisms make them difficult to reproduce in simulations (Möllmann et al., 2015).

Other deterministic and statistical end-to-end models are available to simulate ecosystems dynamics (e.g., Atlantis, OSMOSE, Gompertz models, Shin & Cury, 2001; Fulton et al., 2004; Langanen et al., 2017). These models rely on the definition of various functional relationships. Yet, knowledge about trophic functional relationships is relatively limited (Koen-Alonso & Yodzis, 2005), and model outputs can be significantly affected by the form of trophic functional relationships (Fulton et al., 2003; Kearney et al., 2012; Flynn et al., 2021). Thus, one can re-evaluate classic trophic functional relationships, or one can use models not relying on them. Mullon et al. (2009) suggested an alternative food-web modelling approach which does not rely on specification of functional relationships. Unlike deterministic approaches that consider intrinsic variability as a source of uncertainty in models, the authors suggested that this variability should be explored in a stochastic manner. Instead of adding stochasticity to modelled ecological processes, they developed a constrained non-deterministic food-web model, which allows to not formulate assumptions about uncertain ecological processes. Thus, the developed model accounts for the intrinsic variability of natural systems

## **1.4 Chance and Necessity (CaN)**

Chance and Necessity (CaN) modelling addresses specifically the issue of the stochastic variability of food-webs and does not rely on the specific form of functional relationships (Mullon et al., 2009). It considers that an event is possible only if it complies with a set of



simple structural physical and biological constraints, e.g., population biomass cannot be negative. These structural constraints ensure that the simulated food-web states are biologically and physically possible. For instance, species biomass cannot be negative because it is physically not possible to have a negative weight. Structural constraints ensure that species biomass remains positive or equal to 0. CaN models are designed to reproduce the natural variability of natural systems by exploring the possible trajectories of food-webs. There are two CaN models described in the literature: the Non-Deterministic Network Dynamic model (NDND, Mullan et al., 2009; Planque et al., 2014), and the RCaN model (Planque & Mullan, 2020). The NDND model is designed to explore the possible future trajectories of a predefined food-web and investigate their emerging patterns, such as diet patterns, trophic functional relationships, stability, and synchrony (Mullan et al., 2009; Planque et al., 2014; Lindstrøm et al., 2017). A recent study exploring the possible future trajectories of the Barents Sea food-web was able to reproduce the variability patterns of ecosystem properties of the Barents Sea ecosystem observed during the last three decades (Lindstrøm et al., 2017). The RCaN model aims at reconstructing past trajectories of food-webs using available knowledge (i.e., data and their uncertainties) to investigate the past features of food-webs (Planque & Mullan, 2020). For instance, Planque & Mullan, (2020) applied the RCaN model for the simplified Barents Sea food-web and investigated the past changes in the biomass and trophic flows, and identified trophic control on trophospecies for the time-period 1988-2013.

## **1.5 Model evaluation**

Food-web models are tools that aim to provide information and knowledge on the structure and the functioning of food-webs. The ability of models to address specific questions is central and needs to be assessed more systematically. A first issue is that ecosystem models are often complex, and transparency and reproducibility of model applications are not always ensured (Nichols et al., 2019; Powers & Hampton, 2019). The ODD protocol (Overview, Design concepts, and Details, Grimm et al., 2006, 2010, 2020), which is a standardized protocol aiming at describing models, represented a major advancement in the transparency of model applications. A second issue is that the model performance needs to be evaluated. There are many methods available to evaluate model outputs, e.g., measurement of errors between model outputs and observations (Allen & Somerfield, 2009; Stow et al., 2009; Hipsey et al., 2020), estimations of models' forecast horizons (Petchey et al., 2015), Bayesian model checking (Conn et al., 2018), and sensitivity analysis (Travers et al., 2011; Morris et al., 2014; Hansen et al., 2019). These methods aim at assessing models' skills, models' predictive capacity, or

models' sensitivity to initial conditions regarding the objective for which they were designed. Ecosystem models are general tools designed to address a multitude of questions. Thus, evaluating the performance of the model in a general framework is not particularly relevant. Instead, one should evaluate the performance of ecosystem models to address a specific objective in relation to a model application.

The TRACE (TRANSPARENT and Comprehensive Ecological) documentation (Grimm et al., 2014), which provides a framework for documenting modelling processes, includes some aspects of model evaluation (evaluation of data quality and underlying assumptions of the model applications). Yet, a standardized protocol describing the evaluation methodology of a specific model application still needs to be developed. Such a standardized protocol would allow to increase the transparency and the reproducibility of model application and simplify the communication with non-modelers about food-web model performance.

## **1.6 Nordic Seas**

### **1.6.1 The Barents Sea ecosystem**

The Barents Sea (Figure 1, blue polygon) is a subarctic shelf sea that has experienced important structural and dynamical changes since 1970 (Fossheim et al., 2015; Eriksen et al., 2017; Frainer et al., 2017). It is seasonally covered by sea-ice (the maximal yearly sea ice extent is observed in March and the lowest sea ice extent is observed in September, Onarheim et al., 2018), but annual sea ice cover has decreased by  $0.43 \times 10^6$  km<sup>2</sup> since 1979 (Onarheim & Årthun, 2017). It has affected the biomass and trophic interactions of capelin (*Mallotus villosus*), krill, copepods, and amphipods (Stige et al., 2019). The main pelagic fish, capelin, juvenile herring (*Clupea harengus*) and polar cod (*Boreogadus saida*) are considered as the key species of the Barents Sea food-web, transferring energy from lower trophic levels to higher trophic levels (Hop & Gjørseter, 2013). Pelagic fish stocks displayed large fluctuations, alternating between higher levels of biomass and extremely low levels of biomass since 1983 and the first capelin stock collapse (ICES, 2021b). Over the same time-period, the Barents Sea food-web has been dominated by cod (*Gadus morhua*), which declined in the 1960's before recovering recently and reaching 4500 thousand tons in total stock biomass in 2012, the largest stock size observed since 1955 (ICES, 2021b). Unfortunately, low recruitment rates during the time period 2011-2014 have limited the establishment of strong year classes leading to a decline (2500 thousand tons in 2021, ICES, 2021b). Recent studies suggested that the dynamics of cod is tightly linked to the harvesting rate and capelin abundance (Lindstrøm et al., 2009;

Koen-Alonso et al., 2021). Globally, the Barents Sea food-web has evolved through multiple states since 1970, but none of them lasted over a decade (Johannesen et al., 2012).

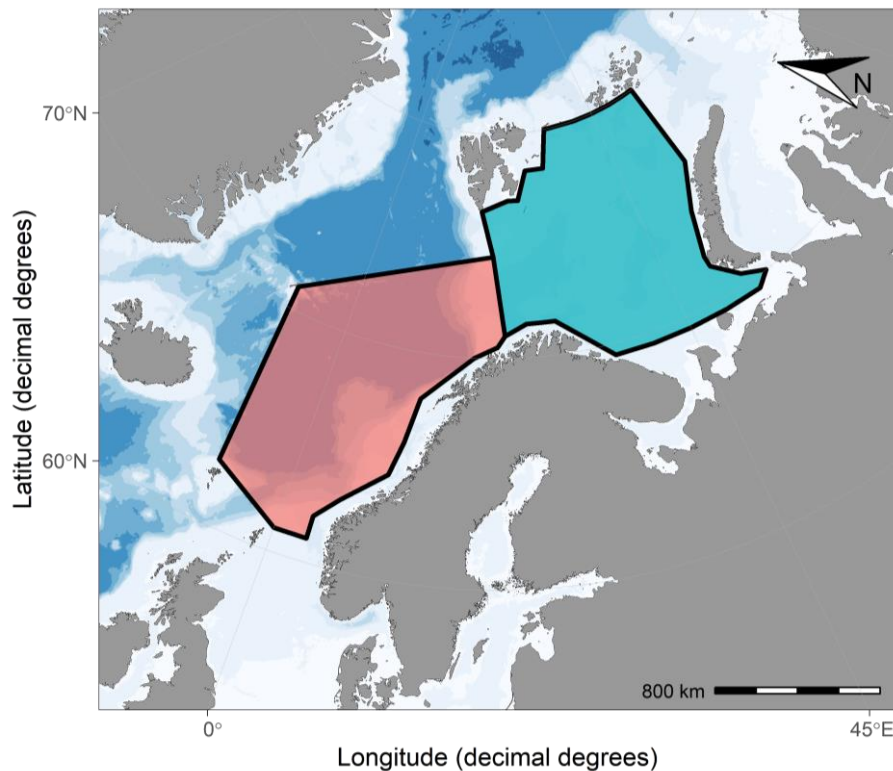


Figure 1. Map of the study areas: the Barents Sea (blue polygon) and the Norwegian Sea (red polygon)

Trophic control between capelin and their prey and predators have been well studied in the Barents Sea. Stige et al. (2014) showed that zooplankton biomass is driven by the predation by capelin (i.e., top-down control), while Stige et al. (2019) also found that capelin dynamics were driven by zooplankton dynamics (i.e., bottom-up control). The major difference in both study is the consideration of reduced sea ice cover and the resulting increase of zooplankton and capelin biomass in the Barents Sea. Yaragina & Dolgov (2009) suggested a wasp-waist control where pelagic fish (i.e., capelin) plays a key role and is assumed to exert a top-down control on zooplankton and a bottom-up control on their predators. Yet, Johannesen et al. (2012) identified fluctuating trophic control between demersal fish, pelagic fish, and zooplankton over decadal timescales.

### 1.6.2 The Norwegian Sea ecosystem

The Norwegian Sea (Figure 1, red polygon) is a deep northern sea (1800m depth in average) adjacent to the Barents Sea and the Arctic Ocean (Blindheim, 2004). The major oceanic current characterizing the Norwegian Sea is an Atlantic water inflow from the North Sea crossing the

area along the Norwegian coast up to the Barents Sea and the Arctic Ocean (Loeng & Drinkwater, 2007). There are also important arctic water inflows from the Greenland Sea and the Icelandic Sea (Blindheim, 2004). There are three major pelagic fish species in the Norwegian Sea: Norwegian spring spawning herring (*Clupea harengus*), Northeast Atlantic mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*). All three species overlap in space during the feeding season (Utne et al., 2012). Several studies have investigated competition between the three species (Prokopchuk & Sentyabov, 2006; Langøy et al., 2012; Utne et al., 2012; Bachiller et al., 2016; Mousing et al., in prep.). The pelagic fish species interact with other species such as amphipods, krill, and mesozooplankton, through both bottom-up and top-down controls (Melle et al., 2004; Olsen et al., 2007). The Norwegian spring spawning herring experienced a large decline in the 1960's, mostly due to a combination of overexploitation and low recruitment (Dragesund et al., 1997), before recovering in 1980's and stabilizing at high biomass levels (ICES, 2021c). Simultaneously, blue whiting biomass increased significantly in the Norwegian Sea (Misund et al., 1998).

## **1.7 Climate change and fisheries effects on ecosystem variability**

Among all external pressures on marine ecosystems, climate change and fisheries are the most important (Lehodey et al., 2006; Halpern et al., 2008a). Climate change has many different manifestations (e.g. ocean acidification, thermohaline circulation alteration, freshwater inflow increase, Doney et al., 2012). This thesis focuses on one specific aspect of climate change, namely temperature change. In the Barents Sea, sea surface temperature increased by 1°C during the time-period 1982-2019 (Timmermans & Ladd, 2019), while temperature increased also in the Norwegian Sea until increased freshwater inflow lowered it since 2010 (ICES, 2021c). Increased temperature matched with observed increases in primary production (PP) in Nordic Seas (Dalpadado et al., 2020; ICES, 2021c). Projections of net primary production in the Barents Sea and the Norwegian Sea, using the ECOSMO (Daewel & Schrum, 2013) and POLCOMS-ERSEM (Wakelin et al., 2012) suggested that net primary production would increase at the horizon 2099 (Holt et al., 2016). Increased temperature is expected to increase organisms' metabolic rates in marine ecosystems (O'Connor et al., 2007; Carozza et al., 2019). Vasseur & McCann (2005) combined a differential equation model estimating biomass densities of prey and predators (see Yodzis & Innes, 1992) to the Metabolic Theory of Ecology (Brown et al., 2004) to estimate the effect of temperature on prey-predator interaction dynamics. They suggested that increasing temperature are likely to destabilize systems by

triggering a shift from a state with a single stable equilibrium to a state with cyclic dynamics. A more recent modelling study did not support these observations and suggested that increased metabolic rates reduced the variability of biomass densities (Fussmann et al., 2014). The observed reduction of variation in population dynamics resulted from a decrease in the energy flow from the prey to the predator for higher temperatures. Ultimately, *Ibid* observed a collapse of predator biomass for extremely high temperature due to starvation.

The first effect of fisheries on the ecosystem dynamics is the decrease of harvested species and more specifically the decrease of large predator stocks (Ward & Myers, 2005). A number of studies suggested that fisheries affect the age-structure of fish communities by removing the largest individuals (Rouyer et al., 2012; Quetglas et al., 2013). Changes in the age-structure of populations may lead to important changes in ecosystem dynamics due to changes in life history traits and demographic features of fish populations (Jørgensen et al., 2007). Based on observed data, Hsieh et al. (2006) showed that harvesting increased the variability of exploited species in the California Current System which was supported by model outputs (Shelton & Mangel, 2011). In the Nordic Seas, fisheries have been linked to the important variations in fish stocks (Dragesund et al., 1997; Toresen & Østvedt, 2000; Hjermmann et al., 2004; Frank et al., 2016; ICES, 2021b, 2021c).

Simulations of future sea surface temperature, based on the RCP8.5 “Business-as-usual” scenario of greenhouse gas emissions (van Vuuren et al., 2011), predict an increase up to 0.5°C at the horizon 2099 (Alexander et al., 2018). Thus, the impact of such sustained increase on the dynamics of marine ecosystems needs to be assessed to better inform future management. Furthermore, previous studies suggested that a stressed ecosystem was more sensitive to additional small perturbations (Möllmann & Diekmann, 2012; Ortuño Crespo & Dunn, 2017), which advocates for investing cumulative impacts of anthropogenic stressors. Especially, the effects of temperature on the ecosystem dynamics should not be treated apart from the effects of fisheries (Shannon et al., 2010; Jarre et al., 2015).

Combined effects can be conceptualized in three broad categories: antagonistic, synergistic, and additive (Crain et al., 2008). Piggott et al. (2015) defined and standardized the concepts of synergism and antagonism in the context of ecological effects. They point out that the direction in which combined stressors operate is essential when defining the nature of combined effects. For instance, while Crain et al. (2008) defined synergism as larger combined effects of stressors than the sum of the individual effects of these stressors, Piggott et al. (2015) make the

difference between positive synergism and negative synergism. Positive synergism corresponds to more positive effects than predicted additively, while negative synergism corresponds to more negative effects than predicted additively.

Combined effects of the temperature and fisheries have been scarcely investigated in the Nordic Seas, but a recent large-scale multi-model study explored the effect of different climate scenarios on mean biomass in multiple marine ecosystems and suggested additive effects of temperature and fisheries on mean biomass (Lotze et al., 2019). In their study, temperature was the largest driver of biomass, while fisheries had a minimal effect. Finally, an application of the Atlantis model for the Benguela ecosystem identified that combined effects of temperature and fisheries were different for the individual species of the Southern Benguela upwelling ecosystem (Ortega-Cisneros et al., 2018).

## 2 Objectives

As mentioned above, changes in food-web dynamics can result from three elements: variations in anthropogenic stressors, changes in internal processes, and stochastic events. The present thesis focuses on investigating how these three elements may contribute to the dynamics of the Barents Sea and the Norwegian Sea food-webs. More specifically, this thesis addresses the following research objectives:

- 1) Explore the possible variability of the Barents Sea food-web, in terms of biomasses and trophic flows among trophospecies, using the NDND model (**Paper I**). This objective will be addressed following three sub-objectives:
  - a) What are the possible food-web configurations of the Barents Sea food-web? My aim is to explore the range of possible configurations of the Barents Sea food-web and to define a reference for its variability accounting for stochastic variability.
  - b) What are the possible trophic pathways in the Barents Sea food-web? My aim is to explore the recurrent trophic pathways of the Barents Sea food-web and to define a reference for the trophic pathway variability in the Barents Sea food-web accounting for stochastic variability.
  - c) How are past changes observed in species dynamics representative of the possible variability of the Barents Sea food-web? My aim is to identify if the

possible and the past configurations of the Barents Sea food-web are consistent with each other. In other terms, I want to identify if the range of past biomass and trophic flow configurations overlap with the possible ones.

- 2) Explore the trophic control in the Barents Sea food-web and the Norwegian Sea pelagic food-web. More specifically,
  - a) Do simulations of possible future trajectories of the Barents Sea food-web support persistent trophic control? (**Paper I**). My aim is to estimate trophic control for trophospecies of the Barents Sea food-web. I also aim to identify if trophic control (i.e., bottom-up, top-down, or wasp-waist) on species is constant over time. Finally, I aim to compare trophic control estimated from simulations to trophic control observed in the past three decades in the Barents Sea food-web.
  - b) Do reconstructions of past trajectories of the Norwegian Sea food-web support bottom-up or top-down controls on zooplankton and small pelagic fish species over the time-period 1988-2020? (**Paper IV**). My aim is to reconstruct ecological time-series of the Norwegian Sea food-web to identify if zooplankton and small pelagic fish dynamics were bottom-up or top-down driven during the time-period 1988-2020.
- 3) Explore the combined effects of temperature and fishing mortality variations on the dynamics of the Barents Sea food-web (**Paper II**). My aim is to assess potential combined effects (i.e., additive, antagonistic, or synergistic effects) of climate change and fisheries on the variability of Barents Sea food-web using a scenario-based approach. I assess the effect of climate change and fisheries by investigating the changes in temporal stability in the individual scenarios.
- 4) Contribute to the development of a standardized protocol aiming at reporting in a transparent manner the evaluation of ecological model applications. My first objective is to participate to discussions concerning the structure and content of such a standardized protocol (**Paper III**). My second objective is to apply the developed protocol to a specific application of the NDND model presented in this thesis.

### 3 Methodological considerations

#### 3.1 Model principles

CaN models are possibilistic mass balanced food-web models (Mullon et al., 2009; Planque et al., 2014; Planque & Mullon, 2020). CaN is closely related to the viability theory (Cury et al., 2005) in the sense that CaN modelling aims at exploring possible trajectories of the ecosystem rather than identifying the optimal one. Chance represents the indeterminacy of ecological processes while necessity corresponds to the structural physical and biological constraints ensuring that the ecosystems sustain itself over time (Planque & Mullon, 2020). The constraints define a set of possible trophic flow values among which trophic flow values are randomly sampled. There are five core constraints in CaN modelling; (1) the food intake of species is limited by satiation, the biomass variations are limited by (2) the upper inertia and (3) the lower inertia, (4) the trophic flows must be positive, and (5) species biomasses need to remain above a threshold value referred to as refuge biomass (Planque et al., 2014).

In the NDND model, possible future biomass trajectories of food-webs are simulated in an iterative manner, i.e., trophic flows are sampled at each time step. The sampled trophic flows define deterministically species biomass at the next time step using the master mass-balanced equation (Eq. 1):

$$B_{i,t+1} = e^{-(\mu_i)} B_{i,t} + \frac{1 - e^{-(\mu_i)}}{\mu_i} \left[ \gamma_i \sum_j F_{ji} \kappa_j + I_i - \sum_j F_{ij} - E_i \right] \quad \text{Eq.1}$$

Where,  $B_{i,t}$  is the biomass of species  $i$  at time step  $t$ ,  $\mu_i$  is the metabolic losses rate of species  $i$ ,  $\gamma_i$  is the assimilation efficiency rate of species  $i$ ,  $\kappa_j$  is the digestibility rate of species  $j$ ,  $F_{ji}$  is the trophic flow from species  $j$  to species  $i$ ,  $F_{ij}$  is the trophic flows from species  $i$  to species  $j$ ,  $I_i$  is the biomass import for species  $i$ , and  $E_i$  is the biomass export for species  $i$ . Estimated biomass ( $B_{i,t+1}$ ) is then used to define the range of possible trophic flows at the next time-step.

The RCaN model aims at reconstructing possible past trajectories of trophospecies. Past biomass trajectories are reconstructed at once. Instead of sampling one trophic flow values at each time-step, the entire time-series of trophic flow is sampled at once. Simulated possible future biomass trajectories are relatively unconstrained while reconstructed ones are further constrained by observed data and their uncertainties. The incorporation of available data and their uncertainties promotes the use of a participatory approach for building and parametrizing



CaN modelling. Furthermore, Planque & Mullon (2020) argue that simplicity of the model structure and parameters facilitates the use of CaN models for communication and participatory management in an Ecosystem-Based fisheries management framework.

## 3.2 Non-trophic model components

The two major non-trophic elements of the CaN models are the import and export terms ( $I_i$  and  $E_i$  in Eq.1). Originally, the import and export terms represented the inflow and outflow of biomass of the study area. Both terms can be used to represent key components of the ecosystem such as primary production (Planque et al., 2014) or losses due to fisheries (see supplementary materials in Lindstrøm et al., 2017). How import and export terms are expressed in CaN models is different between the NDND and the RCaN models. In the NDND model, import and export are expressed explicitly and correspond to input parameters of the model. In the RCaN model, import and export are represented as non-trophic flows (i.e., not affected by *metabolic losses, assimilation, and digestibility*) from or towards outside the model domain, respectively. The two following sections illustrate how primary production and fisheries are implemented in the CaN models using import and export.

### 3.2.1 Primary production

In the NDND model, import of phytoplankton biomass is used as proxy for primary production. Import of phytoplankton is a constant value during the entire simulation process that is defined based on the literature for the parametrization of the models. Rather than representing the real state of phytoplankton, algae, and bacteria present in the food-web, it corresponds to a pool of biomass available for predation for higher trophic levels. In other words, simulated phytoplankton biomass time series corresponds to the remaining biomass after consumption by predators rather than the real dynamics of the phytoplankton. In the RCaN model, however, one can use historical time-series for groups that are not included in the model domain to constrain trophic flows entering the model domain. In other words, the model reconstructs the dynamics of the trophic flows between the group and its predators constrained by historical data, but not the group biomass dynamics. In the Barents Sea RCaN model, presented by Planque & Mullon (2020) and used in **Paper I**, phytoplankton is not included in the model domain, but historical time-series of net primary production are used to constraint the trophic flows from phytoplankton to higher trophic levels. Yet, dynamics of phytoplankton are not explicitly reconstructed in the simulations.

### 3.2.2 Harvesting in CaN models

In CaN models, there are six ways to lose biomass: non-assimilation, non-digestion, metabolism, export, predation, and harvesting. How the latter interacts with the five others led to two hypotheses on the interaction between fishing mortality and other sources of mortality: additivity and compensation (Péron, 2013). In the case of additivity, sources of mortality are considered independent from each other, and the total mortality corresponds to the sum of all sources of mortality. In the case of compensation, one of the sources of mortality affects the other sources of mortality. If the interaction between fishing mortality and other sources of mortality is additive or compensatory is still not clarified in the literature. In common food-web models, such as EwE or Atlantis, fishing mortality is expressed as an additive process in the model structure (Heymans et al., 2016; Audzijonyte et al., 2019). Yet, it is expected that fishing mortality is on a continuum between fully additive and fully compensatory (Myers & Quinn II, 2002; Péron, 2013). Fisheries in the NDND model are assumed to be compensatory (i.e., losses due to fisheries are compensated by predation interactions).

In the NDND model, fished biomass corresponds to an annual export of biomass for harvested species. The value of harvested biomass is estimated in two different ways: (1) harvest control rules (HCR), and (2) as constant annual catches. In fisheries science, HCRs are used to estimate the fishing mortality rate as a function of the spawning stock biomass. Based on the estimated fishing mortality rate, the number of individuals to catch is defined using the Baranov equation (Baranov, 1918; Branch, 2009). In **Paper I** and **II**, The HCRs are defined for fish species and resemble fishing regulations operating at present. The HCRs in the NDND model rely on three assumptions: (1) the catch/stock ratio is considered equivalent in biomass and number of individuals, (2) the fishing mortality is estimated based on the total stock biomass instead of the spawning stock biomass, and (3) HCRs for dominant species of harvested species are used as HCRs for the whole trophospecies (e.g., in **Paper I**, the HCR's parameters for cod are used to define the HCR for demersal fish). Figure 2 summarize how HCRs are defined.

In **Paper II**, harvesting of benthos and marine mammals was added to the existing fisheries module of the NDND model. Given that no HCR was defined for either group in Nordic Seas in the literature, harvesting was implemented as an annual catch (NAMMCO – North Atlantic Marine Mammal Commission, 2021). For marine mammals, annual catches are reported as individuals. Thus, conversion factors from number of individuals to  $\text{tons}\cdot\text{km}^{-2}$  was applied.

In the RCaN model, as for phytoplankton, fisheries are outside the model's domain. Thus,

historical catches time-series are used to constrain the reconstructions of non-trophic flows from harvested trophospecies to fisheries (i.e., flows towards outside the model's domain).

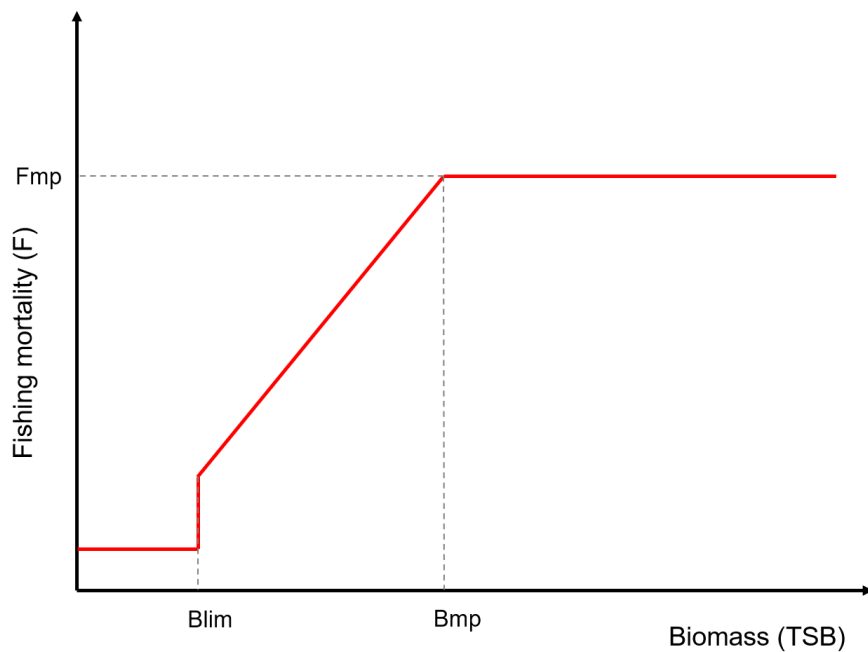


Figure 2. Harvest control rule (HCR) pattern implemented in the NDND model. The red line corresponds to the fishing mortality as function of total stock biomass (TSB). The HCR can be divided in three phases: (1) When  $TSB < Blim$ , then  $F=0$ , (2) When  $Blim < TSB < Bmp$ , then  $F$  increases linearly, and (3) When  $TSB > Bmp$ , then  $F=Fmp$ . When  $F=Fmp$ , harvested biomass is estimated using the Baranov equation (Baranov, 1918; Branch, 2009)

### 3.3 Implementation of climate in CaN models

The CaN models rely on six input parameters (*assimilation efficiency, digestibility, other losses, inertia, satiation, and refuge biomass*). In addition to these six input parameters, the NDND model requires values for the *initial biomass, import and export*. Among the input parameters, other losses, inertia, and satiation are defined using the metabolic theory of ecology (MTE, Brown et al., 2004) and life history theory. Conventionally, changes in metabolic rates due to variations in temperatures are estimated using  $Q_{10}$ . It expresses the change in metabolic rate values for an increase in temperature across a range of  $10^{\circ}\text{C}$  (Gillooly et al., 2001). Gillooly et al. (2001) pointed out that using  $Q_{10}$  can lead to errors larger than 15% in the estimations of changes of metabolic rates in response to changes in temperature. Instead, the authors suggested to use the MTE to account for body-size and temperature dependence of metabolic rates. Applying Eq.2, where  $E$  (activation energy) =  $0.63 \text{ eV}$ ,  $k$  (Boltzmann constant) =  $8.26 \cdot 10^{-5}$ , and an initial temperature ( $T$ ) of  $6^{\circ}\text{C}$  leads an increase of 10% in metabolic rate values for an increase by  $1^{\circ}\text{C}$ .

$$\frac{B(T + \Delta T)}{B(T)} = \frac{B_0 M^{3/4} \cdot e^{-E/k(T+\Delta T)}}{B_0 M^{3/4} \cdot e^{-E/kT}} = \frac{e^{-E/k(T+\Delta T)}}{e^{-E/kT}} \quad \text{Eq.2}$$

## 4 Summary of results

### 4.1 Paper I: Multiple configurations and fluctuating trophic control in the Barents Sea food-web

This paper focus on identifying the possible biomass configurations and trophic pathways of the Barents Sea food-web (Figure 3), as well as identifying if trophic control on Barents Sea species is persistent over time. In that respect, we aimed at defining a reference for the variability of the Barents Sea food-web.

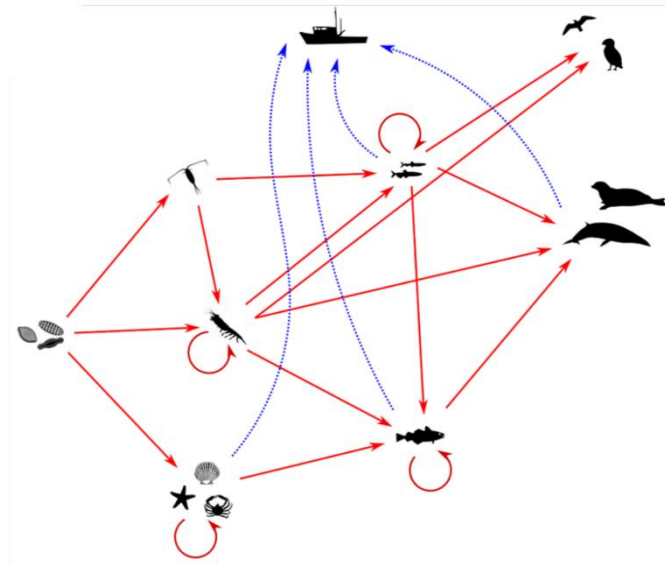


Figure 3. Simplified food-web of the Barents Sea. Each icon corresponds to one trophospecies (i.e., phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, marine mammals, and birds; from left to right and top to bottom). Red-full arrows correspond to trophic flows. Blue-dashed arrows represent the non-trophic flows to the fisheries.

We used the Non-Deterministic Network Dynamic model (NDND) to simulate possible biomass and trophic flow trajectories of the Barents Sea food-web. As principal component analysis performed on autocorrelated multivariate time-series can be spurious (Planque & Arneberg, 2018), we explored the possible food-web configurations in simulated time-series using dynamical principal component analysis to account for temporal autocorrelation. We applied this method to identify food-web configurations based on simulated biomass and trophic flows. We found four biomass configurations corresponding to two gradients of biomass (Figure 4). The first one opposed pelagic fish and omnivorous zooplankton while the second one opposed demersal fish and marine mammals. We also concluded that there were

three possible trophic pathways in the Barents Sea food-web: (1) a pelagic, (2) a planktonic, and (3) a benthic-demersal trophic pathway (Figure 5 in **Paper I**).

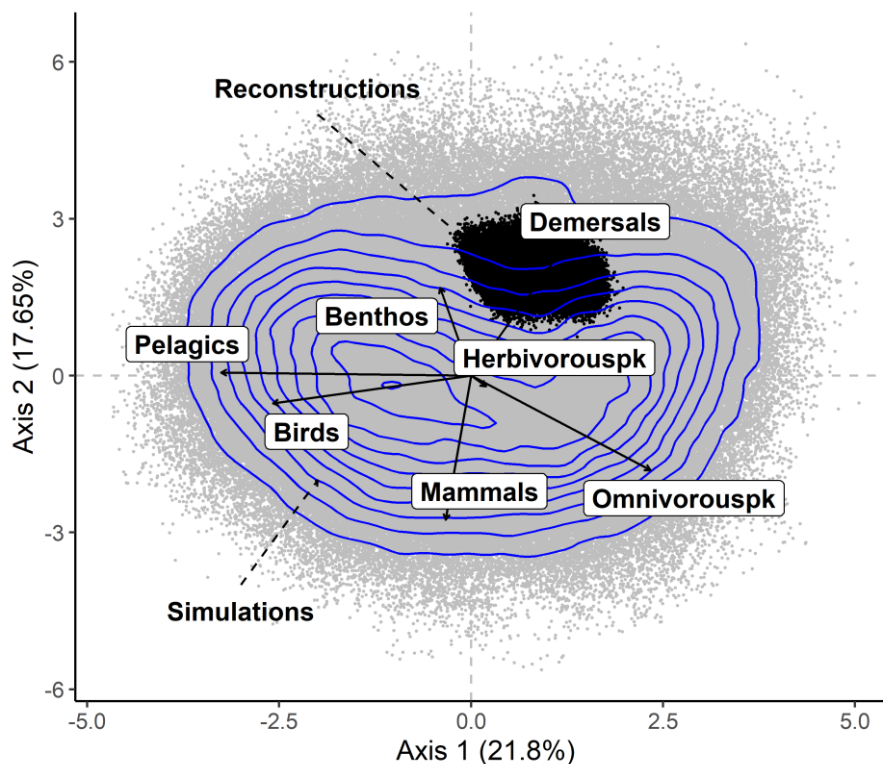
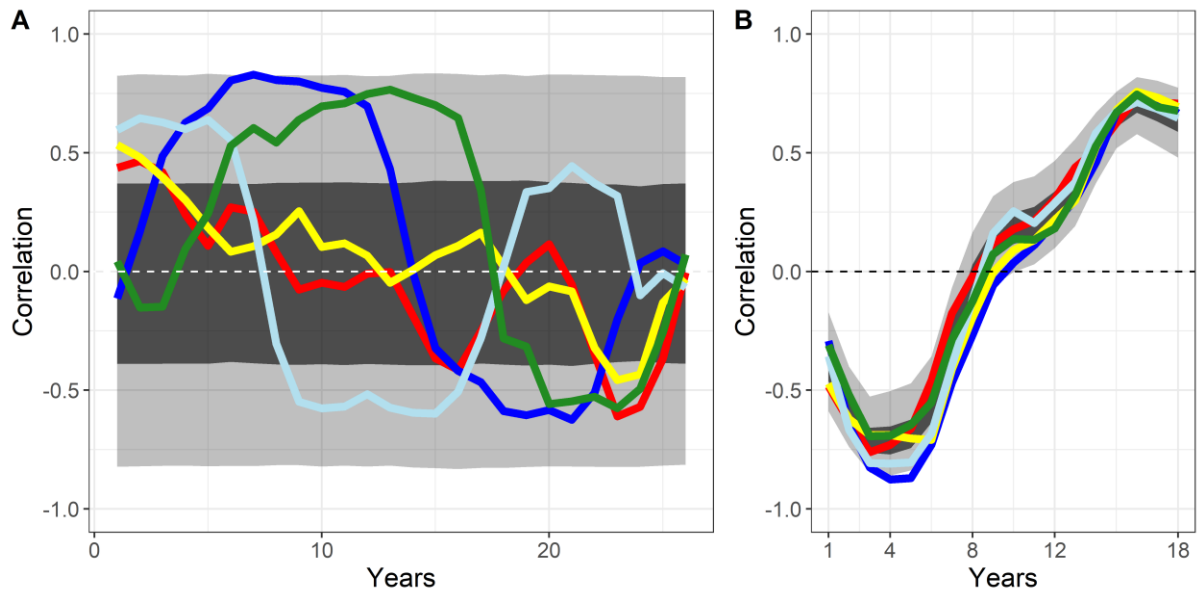


Figure 4. Simulated (grey points) vs. reconstructed (black points) biomass configurations in the Barents Sea food-web. Each point represents the biomass configuration for one year. Arrows with trophospecies names corresponds to the projection of the variables on the PCA-space. Blue lines correspond to the density lines of configurations, i.e., the more line, the denser.

We then reconstructed past biomass and trophic flow trajectories using the RCaN model to assess whether past dynamics of the Barents Sea food-web are representative of its possible variability. The reconstructions range of reconstructed food-web configurations completely overlapped with the range of simulated configurations, both for biomass and trophic flow configurations (Figure 4 and Figure 5 in **Paper I**). Yet, the range of reconstructed configurations was smaller than the range of simulated configurations. The projection of reconstructed biomass configurations showed that demersal fish was dominant in the Barents Sea food-web (Figure 4) and the major trophic pathway was the benthic-demersal one (Figure 5 in **Paper I**).

We found persistent trophic control in the Barents Sea food-web neither over 379 years (Figure 6 in **Paper I**) nor over 40 years (Figure 7 in **Paper I**). Trophic control in the simulations of the Barents Sea food-web were fluctuating at interdecadal timescales, with correlation values varying between -0.8 and 0.9 (Figure 5A). A similar pattern was visible for the reconstructions,

where correlation varied between -0.8 and 0.8 (Figure 5B). This pattern of fluctuating trophic control at interdecadal timescale was present for all trophic interactions considered in the study (see supplementary material Figure 8 and 9 in **Paper I**).



*Figure 5. Fluctuating trophic control between demersal and pelagic fish in simulated food-web trajectories (A) and reconstructed ones (B). Correlation corresponds to the Pearson correlation between demersal and pelagic fish biomass estimated for a sliding window of 15 years. Dark grey envelopes contain 50% of estimated correlation values. The light grey envelopes contain 95% of estimated correlation values. Individual trajectories (dark blue, cyan, yellow, green, red) correspond to five randomly selected trajectories of correlations between demersal fish and pelagic fish biomass.*

This study defines a baseline for the variability of the Barents Sea food-web by exploring the possible range of stochastic variability. The possible range of stochastic variability is larger than the observed past variability of the Barents Sea food-web. Past configurations dominated by demersal fish correspond to one of the four identified possible food-web configurations, while the past trophic pathway represent a configuration where the trophic flows transiting through demersal fish are dominant. Furthermore, this study suggests that fluctuating trophic control is to be expected in the Barents Sea food-web. This finding is supported by Johannesen et al. (2012), who first suggested fluctuating trophic control based on historical data. Finally, while stochasticity is considered as a source of uncertainty in management policies (Link et al., 2012), **Paper I** highlights the importance of considering stochastic variability for future management decisions.

## 4.2 Paper II: Combined effects of temperature and fishing mortality on the Barents Sea ecosystem stability

This paper focuses on the effect of temperature and fishing mortality on the temporal stability

of the Barents Sea food-web. We explored their effects independently before investigating if their combined effects on the temporal stability were antagonistic, additive, or synergistic. To this end, we used a scenario-based approach with four scenarios of temperature and fishing mortality (i.e., 16 crossed scenarios of temperature and fishing mortality in total) for which we simulated possible biomass trajectories of the Barents Sea food-web using the NDND model. For each trajectory, we estimated the stability for the whole Barents Sea food-web and individual species.

We found that, although species biomass was affected by increasing temperature and fishing mortality (Figure 6), stability was weakly affected (Figure 7). Increasing temperature negatively affected species biomass (Figure 6A) as well as stability (Figure 7A), while higher fishing mortality triggered compensatory dynamics between both fish species (i.e., pelagic, and demersal fish, Figure 6B) but had no effect on stability (Figure 7B). We attributed the relative absence of effects on stability to the co-variability between the average biomass and its variance, where average biomass and variance had a positive linear relationship (see supplementary materials Figure S6 and S7 in **Paper II**).

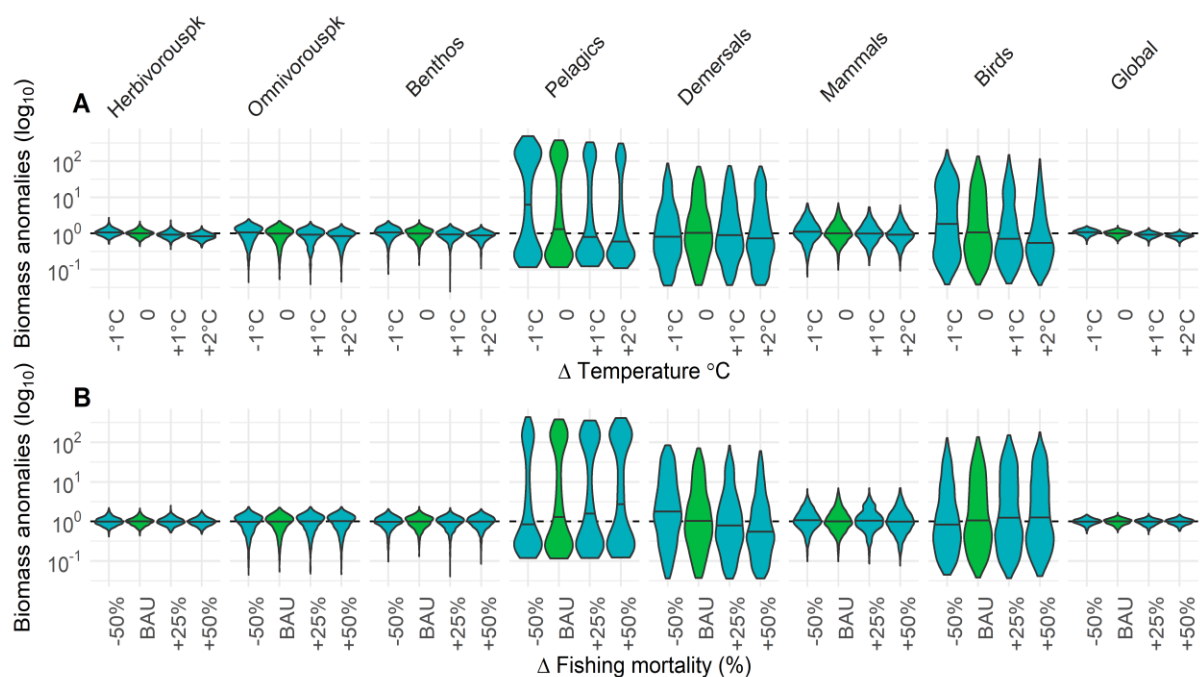


Figure 6. Effect of temperature (A) and fisheries (B) on species and food-web average biomass. Each violinplot corresponds to a scenario of temperature and fishing mortality. The green violinplot indicates the reference scenario (i.e., the scenario with no change in temperature and fishing mortality). Black line in violinplots corresponds to the median biomass and temporal stability.

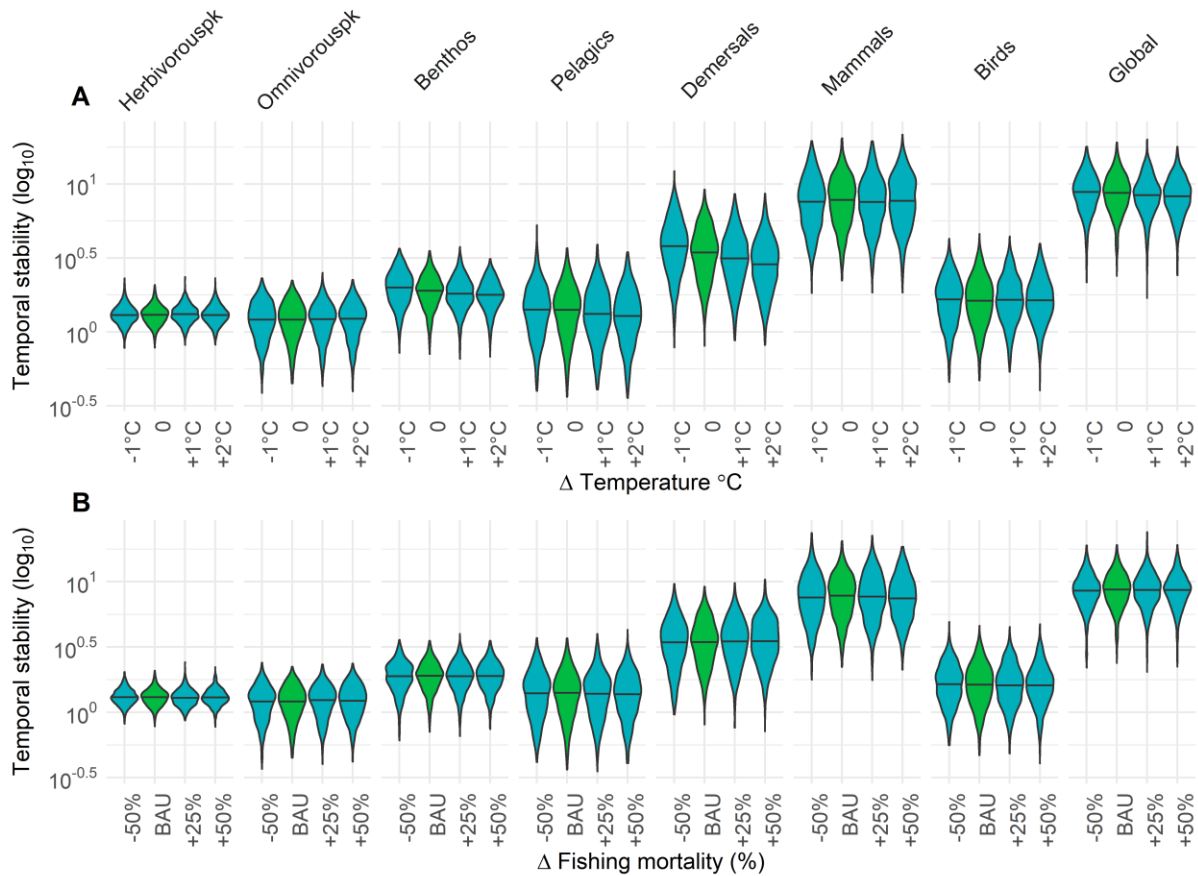


Figure 7. Effect of temperature (A) and fisheries (B) on species and food-web temporal stability Each violinplot corresponds to a scenario of temperature and fishing mortality. The green violinplot indicates the reference scenario (i.e., the scenario with no change in temperature and fishing mortality). Black line in violinplots corresponds to the median biomass and temporal stability.

We identified combined effects of temperature and fisheries by comparing the simulated effects to the sum of the individual effects of temperature and fisheries. No deviation from the sum of individual effects corresponded to additive effects of climate and fishing. A positive deviation indicated synergism while a negative deviation indicated antagonism between climate and fisheries. We found that increased fishing intensity (higher  $Fmp$ ) amplified the effects of increasing temperature on stability (Figure 8). We also highlighted that increasing fishing mortality had positive effects on stability. For harvested species, we observed synergistic effects in scenario of colder temperature and antagonistic effects for scenarios of warmer temperatures, regardless of the fisheries. Finally, we observed a shift from synergistic to antagonistic effects for increasing fishing mortality in scenarios of colder temperature, and vice versa for scenarios of warmer temperature.



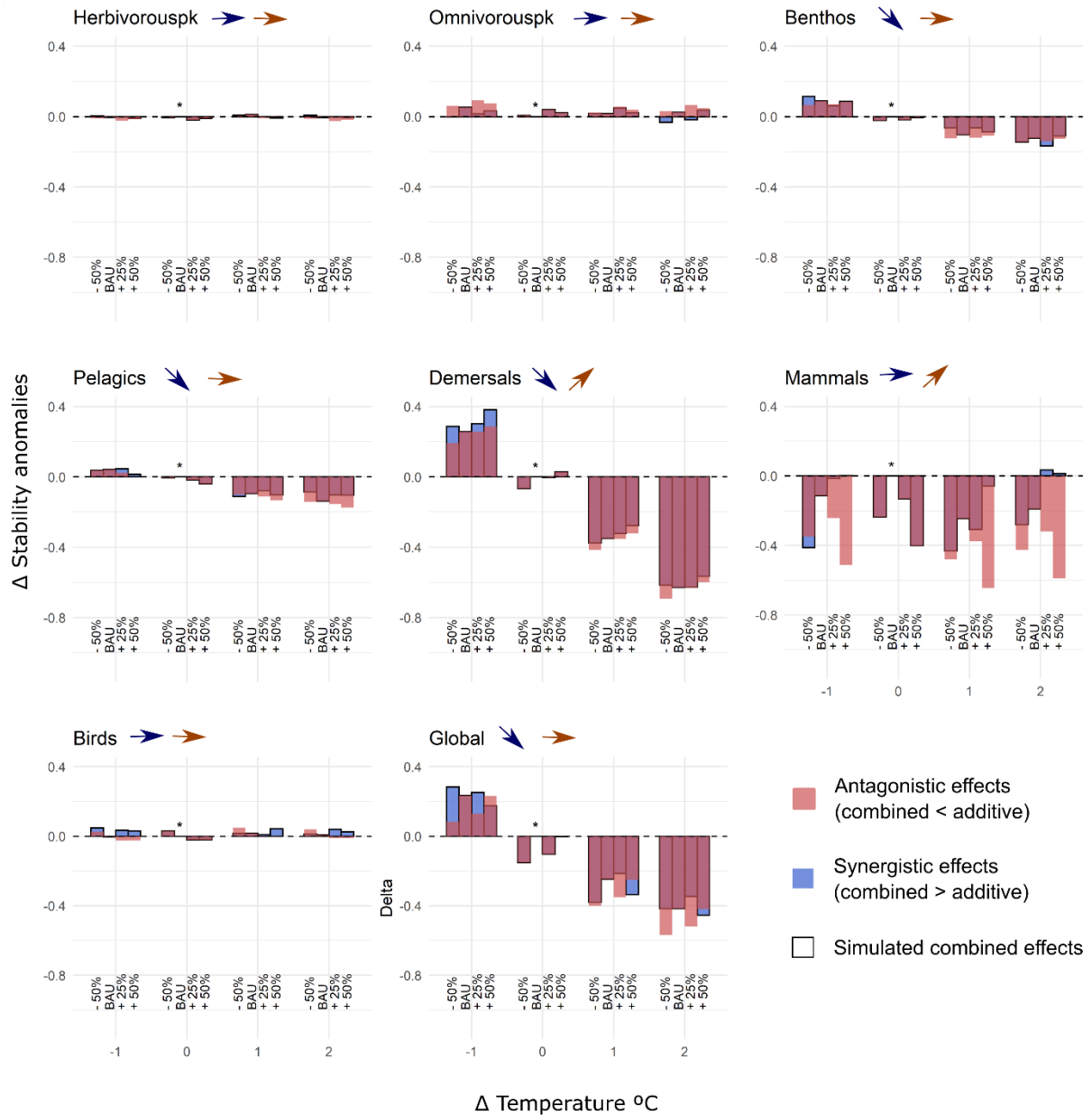


Figure 8. Combined effects of temperature and fishing mortality on the species and food-web temporal stability. Each barplot corresponds to a combined scenario temperature and fishing mortality. The reference scenarios (i.e., no change in temperature and fishing mortality) is identified by “\*”. The black-framed bars correspond to the simulated effect of temperature and fishing mortality. Total overlap between the simulated and the sum of the individual effects of both drivers indicates additive effects. Larger simulated effects (the blue bar larger than the red one) indicate synergistic effects, and smaller simulated effects (the red bar larger than the blue one) indicates antagonistic effects. Blue arrows beside groups’ names summarize the effect of temperature on the group’s temporal stability. The orange arrows summarize the effect of fisheries on the group’s temporal stability.

The negative effect of temperature on biomass is not supported by modelling studies suggesting that species biomass should increase in polar ecosystems at the horizon 2100 (Bryndum-Buchholz et al., 2019; Lotze et al., 2019). Surprisingly, the effects of fisheries on the species biomass does not propagate to lower trophic levels due to decoupled dynamics between zooplankton species and pelagic fish. In the literature, covariance of mean biomass and variance is expected to increase the stability of the ecosystem (Grman et al., 2010), while

synchrony is expected to destabilize it (Loreau & de Mazancourt, 2008). We suggest that covariance of mean biomass and variance, and synchrony in species dynamics compensate each other, maintaining a constant value of stability. The synergism between temperature and fisheries on the Barents Sea food-web we found in this study was only partly consistent with the past literature. Based on observations, Hsieh et al. (2006) suggested that harvesting increased the variability of exploited species, which supports our results. Contrarily modelling studies using ATLANTIS suggested that temperature and fisheries effects on the US Northeastern Shelf were mostly additive (Nye et al., 2013), while their nature was species dependent in the Benguela upwelling system (Ortega-Cisneros et al., 2018).

### **4.3 Paper III: A standard protocol for describing the evaluation of models**

This paper aims at presenting a standardized protocol to report the evaluation of model applications: the OPE protocol (Objectives, Patterns, Evaluation). The “Objectives” section describes the context and the objective of the model application. It should also inform on potential specific model setup in relation to the objective. In this section, one should describe all deviations of the initial model description that is required to address the objective (e.g., additional submodels, variables, or changes in the temporal or spatial scale of the model). The “Patterns” section provides a description of the ecological patterns used for the evaluation of the model in relation to the objective. More than just describing the patterns, one should describe the motivation for choosing an ecological pattern. In this section, the model user is asked to describe the type and sources of independent data (i.e., existing data that are not built by the evaluated model) used to evaluate the model. It includes the uncertainty associated to independent data. The user should also indicate which model outputs are used for the evaluation and if these outputs have uncertainties. The “Evaluation” section describes the evaluation methodology and the rationale behind its use. It is also the section where the user can describe a sensitivity analysis to the model structure or model parameters and its outcomes (if a sensitivity analysis was performed). The last questions of the OPE protocol focus rather on the limitations of the evaluation methodology (i.e., computational limitations or sensitivity of the evaluation outcomes to the chosen methodology). In total, the OPE protocol comprises 25 questions aiming at reporting in a transparent manner the evaluation of a specific model application.

This paper also presents case studies application of the OPE protocol for the following

ecological model applications: 1) estimating trophic levels of ecological groups of the Barents Sea in 2000 with an Ecopath model, 2) assessing the cumulative impact of fisheries and climate in the Norwegian and Barents Seas using an ATLANTIS model, 3) assessing the persistence of trophic control in the Barents Sea food-web in the Barents Sea using the NDND model, 4) reconstructing and predicting interannual-to-decadal variations in hydrology, biogeochemistry, and phytoplankton biomass in the Barents Sea ecosystem, 5) quantifying in field biomass estimates of *Calanus finmarchicus* in the Norwegian Sea as a function of the sampling design with the NORWECOM model, and 6) quantify the association between the dynamics of capelin and its main two prey (krill and *Calanus* species) in the Barents Sea with a Gompertz model.

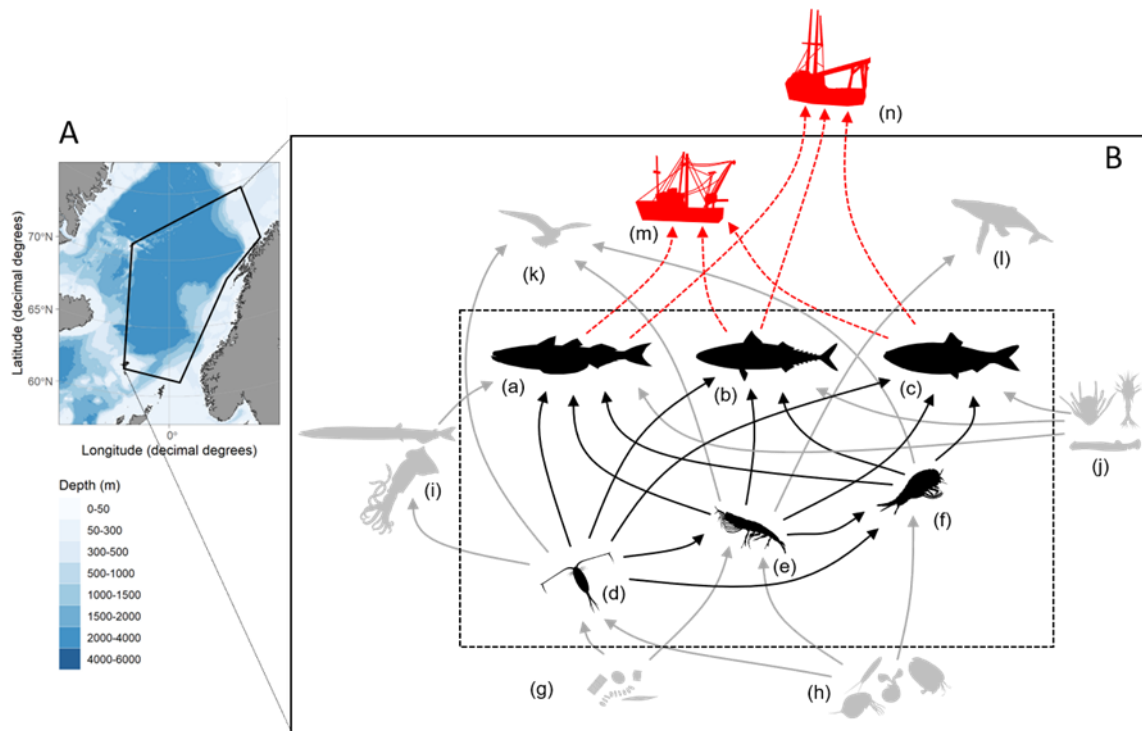
The reporting of model evaluation for the six cases studies presented in the paper led to additional discussion among the co-authors. First, in some cases, additional evaluation steps are not accounted for in the protocol. These steps do neither rely on the comparison of patterns between model outputs and independent data, nor on the sensitivity analysis of the model to input parameters. Second, for a better understanding of the applied protocol, it appeared necessary to provide some background on the model application. Therefore, we added introductory paragraphs summarizing the history of the models and their development.

Unfortunately, documenting model evaluation is not a standard practice among the ecological modeler community because it is time-consuming and little rewarding. By presenting a standardized protocol for reporting the model evaluation in relation to an objective, we aim to provide a tool for better communication about model evaluation and hope to develop a culture of documenting model evaluation such as it is the case with the ODD protocol. However, a lot of work to promote the use of the OPE protocol is still needed to reach this goal. Furthermore, as for the ODD protocol, which was revised two times since its initial development (Grimm et al., 2006, 2010, 2020), the presented OPE protocol is work-in-progress. Future feedbacks and discussions on the OPE protocol are expected to lead to revisions in the present protocol.

#### **4.4 Paper IV: Quantification of trophic interactions in the Norwegian Sea pelagic food-web over multiple decades**

This paper focus on trophic control in the Norwegian Sea pelagic food-web (Figure 9) during the last three decades. We reconstructed possible past dynamics of Norwegian Sea pelagic food-web using the RCaN model and investigated if the reconstructions are supportive of bottom-up or top-down control of zooplankton and small pelagics, and of competition between small pelagics during the last three decades. Therefore, we used available time-series and

known uncertainties for the trophic groups of the Norwegian Sea pelagic food-web to constrain the reconstructions of past trajectories. Trophic control was estimated based on the relationship between the total consumption of a species and the growth, and the relationship between predation and growth for bottom-up and top-down control, respectively.



*Figure 9. Schematic representation of the Norwegian Sea pelagic food-web. (A) Geographic extent of the Norwegian Sea used to parametrize the RCaN model. (B) the food-web topology, where the black full-lined box corresponds to the geographical extent of the Norwegian Sea. Black icons inside the black-dashed box corresponds to trophospecies inside the model domain (i.e., copepods, krill, amphipods, mackerel, herring, blue whiting). Grey icons correspond to trophospecies outside the model domain (i.e., the dynamics of these groups are not reconstructed). Red icons correspond to fisheries. Black arrows correspond to trophic flows inside the model domain. Grey arrows correspond to trophic flows entering or exiting the model domain. Red arrows correspond to non-trophic flows towards fisheries.*

First, with the available data and their uncertainties, it was possible to reconstruct past trajectories of the food-web. The reconstructions showed lower uncertainties for fish species (i.e., herring, blue whiting, and mackerel), while zooplankton species reconstructed trajectories displayed relatively large uncertainties (Figure 10). In the reconstructions, we found a positive linear relationship between the consumption of zooplankton by herring and herring biomass growth indicating bottom-up control on herring dynamics (Figure 11-left panel). Contrarily, we did not find any relationship between the predation on herring and herring biomass growth (Figure 11-middle panel). It means that there was no top-down control on herring in the reconstructions of the Norwegian Sea pelagic food-web. Furthermore, the distribution of correlation calculated for individual reconstructed trajectories supported the presence of bottom-up control and the absence of top-down control on herring (Figure 11-right panel). The

same analysis displayed similar trophic interactions for the other species of the Norwegian Sea pelagic food-web (Figure 6 in **Paper IV**). Yet, amphipods displayed a different pattern where their dynamics are top-down and bottom-up driven (Figure 6 – top-right panel in **Paper IV**). The results also suggest that competition for amphipods between small pelagic fish of the Norwegian Sea pelagic food-web is weak while it is null for the two other preys (Figure 8 in **Paper IV**).

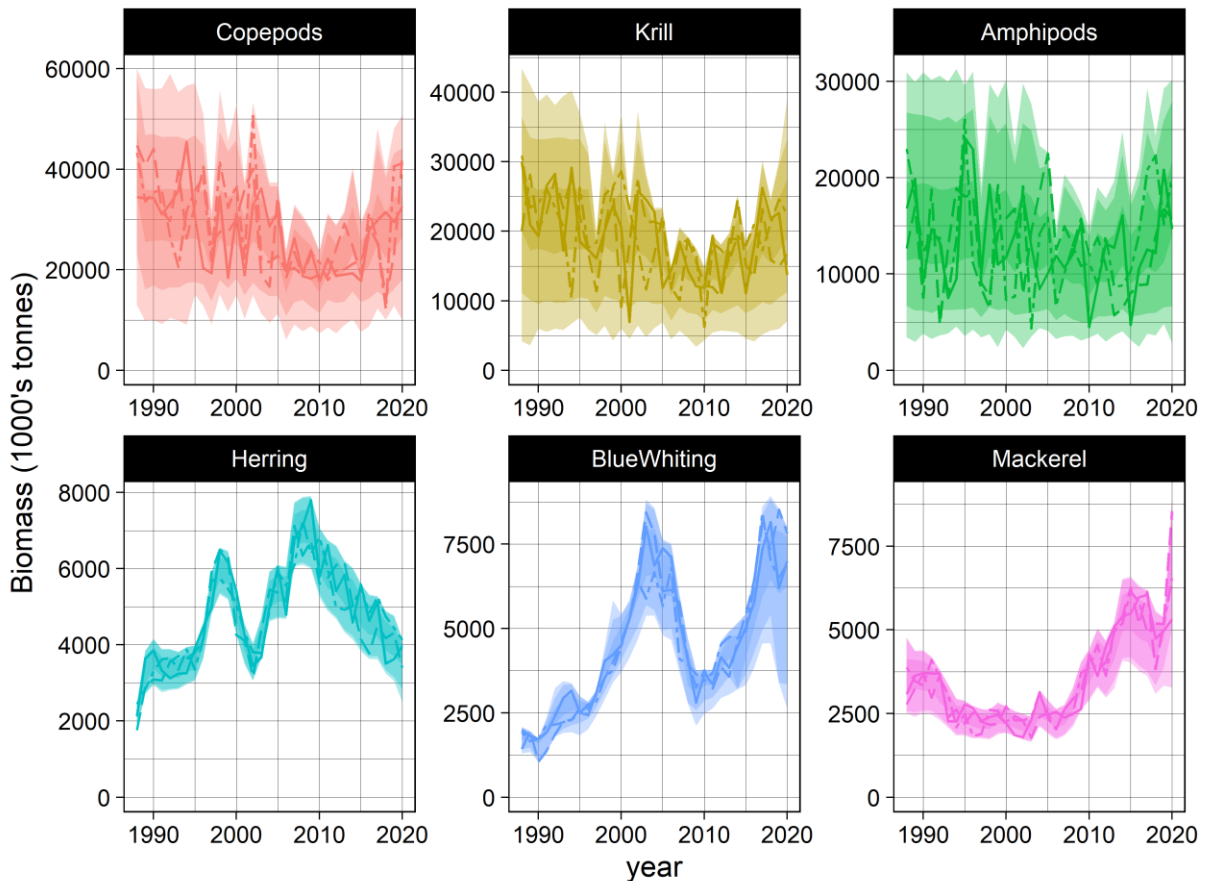


Figure 10. Reconstructed biomass time-series of copepods, krill, amphipods, herring, blue whiting, and mackerel using the RCaN model for the Norwegian Sea pelagic food-web. The envelopes contain 100% (light), 95% (medium) and 50% (dark) of the reconstructed time-series. The plain, dashed, and dashed-dotted lines correspond to three individual reconstructed time-series.

The results presented in **Paper IV** are in contrast with previous studies suggesting that the combination of higher herring biomass and the entry of blue whiting in the Norwegian Sea were concomitant with low copepod biomass in the following year (Olsen et al., 2007). Furthermore, Huse et al. (2012) and Olafsdottir et al. (2016) suggested that small pelagic fish compete for the access to limited resources. The inconsistency between our results and the previous studies may result from differences in the spatiotemporal dynamics of small pelagic fish species in the Norwegian Sea (i.e, different timing in feeding season, migration patterns,

timing in seasonal development of zooplankton, fish species co-occurrence). The sensitivity of the model conclusion to input parameters and data time-series used to constrain the reconstructions of food-web dynamics was evaluated (see supplementary materials S5 in **Paper IV**). The conclusions of the model were relatively robust to variations in the input parameter values. However, there were three cases for which the study's conclusions were altered. First, for extremely low primary production levels (10% of the baseline values), the model could not reconstruct past trajectories. Second, for extremely high fisheries (100% of the baseline values), the sampling of the possible trajectories was suboptimal. Third, for strong increase or decrease of metabolic losses, there was no solution for the sampling of trophic flows.

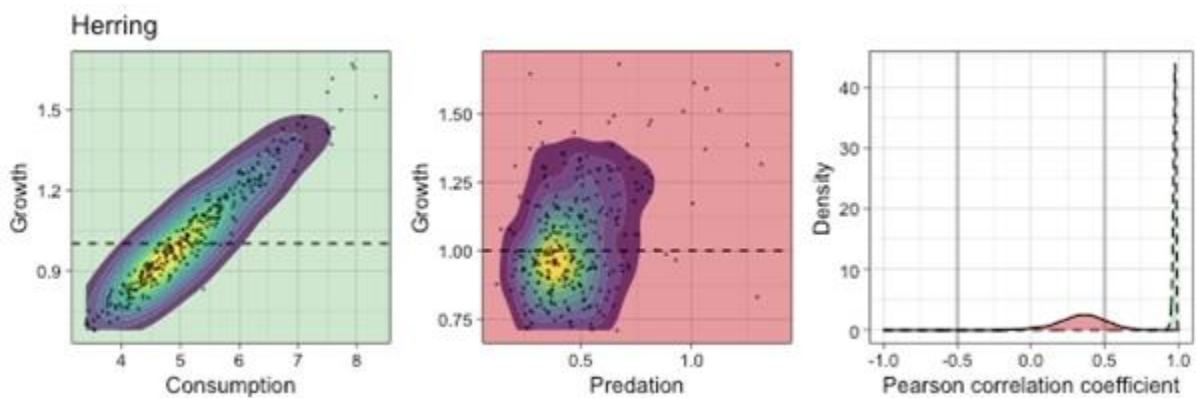


Figure 11. Relationship between herring growth and relative prey consumption (left panel), and relative predation on herring (middle panel). Each dot represents a reconstructed trajectory. The density plot helps to visualize the scatterplot of reconstructed trajectories. The distribution of correlation values between herring growth and relative predation (red) and relative consumption (green) are shown on the right panel.

The RCaN model as it is applied in this study illustrate how CaN models can be used in a participatory modelling approach for integrated ecosystem assessment. It relies on principles that are simple, easily communicable, and understandable by a wider community. Furthermore, actual RCaN models can be easily updated by adding new data to the model, which is relatively straightforward. RCaN reconstructions can also be used to identify where data is lacking or is of insufficient quality

## 5 Discussion

### 5.1 Exploring the possible variability of the Barents Sea food-web.

The range of past ecosystem configurations of the Barents Sea food-web represented only a fraction of the possible variability displayed in the NDND simulations (**Paper I**). This result advocates for considering stochasticity in the development of management policies.

Stochasticity is commonly considered a source of uncertainty for management (Link et al., 2012). Adaptive management aims at accounting for this uncertainty in the decision-making process (Walters, 1986). Yet, although adaptive management is highly recommended and supported in the literature, only few examples of successful adaptive management plan have been implemented (Westgate et al., 2013). Given that the NDND model explores the possible futures of the natural system by accounting for the uncertainties about them, it can be used for testing possible management strategies in a management strategy evaluation framework (MSE, (Punt et al., 2016). MSEs aim at identifying the possible trade-off in performance of different management strategies through a simulation-based approach, while accounting for uncertainties. Usually, MSE are performed in single-species context (ICES, 2020). Yet, single-species approach does not account for biological interactions between species (e.g., predation). Using ecosystem models to perform MSE allows to account for species interactions and the direct effect between fisheries and the ecosystem (Perryman et al., 2021). The implementation of HCRs in the NDND model to estimate annual catches for fish trophospecies could possibly allow to test for multiple management strategies in a multi-species framework that accounts for species interactions and evaluate them to exclude non-relevant management strategies.

The NDND model, used in **Paper I** and **Paper II**, includes a harvesting module that allows to run various HCRs for individual trophospecies. In **Paper I**, we used the HCRs defined for cod and capelin to estimate annual catches of demersal fish and pelagic fish, respectively. Although, the implemented HCRs are simplifications of the real HCRs used for the management of the cod and capelin stocks, it is possible to define more complex HCRs and test for different long-term management strategies for fisheries that account for the stochastic variability of the ecosystem. Furthermore, recent development of management strategies advocate for ecosystem-based management and a shift from single-species management to multi-species management (e.g., Olsen et al., 2007; Moffitt et al., 2016). The NDND model allows to test for fisheries management strategies and their impact on the dynamics of all trophospecies of the food-web. A previous modelling study used a stochastic viability approach to identify strategies ensuring ecological conservation of natural resources and economical sustainability (Doyen et al., 2012). *Ibid* advocate for the use of stochastic viability for ecosystem-based management because it can deal with core element of ecosystem-based management (i.e., risk, precaution, and sustainability).

Nonetheless, such an approach to test management strategies would imply identifying the forecast horizon, i.e., the time horizon for which predictions are informative for decision

making (Petchey et al., 2015), of the NDND model. Anderson & Gillooly (2020) showed that species forecast horizon was dependent on the length of the generation time (i.e., the lifespan of individuals). The forecast horizon of species with short generation time was shorter. In the NDND model, the *inertia* parameter is related to the average lifespan of individual species (Mullon et al., 2009) and it was lower for short-lived species such as herbivorous zooplankton (lower *inertia* value indicates higher “biological” inertia for trophospecies). Thus, it is expected that the forecast horizon for these species should be shorter than the one of species with longer lifespans (e.g., marine mammals). Furthermore, as the NDND model simulates relatively unconstrained trajectories of the food-web, the forecast horizon is expected to be relatively short.

Deterministic food-web models, such as EwE and Atlantis, account for many ecological processes in hope of better representing the real food-web dynamics. Their complexity increased by adding parameters (Fulton, 2010) leading to more uncertainty in model predictions (Evans, 2012). The NDND model represents a shift in the way of constructing a food-web model. Instead of including many ecological processes increasing the model complexity, it accounts only for structural biological constraints (i.e., *satiation*, *inertia*, positive trophic flows, biomass over *refuge biomass*). These constraints define the range of possible trophic flow values that comply with them. This range of possible values is then explored in a stochastic manner, which implies that simulated trajectories can be highly variable. As one can consider deterministic food-web models too constrained to reproduce the variability patterns of natural systems, one can also consider that the NDND model is too weakly constrained. It means that the simulated variability presented in **Paper I** would include food-web configurations of the Barents Sea that are unrealistic. A possible development of the NDND model in the future could imply to further constrain the NDND simulations by including ecological processes that can affect trophodynamics of the Barents Sea food-web, such as species distribution overlap. However, one needs to be careful to not include ecological processes that would not affect the range of possible food-web configurations while significantly increasing the simulation time.

## 5.2 Trophic control in the Nordic Seas

### 5.2.1 Fluctuating trophic control in the Barents Sea

The results in **Paper I** show that trophic control is variable over time and fluctuates at interdecadal timescale in the Barents Sea for most trophic interactions. Yaragina & Dolgov



(2009) suggested a wasp-waist control where pelagic fish exerted bottom-up control on predators and top-down control on zooplankton, the latter being supported by statistical model outputs (Stige et al., 2014). Fluctuating trophic control in the Barents Sea was first suggested based on past observations over the time period 1970-2009 (Johannesen et al., 2012). **Paper I** shows that fluctuations in trophic control are to be expected in the Barents Sea food-web, and result from food-web stochastic dynamics. Fluctuating trophic control between cod and its prey has been described in the North Pacific ecosystem as well, but it was attributed to a rapid warming in 1970's (Litzow & Ciannelli, 2007) rather than stochastic trophic interactions. Rather than triggering shifts in trophic control, it is likely that increasing temperatures affect the timescale of trophic control fluctuations due to higher turnover rates in species biomass, but this needs to be tested.

### **5.2.2 Trophic control in the Norwegian Sea**

In **Paper IV**, the RCaN model was used to reconstruct past trajectories in a zooplankton multi-species (amphipods, krill, and copepods) context. Trophic control in the reconstructions support the hypothesis of a bottom-up driven Norwegian Sea pelagic food-web while it is in conflict with the top-down hypothesis, i.e., growth of predators' biomass was positively correlated to the trophic flows from their preys, and growth of prey biomass was not correlated to trophic flows to their predators. The performed sensitivity analysis on the model parametrization and the observed data time-series presented in the supplementary materials S5 of **Paper IV** shows that the conclusions from this study are relatively robust, but they conflict with past studies suggesting top-down control on zooplankton by herring in the Norwegian Sea (Olsen et al., 2007). This study estimated trophic control in a single prey-predator context, i.e., Norwegian spring-spawning herring and *Calanus finmarchicus*. The results in **Paper IV** advocate for the development of multi-species approaches to improve the assessment of key ecological properties of ecosystems, among which ecosystem models.

## **5.3 The combined effects of climate and fisheries on ecosystem stability**

### **5.3.1 Synergistic effect of temperature and fisheries**

A major result of **Paper II** is the synergism between temperature and fisheries, although the responses of stability to both drivers were relatively weak. Previous studies showed that harvested species displayed higher variability than non-harvested species (Hsieh et al., 2006). A more recent modelling study suggested that in an environmentally variable system, increased

fishing mortality led to higher species variability (Shelton & Mangel, 2011). The increased variability of harvested species is expected to result from the age-structure truncation of fish stocks by fisheries (Hsieh et al., 2006; Rouyer et al., 2012; Quetglas et al., 2013). In fact, three hypotheses were suggested to explain the changes in temporal variability of harvested fish stocks due to fisheries (Anderson et al., 2008). First, the variations in abundances can result from variations in fishing intensity (Jonzén et al., 2002). Second, age-truncated stocks may be more sensitive to environmental variations (Hsieh et al., 2006). Third, juvenescent populations are expected to be less stable due to differences in demographic parameters (Hsieh et al., 2005). Anderson et al. (2008) only found empirical evidence for the latter hypothesis. Given that trophospecies in the NDND model are not age-structured, the results presented in **Paper II** suggest that fisheries directly affect the stability of harvested species. This finding supports the first hypothesis rather than the two other ones. Nonetheless, the analysis in **Paper II**, also revealed a negative trend in species stability in response to temperature increase only for harvested species. This observation is in line with previous studies suggesting that fisheries increase the sensitivity of species dynamics to climate variability (Perry et al., 2010). Again, without affecting the age-structure that is not defined for trophospecies in the NDND model, this result suggest that harvesting amplifies the effect of climate change on species intrinsic variability. These results illustrate the need to account for both fisheries and climate change in decision-making for management. It advocates for the use of ecosystem-based management for fisheries to account for all the cumulative effects of anthropogenic drivers in management policies (Halpern et al., 2008b; Skern-Mauritzen et al., 2018).

### 5.3.2 Taylor's law

The results in **paper II**, show that temporal stability (the inverse of the coefficient of variation, i.e., the mean divided by the standard deviation) displayed weak median responses to combined variations of temperature and fishing mortality. There are the two possible explanations for the reduced response in stability to temperature and fishing mortality variations: (1) fisheries and temperature did not affect the mean biomass nor the variance, or (2) mean biomass and variance covary in such way that stability remains unchanged. Hypothesis (1) is not support by the results in **Paper II**, given that they showed an effect of temperature and fishing individual species biomass. Thus, the investigation of mean-variance scaling relationships (Cottingham et al., 2001) showed that the variance increases for higher mean biomass (Figure S6 and S7 in supplementary material **Paper II**). Such relationship corresponds to a Taylor's law, which relates the logarithm of variance to the logarithm of biomass linearly (Taylor, 1961). The slope

of the identified Taylor's law is close to 1 (Figure S6 and S7 in supplementary material **Paper II**) which indicates that mean biomass and variance covary in such way that stability remains unchanged, supporting hypothesis (2).

Despite covariation between mean biomass and variance, fisheries management policies aim at maintaining stable and sustainable fish stocks over time. In the case of stocks which have declined, management aims at restoring the state of the stocks by reaching identical biomass levels than historical ones. The Taylor's law identified between mean biomass and variance indicates that aiming for higher levels of biomass might not be sufficiently robust to define management policies, given that higher biomass induces higher biomass variability. It advocates for the use of ecological indicators that integrate biomasses to other key characteristics of the ecosystem functioning, to summarize the effect of stressors on the ecosystem dynamics (Coll et al., 2016). For instance, the IndiSeas working group has provided several studies focusing on identifying relevant ecological indicators of the effect of fisheries (e.g., Coll et al. 2016). They also assessed their sensitivity to environmental changes (e.g., Shin et al. 2018), and evaluated their performance at identifying threshold for ecosystem-based management (e.g., Fu et al., 2019).

### **5.3.3 Compensatory vs. additive fisheries**

In the RCaN model, available catch time-series are used to constrain reconstructions of past trajectories (Planque & Mullon, 2020). In other words, annual flows to fisheries are equal to the reported annual catches with an uncertainty of 10% (see supplementary materials S3 in **Paper IV**). Yet, the *inertia* constraint in the original RCaN model is not dependent on the amount of harvested biomass (Planque & Mullon, 2020). It means that the maximum annual biomass decrease is dependent on the state of the food-web and that fisheries does not affect it. Thus, as the harvested biomass is defined as a constraint in the model (i.e., the reconstruction must comply with the historical time-series of harvested biomass), trophic flow values must comply with the remaining biomass left after harvesting to respect the inertia constraint. In that sense, fishing mortality is fully compensatory in the RCaN model. Up to now, it is not possible to explore partial or full additivity of fishing mortality in the RCaN model.

In the NDND model, harvesting is explicitly modelled as a compensatory process such as the sum of losses due to predation and the losses due to fisheries cannot exceed the inertia constraint. Other ecosystem models consider fishing mortality as additive (Heymans et al., 2016; Audzijonyte et al., 2019). Whether fishing mortality is additive or compensatory is still

an ongoing debate in the literature (Froese et al., 2016; Walters & Christensen, 2019). But, it is expected that the degree of fishing mortality compensation is on a continuum between compensatory and additive (Myers & Quinn II, 2002; Péron, 2013). A simple exploration of the compensation degree of fishing mortality using NDND simulations revealed that low increase (25%) in additive fishing mortality triggers significant changes in species biomass (Figure 12, E. Sivel unpublished data). This exploration is only a preliminary result that requires further investigation to better assess the effect of case where fishing mortality is partially additive.

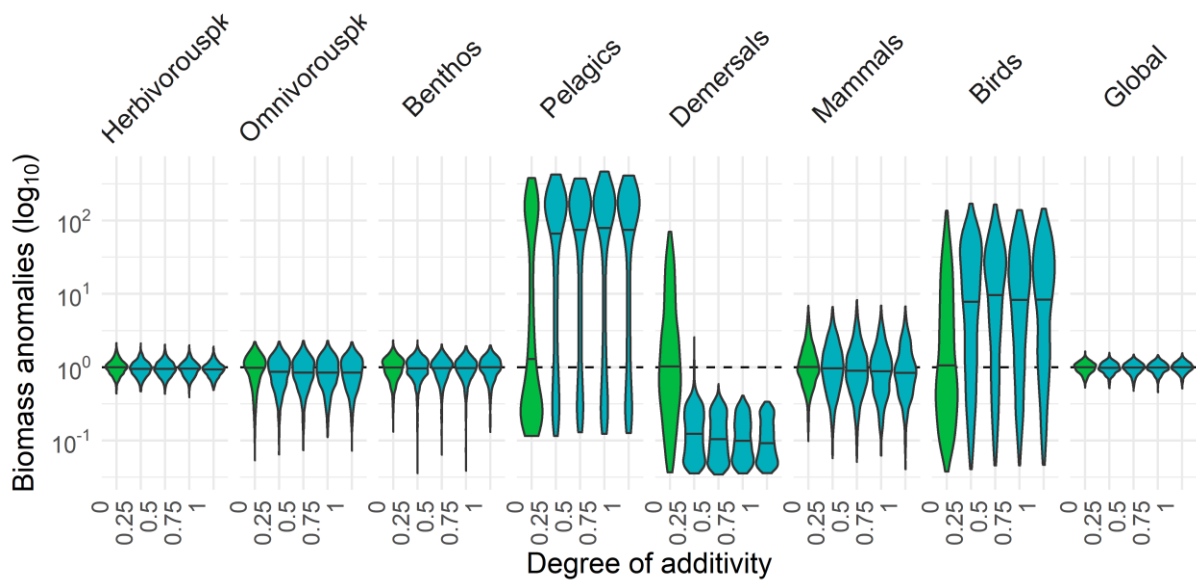


Figure 12. Distribution of mean biomass for different degrees of additivity of fisheries to other sources of mortality, i.e., predation. Violin plots corresponds to simulations with different values of additivity. The green violin, i.e., degree of additivity = 0, correspond to the configuration of fisheries compensation in both applications of the NDND model (**Paper I** and **Paper II**). Increased additivity of fisheries significantly affects the mean biomass of pelagic fish, demersal fish, and birds for relatively low degree of additivity (>25%). The observed pattern is similar to the pattern of the effect of fisheries on species biomass.

## 5.4 Model evaluation

### 5.4.1 OPE protocol

The protocol for reporting the evaluation of models regarding to a specific objective (OPE protocol, **Paper III**) is the result of a collaborative work between ecosystems modelers. The initial objective was to explore and identify suitable tools and methods to assess the performance of ecosystem models. Model evaluation is a time-consuming and complex work, and dedicated tools for reporting it were not available. The presented protocol in **Paper III** is the result from a collaborative work among a group of ecosystem modelers. Beside the 25 questions of the protocol, the discussions highlighted that the evaluation should always be

performed in relation to a specific objective. Ecosystem models are generic tools designed to address a multitude of scientific questions. Hence, instead of evaluating the global performance of ecosystem models, the performance of the model to answer the specific scientific question for which it was applied should be evaluated. The aim of developing such a protocol is to contribute to the development of a culture of reporting model evaluation by providing standardized tools to do so. As for the initial ODD protocol (Grimm et al., 2006), the current OPE protocol must be considered as in development. The development of the reporting culture and feedback from model users would allow to improve it and make it more adapted to the needs of model users.

The OPE protocol was applied in the different application of CaN models I present in this thesis. The major lesson learned from these applications is that model evaluation should be part of the study design. In the case of the applications of the OPE protocol to the NDND model (Supplementary material in **Paper III** and in **Paper II**), the protocol was prepared *a posteriori* to the model evaluation process. It showed that some elements of the evaluation could have been conducted differently if the protocol would have been filled *a priori* to the model evaluation process. For instance, in the case study in **Paper III**, the evaluation of the model application is done based on a visual inspection of the overlap between simulated and reconstructed data (see Figure 4). Yet, one could have defined a threshold value of the percentage of overlap between the range of simulated and reconstructed data. In that sense, the applications of the OPE protocol to the CaN model applications showed that the culture of evaluating model application is still poorly developed as evaluation is considered as a time-consuming and little rewarding process. Model evaluation is often the topic of separate studies (e.g., Hansen et al., 2019) or it is not presented. The applications of the OPE protocol pointed out that protocol could be used a tool to include a systematic thinking of model evaluation while defining the study design.

#### **5.4.2 Sensitivity analysis**

Input parameters of the CaN models can be derived from first principles or from observations. In both cases, estimated parameter values are associated with uncertainties that can vary in time and space. These uncertainties can significantly affect the model outputs. Thus, the robustness of presented conclusions needs to be assessed with respect to the uncertainty in input parameters in CaN models. The robustness of the RCaN model to input parameters was assessed and presented in the supplementary materials of **Paper IV**. The sensitivity analysis

showed that the conclusions on trophic control in the Norwegian Sea pelagic food-web are robust. Only extreme modifications of the initial model setup (e.g., an increase of 100% of harvesting on all fish species, decrease of primary production to 10 % of the baseline conditions) significantly altered the conclusions.

No sensitivity analysis was performed on the applications of the NDND model presented in this thesis (**Paper I, Paper II**). In **Paper II**, lower trophic levels are not affected by variations of fishing mortality. In the available literature based on observations, the absence of harvesting effect on lower trophic levels in the Barents is due to a decoupling between the zooplankton and capelin dynamics, which resulted from increased primary production (Dalpadado et al., 2020). This increase in primary production in the Barents ensued increasing sea-ice free areas due to higher temperatures (Dalpadado et al., 2020). However, modelling outputs suggested that increasing temperature had the opposite effect on primary production (Holt et al., 2016). Reconstructions of past food-web dynamics for the Barents Sea using the RCaN model with identical parametrization as the NDND model in the **Paper I** (Planque & Mullon, 2020) suggested that zooplankton dynamics could be reconstructed with substantially lower phytoplankton import (unpublished data), which is used as a proxy for primary production. Similarly, the sensitivity analysis on the RCaN model for the Norwegian Sea pelagic food-web presented in **Paper IV** suggests that, although reduced primary production lowers the biomass of individual groups, it did not affect the conclusions of the study. Thus, how changes in primary production can affect conclusions presented in **Paper I** and **Paper II** requires further investigations.

## 6 Conclusion

The present thesis addressed four research questions articulated around the use of Chance and Necessity modelling to investigate the drivers of variability in the Nordic Seas' food-webs. First, I aimed at exploring the possible stochastic variability of the Barents Sea food-web to define a reference for its variability and compare it to the observed variability over the last three decades. I found that the past variability of the Barents Sea food-web corresponded only to a fraction of its possible variability (**Paper I**). It shows that the Nordic Seas' food-web dynamics can be affected by other drivers than variations in anthropogenic stressors. Second, I explored trophic control in the Nordic Seas' food-webs. With the NDND model, I tested for persistent trophic control over time in the Barents Sea food-web. I found fluctuating trophic control at inter-decadal timescale is to be expected and that it emerged from internal dynamics

and stochastic variability of the Barents Sea food-web (**Paper I**). With the RCaN model, we reconstructed the past dynamics of the Norwegian Sea pelagic food-web and identified trophic control of zooplankton groups and planktivorous fish. The results support bottom-up control of planktivorous species by zooplankton, but not top-down control of copepods and krill (**Paper IV**). Third, I investigated the effects of climate change and fisheries on the stability of the Barents Sea food-web. The results suggested that temperature and fisheries have synergistic effects, where harvesting amplifies the negative effects of increasing temperature on species stability (**Paper II**). Fourth, I contributed to the elaboration of a standardized protocol to report the model evaluation process and applied it to the NDND model (**Paper III**).

The CaN models are novel food-web models that simulate a wide range of possible trajectories of the food-web. As such it should not be used as a predictive tool to project future trajectories of the ecosystem. Instead, the results I presented in this thesis illustrate that CaN models can be used a tool to explore the variability emerging from internal dynamics and stochastic events, and thus, provide relevant knowledge for adaptive management of the Nordic Seas natural resources. CaN models could be used to test management strategies, such as HCRs, or to define management goals, such as identifying the point of no return concerning increasing temperature, while accounting for internal dynamics and stochasticity. The results also advocate for the use of ecosystem-based approach for managing natural resources. We found that a whole-ecosystem approach using the RCaN model provide different conclusions than the historically single-species approaches used for management policies. Furthermore, the results showed that individual anthropogenic stressors should not be considered separately to assess their impact of the ecosystem dynamics.

## 7 References

- Alexander, M. A., Scott, J. D., Friedland, K. D., Mills, K. E., Nye, J. A., Pershing, A. J., & Thomas, A. C. (2018). Projected sea surface temperatures over the 21st century: Changes in the mean, variability and extremes for large marine ecosystem regions of Northern Oceans. *Elementa: Science of the Anthropocene*, 6, 9. <https://doi.org/10.1525/elementa.191>
- Allen, J. I., & Somerfield, P. J. (2009). A multivariate approach to model skill assessment. *Journal of Marine Systems*, 76(1), 83–94. <https://doi.org/10.1016/j.jmarsys.2008.05.009>
- Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., & Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature*, 452(7189), 835–839. <https://doi.org/10.1038/nature06851>
- Anderson, D. M., & Gillooly, J. F. (2020). Allometric scaling of Lyapunov exponents in chaotic populations. *Population Ecology*, 62(3), 364–369. <https://doi.org/10.1002/1438->

- Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Progress in Oceanography*, *136*, 60–70. <https://doi.org/10.1016/j.pocean.2015.05.002>
- Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., & Fulton, E. A. (2019). Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. *Methods in Ecology and Evolution*, *10*(10), 1814–1819. <https://doi.org/10.1111/2041-210X.13272>
- Bachiller, E., Skaret, G., Nøttestad, L., & Slotte, A. (2016). Feeding Ecology of Northeast Atlantic Mackerel, Norwegian Spring-Spawning Herring and Blue Whiting in the Norwegian Sea. *PLOS ONE*, *11*(2), e0149238. <https://doi.org/10.1371/journal.pone.0149238>
- Baranov, F. I. (1918). On the question of the biological basis of fisheries. *Izvestiya*, *1*, 81–128.
- Blindheim, J. (2004). Oceanography and climate. In *The Norwegian Sea Ecosystem* (H. R. Skjoldal, R. Sætre, A. Færnø, O. A. Misund, and I. Røttingen, pp. 65–96). Tapir Academic Press.
- Boettiger, C. (2018). From noise to knowledge: How randomness generates novel phenomena and reveals information. *Ecology Letters*, *21*(8), 1255–1267. <https://doi.org/10.1111/ele.13085>
- Branch, T. A. (2009). Differences in predicted catch composition between two widely used catch equation formulations. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(1), 126–132. <https://doi.org/10.1139/F08-196>
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771–1789. <https://doi.org/10.1890/03-9000>
- Bryndum-Buchholz, A., Tittensor, D. P., Blanchard, J. L., Cheung, W. W. L., Coll, M., Galbraith, E. D., Jennings, S., Maury, O., & Lotze, H. K. (2019). Twenty-first-century climate change impacts on marine animal biomass and ecosystem structure across ocean basins. *Global Change Biology*, *25*(2), 459–472. <https://doi.org/10.1111/gcb.14512>
- Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J. M., & Pelejero, C. (2011). Effects of climate change on Mediterranean marine ecosystems: The case of the Catalan Sea. *Climate Research*, *50*(1), 1–29. <https://doi.org/10.3354/cr01040>
- Cardinale, M., Svedäng, H., Bartolino, V., Maiorano, L., Casini, M., & Linderholm, H. (2012). Spatial and temporal depletion of haddock and pollack during the last century in the Kattegat-Skagerrak. *Journal of Applied Ichthyology*, *28*(2), 200–208. <https://doi.org/10.1111/j.1439-0426.2012.01937.x>
- Carozza, D. A., Bianchi, D., & Galbraith, E. D. (2019). Metabolic impacts of climate change on marine ecosystems: Implications for fish communities and fisheries. *Global Ecology and Biogeography*, *28*(2), 158–169. <https://doi.org/10.1111/geb.12832>
- Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling*, *172*(2), 109–139. <https://doi.org/10.1016/j.ecolmodel.2003.09.003>
- Christensen, V., Walters, C. J., & Pauly, D. (2005). *Ecopath with Ecosim: A User's Guide*.



University of British Columbia.

Coll, M., Shannon, L. J., Kleisner, K. M., Juan-Jordá, M. J., Bundy, A., Akoglu, A. G., Banaru, D., Boldt, J. L., Borges, M. F., Cook, A., Diallo, I., Fu, C., Fox, C. J., Gascuel, D., Gurney, L. J., Hattab, T., Heymans, S. J. J., Jouffre, D., Knight, B. R., ... Shin, Y.-J. (2016). Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. *Ecological Indicators*, *60*, 947–962. <https://doi.org/10.1016/j.ecolind.2015.08.048>

Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., & Hooten, M. B. (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs*, *88*(4), 526–542. <https://doi.org/10.1002/ecm.1314>

Cottingham, K. L., Brown, B. I., & Lennon, J. T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, *4*(1), 72–85. <https://doi.org/10.1046/j.1461-0248.2001.00189.x>

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315. <https://doi.org/10.1111/j.1461-0248.2008.01253.x>

Cury, P. M., Mullan, C., Garcia, S. M., & Shannon, L. J. (2005). Viability theory for an ecosystem approach to fisheries. *ICES Journal of Marine Science*, *62*(3), 577–584. <https://doi.org/10.1016/j.icesjms.2004.10.007>

Daewel, U., & Schrum, C. (2013). Simulating long-term dynamics of the coupled North Sea and Baltic Sea ecosystem with ECOSMO II: Model description and validation. *Journal of Marine Systems*, *119–120*, 30–49. <https://doi.org/10.1016/j.jmarsys.2013.03.008>

Dalpadado, P., Arrigo, K. R., van Dijken, G. L., Skjoldal, H. R., Bagøien, E., Dolgov, A. V., Prokopchuk, I. P., & Sperfeld, E. (2020). Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea. *Progress in Oceanography*, *185*, 102320. <https://doi.org/10.1016/j.pocean.2020.102320>

Donadi, S., Austin, Å. N., Bergström, U., Eriksson, B. K., Hansen, Joakim. P., Jacobson, P., Sundblad, G., van Regteren, M., & Eklöf, Johan. S. (2017). A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20170045. <https://doi.org/10.1098/rspb.2017.0045>

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science*, *4*(1), 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>

Doyen, L., Thébaud, O., Béné, C., Martinet, V., Gourguet, S., Bertignac, M., Fifas, S., & Blanchard, F. (2012). A stochastic viability approach to ecosystem-based fisheries management. *Ecological Economics*, *75*, 32–42. <https://doi.org/10.1016/j.ecolecon.2012.01.005>

Dragesund, O., Johannessen, A., & Ulltang, Ø. (1997). Variation in migration and abundance of norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia*, *82*(2), 97–105. <https://doi.org/10.1080/00364827.1997.10413643>

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci,

B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., ... Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, 31(21), 4773–4787. <https://doi.org/10.1016/j.cub.2021.08.062>

Eriksen, E., Skjoldal, H. R., Gjøsæter, H., & Primicerio, R. (2017). Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progress in Oceanography*, 151, 206–226. <https://doi.org/10.1016/j.pocean.2016.12.009>

Evans, K., Brown, J. N., Sen Gupta, A., Nicol, S. J., Hoyle, S., Matear, R., & Arrizabalaga, H. (2015). When 1+1 can be >2: Uncertainties compound when simulating climate, fisheries and marine ecosystems. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 312–322. <https://doi.org/10.1016/j.dsr2.2014.04.006>

Evans, M. R. (2012). Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), 181–190. <https://doi.org/10.1098/rstb.2011.0172>

Finney, B. P., Alheit, J., Emeis, K.-C., Field, D. B., Gutiérrez, D., & Struck, U. (2010). Paleoecological studies on variability in marine fish populations: A long-term perspective on the impacts of climatic change on marine ecosystems. *Journal of Marine Systems*, 79(3), 316–326. <https://doi.org/10.1016/j.jmarsys.2008.12.010>

Flynn, K. J., Speirs, D. C., Heath, M. R., & Mitra, A. (2021). Subtle Differences in the Representation of Consumer Dynamics Have Large Effects in Marine Food Web Models. *Frontiers in Marine Science*, 8, 1699. <https://doi.org/10.3389/fmars.2021.638892>

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5(7), 673–677. <https://doi.org/10.1038/nclimate2647>

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences*, 114(46), 12202–12207. <https://doi.org/10.1073/pnas.1706080114>

Frank, K. T. (2005). Trophic Cascades in a Formerly Cod-Dominated Ecosystem. *Science*, 308(5728), 1621–1623. <https://doi.org/10.1126/science.1113075>

Frank, K. T., Petrie, B., Leggett, W. C., & Boyce, D. G. (2016). Large scale, synchronous variability of marine fish populations driven by commercial exploitation. *Proceedings of the National Academy of Sciences of the United States of America*, 113(29), 8248–8253. <https://doi.org/10.1073/pnas.1602325113>

Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O. L. F., Demirel, N., Tsikliras, A. C., & Holt, S. J. (2016). A critique of the balanced harvesting approach to fishing. *ICES Journal of Marine Science*, 73(6), 1640–1650. <https://doi.org/10.1093/icesjms/fsv122>

Fu, C., Xu, Y., Bundy, A., Grüss, A., Coll, M., Heymans, J. J., Fulton, E. A., Shannon, L., Halouani, G., Velez, L., Akoglu, E., Lynam, C. P., & Shin, Y.-J. (2019). Making ecological indicators management ready: Assessing the specificity, sensitivity, and threshold response of ecological indicators. *Ecological Indicators*, 105, 16–28.

<https://doi.org/10.1016/j.ecolind.2019.05.055>

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, 81(1), 171–183. <https://doi.org/10.1016/j.jmarsys.2009.12.012>

Fulton, E. A., Smith, A. D. M., & Johnson, C. R. (2003). Mortality and predation in ecosystem models: Is it important how these are expressed? *Ecological Modelling*, 169(1), 157–178. [https://doi.org/10.1016/S0304-3800\(03\)00268-0](https://doi.org/10.1016/S0304-3800(03)00268-0)

Fulton, E. A., Smith, A. D. M., & Johnson, C. R. (2004). Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. *Ecological Modelling*, 174(3), 267–307. <https://doi.org/10.1016/j.ecolmodel.2003.09.027>

Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A., & Rall, B. C. (2014). Ecological stability in response to warming. *Nature Climate Change*, 4(3), 206–210. <https://doi.org/10.1038/nclimate2134>

Garcia, T., Planque, B., Arneberg, P., Bogstad, B., Skagseth, Ø., & Tiedemann, M. (2021). An appraisal of the drivers of Norwegian spring-spawning herring (*Clupea harengus*) recruitment. *Fisheries Oceanography*, 30(2), 159–173. <https://doi.org/10.1111/fog.12510>

Gatti, G., Bianchi, C. N., Parravicini, V., Rovere, A., Peirano, A., Montefalcone, M., Massa, F., & Morri, C. (2015). Ecological Change, Sliding Baselines and the Importance of Historical Data: Lessons from Combining Observational and Quantitative Data on a Temperate Reef Over 70 Years. *PLOS ONE*, 10(2), e0118581. <https://doi.org/10.1371/journal.pone.0118581>

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of Size and Temperature on Metabolic Rate. *Science*, 293(5538), 2248–2251. <https://doi.org/10.1126/science.1061967>

Grimm, V., Augusiak, J., Focks, A., Frank, B. M., Gabsi, F., Johnston, A. S. A., Liu, C., Martin, B. T., Meli, M., Radchuk, V., Thorbek, P., & Railsback, S. F. (2014). Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. *Ecological Modelling*, 280, 129–139. <https://doi.org/10.1016/j.ecolmodel.2014.01.018>

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., ... DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198(1), 115–126. <https://doi.org/10.1016/j.ecolmodel.2006.04.023>

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, 221(23), 2760–2768. <https://doi.org/10.1016/j.ecolmodel.2010.08.019>

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A. S. A., Milles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohwäder, M.-S., Stillman, R. A., Thiele, J. C., & Ayllón, D. (2020). The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. *Journal of Artificial Societies and Social Simulation*, 23(2), 7. <https://doi.org/10.18564/jasss.4259>

Grman, E., Lau, J. A., Schoolmaster, D. R., & Gross, K. L. (2010). Mechanisms contributing

to stability in ecosystem function depend on the environmental context. *Ecology Letters*, *13*(11), 1400–1410. <https://doi.org/10.1111/j.1461-0248.2010.01533.x>

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008a). A Global Map of Human Impact on Marine Ecosystems. *Science*, *319*(5865), 948–952. <https://doi.org/10.1126/science.1149345>

Halpern, B. S., McLeod, K. L., Rosenberg, A. A., & Crowder, L. B. (2008b). Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean & Coastal Management*, *51*(3), 203–211. <https://doi.org/10.1016/j.ocecoaman.2007.08.002>

Hansen, C., Drinkwater, K. F., Jähkel, A., Fulton, E. A., Gorton, R., & Skern-Mauritzen, M. (2019). Sensitivity of the Norwegian and Barents Sea Atlantis end-to-end ecosystem model to parameter perturbations of key species. *PLOS ONE*, *14*(2), e0210419. <https://doi.org/10.1371/journal.pone.0210419>

Hastings, A., Abbott, K. C., Cuddington, K., Francis, T. B., Lai, Y.-C., Morozov, A., Petrovskii, S., & Zeeman, M. L. (2021). Effects of stochasticity on the length and behaviour of ecological transients. *Journal of The Royal Society Interface*, *18*(180), 20210257. <https://doi.org/10.1098/rsif.2021.0257>

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., & Genner, M. J. (2020). Climate Change Drives Poleward Increases and Equatorward Declines in Marine Species. *Current Biology*, *30*(8), 1572–1577. <https://doi.org/10.1016/j.cub.2020.02.043>

Hervann, P.-Y., & Gascuel, D. (2020). Exploring the impacts of fishing and environment on the Celtic Sea ecosystem since 1950. *Fisheries Research*, *225*, 105472. <https://doi.org/10.1016/j.fishres.2019.105472>

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*, *331*, 173–184. <https://doi.org/10.1016/j.ecolmodel.2015.12.007>

Hipsey, M. R., Gal, G., Arhonditsis, G. B., Carey, C. C., Elliott, J. A., Frassl, M. A., Janse, J. H., de Mora, L., & Robson, B. J. (2020). A system of metrics for the assessment and improvement of aquatic ecosystem models. *Environmental Modelling & Software*, *128*, 104697. <https://doi.org/10.1016/j.envsoft.2020.104697>

Hjermann, D. Ø., Bogstad, B., Dingsør, G. E., Gjøsæter, H., Ottersen, G., Eikeset, A. M., & Stenseth, N. C. (2010). Trophic interactions affecting a key ecosystem component: A multistage analysis of the recruitment of the Barents Sea capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(9), 1363–1375. <https://doi.org/10.1139/F10-064>

Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. (2004). Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proceedings of the National Academy of Sciences*, *101*(32), 11679–11684. <https://doi.org/10.1073/pnas.0402904101>

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The Impact of Climate Change on the World's Marine Ecosystems. *Science*, *328*(5985), 1523–1528. <https://doi.org/10.1126/science.1189930>

Holt, J., Schrum, C., Cannaby, H., Daewel, U., Allen, I., Artioli, Y., Bopp, L., Butenschon, M., Fach, B. A., Harle, J., Pushpadas, D., Salihoglu, B., & Wakelin, S. (2016). Potential impacts of climate change on the primary production of regional seas: A comparative analysis of five European seas. *Progress in Oceanography*, 140, 91–115. <https://doi.org/10.1016/j.pocean.2015.11.004>

Hop, H., & Gjørseter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*, 9(9), 878–894. <https://doi.org/10.1080/17451000.2013.775458>

Hsieh, C., Glaser, S. M., Lucas, A. J., & Sugihara, G. (2005). Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature*, 435(7040), 336–340. <https://doi.org/10.1038/nature03553>

Hsieh, C., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., & Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature*, 443(7113), 859–862. <https://doi.org/10.1038/nature05232>

Huse, G., Holst, J. C., Utne, K., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., Fenchel, T., & Uiblein, F. (2012). Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea – results of the INFERNO project. *Marine Biology Research*, 8(5–6), 415–419. <https://doi.org/10.1080/17451000.2011.653372>

ICES. (2020). The third Workshop on Guidelines for Management Strategy Evaluations (WKGME3). *ICES Scientific Reports*, 2(116), 112 pp. <https://doi.org/doi.org/10.17895/ices.pub.7627>

ICES. (2021a). Herring (*Clupea harengus*) in subareas 1, 2, and 5, and in divisions 4.a and 14.a, Norwegian spring-spawning herring (Northeast Atlantic and Arctic Ocean). *Report of the ICES Advisory Committee, 2021*. <https://doi.org/10.17895/ices.advice.7765>.

ICES. (2021b). Working Group on the Integrated Assessments of the Barents Sea (WGIBAR). *ICES Scientific Reports*, 3(77), 236 pp. <https://doi.org/10.17895/ICES.PUB.8241>

ICES. (2021c). Working Group on the Integrated Assessments of the Norwegian Sea (WGINOR; outputs from 2020 meeting). *ICES Scientific Reports*, 3(35), 114 pp. <https://doi.org/10.17895/ICES.PUB.8021>

Jarre, A., Hutchings, L., Kirkman, S. P., Kreiner, A., Tchupalanga, P. C. M., Kainge, P., Uanivi, U., van der Plas, A. K., Blamey, L. K., Coetzee, J. C., Lamont, T., Samaai, T., Verheye, H. M., Yemane, D. G., Axelsen, B. E., Ostrowski, M., Stenevik, E. K., & Loeng, H. (2015). Synthesis: Climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fisheries Oceanography*, 24(S1), 122–149. <https://doi.org/10.1111/fog.12086>

Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjørseter, H., Knutsen, T., Skern-Mauritzen, M., & Stiansen, J. E. (2012). Changes in Barents Sea ecosystem state, 1970–2009: Climate fluctuations, human impact, and trophic interactions. *ICES Journal of Marine Science*, 69(5), 880–889. <https://doi.org/10.1093/icesjms/fss046>

Jonzén, N., Ripa, J., & Lundberg, P. (2002). A Theory of Stochastic Harvesting in Stochastic Environments. *The American Naturalist*, 159(5), 427–437. <https://doi.org/10.1086/339456>

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande,

- B., Gårdmark, A. G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., & Rijnsdorp, A. D. (2007). Ecology: Managing Evolving Fish Stocks. *Science*. <https://doi.org/10.1126/science.1148089>
- Kearney, K. A., Stock, C., Aydin, K., & Sarmiento, J. L. (2012). Coupling planktonic ecosystem and fisheries food web models for a pelagic ecosystem: Description and validation for the subarctic Pacific. *Ecological Modelling*, 237–238, 43–62. <https://doi.org/10.1016/j.ecolmodel.2012.04.006>
- Kleisner, K. M., Fogarty, M. J., McGee, S., Hare, J. A., Moret, S., Perretti, C. T., & Saba, V. S. (2017). Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography*, 153, 24–36. <https://doi.org/10.1016/j.pocean.2017.04.001>
- Koen-Alonso, M., Lindstrøm, U., & Cuff, A. (2021). Comparative Modeling of Cod-Capelin Dynamics in the Newfoundland-Labrador Shelves and Barents Sea Ecosystems. *Frontiers in Marine Science*, 8, 139. <https://doi.org/10.3389/fmars.2021.579946>
- Koen-Alonso, M., & Yodzis, P. (2005). Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(7), 1490–1512. <https://doi.org/10.1139/f05-087>
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151546. <https://doi.org/10.1098/rspb.2015.1546>
- Lande, R. (1993). Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *The American Naturalist*, 142(6), 911–927. <https://doi.org/10.1086/285580>
- Landres, P. B., Morgan, P., & Swanson, F. J. (1999). Overview of the Use of Natural Variability Concepts in Managing Ecological Systems. *Ecological Applications*, 9(4), 1179–1188. [https://doi.org/10.1890/1051-0761\(1999\)009\[1179:OOTUON\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2)
- Langangen, Ø., Ohlberger, J., Stige, L. C., Durant, J. M., Ravagnan, E., Stenseth, N. C., & Hjermann, D. Ø. (2017). Cascading effects of mass mortality events in Arctic marine communities. *Global Change Biology*, 23(1), 283–292. <https://doi.org/10.1111/gcb.13344>
- Langøy, H., Nøttestad, L., Skaret, G., Broms, C., & Fernö, A. (2012). Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Marine Biology Research*, 8(5–6), 442–460. <https://doi.org/10.1080/17451000.2011.642803>
- Lawton, J. H. (1988). More time means more variation. *Nature*, 334(6183), 563–563. <https://doi.org/10.1038/334563a0>
- Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.-M., Hare, S. R., Ottersen, G., Perry, R. I., Roy, C., Lingen, C. D. van der, & Werner, F. (2006). Climate Variability, Fish, and Fisheries. *Journal of Climate*, 19(20), 5009–5030. <https://doi.org/10.1175/JCLI3898.1>

- Levin, S. A. (1998). Ecosystems and the Biosphere as Complex Adaptive Systems. *Ecosystems*, 1(5), 431–436. <https://doi.org/10.1007/s100219900037>
- Levin, S. A. (2005). Self-organization and the emergence of complexity in ecological systems. *Bioscience*, 55(12), 1075–1079. [https://doi.org/10.1641/0006-3568\(2005\)055\[1075:SATEOC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[1075:SATEOC]2.0.CO;2)
- Levin, S. A., Xepapadeas, T., Crépin, A.-S., Norberg, J., Zeeuw, A. de, Folke, C., Hughes, T., Arrow, K., Barrett, S., Daily, G., Ehrlich, P., Kautsky, N., Mäler, K.-G., Polasky, S., Troell, M., Vincent, J. R., & Walker, B. (2013). Social-ecological systems as complex adaptive systems: Modeling and policy implications. *Environment and Development Economics*, 18(2), 111–132. <https://doi.org/10.1017/S1355770X12000460>
- Lilly, G. R., Nakken, O., & Bratley, J. (2013). A review of the contributions of fisheries and climate variability to contrasting dynamics in two Arcto-boreal Atlantic cod (*Gadus morhua*) stocks: Persistent high productivity in the Barents Sea and collapse on the Newfoundland and Labrador Shelf. *Progress in Oceanography*, 114, 106–125. <https://doi.org/10.1016/j.pocean.2013.05.008>
- Lindstrøm, U., Planque, B., & Subbey, S. (2017). Multiple Patterns of Food Web Dynamics Revealed by a Minimal Non-deterministic Model. *Ecosystems*, 20(1), 163–182. <https://doi.org/10.1007/s10021-016-0022-y>
- Lindstrøm, U., Smout, S., Howell, D., & Bogstad, B. (2009). Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(21), 2068–2079. <https://doi.org/10.1016/j.dsr2.2008.11.017>
- Link, J. S., Ihde, T. F., Harvey, C. J., Gaichas, S. K., Field, J. C., Brodziak, J. K. T., Townsend, H. M., & Peterman, R. M. (2012). Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management. *Progress in Oceanography*, 102, 102–114. <https://doi.org/10.1016/j.pocean.2012.03.008>
- Litzow, M. A., & Ciannelli, L. (2007). Oscillating trophic control induces community reorganization in a marine ecosystem. *Ecology Letters*, 10(12), 1124–1134. <https://doi.org/10.1111/j.1461-0248.2007.01111.x>
- Loeng, H., & Drinkwater, K. (2007). An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(23), 2478–2500. <https://doi.org/10.1016/j.dsr2.2007.08.013>
- Longhurst, A. R. (2010). *Mismanagement of marine fisheries*. Cambridge University Press.
- Loreau, M., & de Mazancourt, C. (2008). Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. *The American Naturalist*, 172(2), E48–E66. <https://doi.org/10.1086/589746>
- Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J. L., Bopp, L., Büchner, M., Bulman, C. M., Carozza, D. A., Christensen, V., Coll, M., Dunne, J. P., Fulton, E. A., Jennings, S., ... Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences*, 116(26), 12907–12912. <https://doi.org/10.1073/pnas.1900194116>

- Lotze, H. K., & Worm, B. (2009). Historical baselines for large marine animals. *Trends in Ecology & Evolution*, 24(5), 254–262. <https://doi.org/10.1016/j.tree.2008.12.004>
- McClenachan, L., Ferretti, F., & Baum, J. K. (2012). From archives to conservation: Why historical data are needed to set baselines for marine animals and ecosystems. *Conservation Letters*, 5(5), 349–359. <https://doi.org/10.1111/j.1755-263X.2012.00253.x>
- McKechnie, I., Lepofsky, D., Moss, M. L., Butler, V. L., Orchard, T. J., Coupland, G., Foster, F., Caldwell, M., & Lertzman, K. (2014). Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. *Proceedings of the National Academy of Sciences*, 111(9), E807–E816. <https://doi.org/10.1073/pnas.1316072111>
- Melle, W., Ellertsen, B., & Skjoldal, H. R. (2004). Zooplankton: The link to higher trophic levels. In *The Norwegian Sea ecosystem* (H. R. Skjoldal, R. Sætre, A. Færnø, O. A. Misund, and I. Røttingen, pp. 137–202). Tapir Academic Press.
- Misund, O. A., Vilhjálmsson, H., Jákupsstovu, S. H. í, Røttingen, I., Belikov, S., Asthorsson, O., Blindheim, J., Jónsson, J., Krysov, A., Malmberg, S. A., & Sveinbjórsson, S. (1998). Distribution, migration and abundance of norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian sea as recorded by coordinated surveys in spring and summer 1996. *Sarsia*, 83(2), 117–127. <https://doi.org/10.1080/00364827.1998.10413677>
- Moffitt, E. A., Punt, A. E., Holsman, K., Aydin, K. Y., Ianelli, J. N., & Ortiz, I. (2016). Moving towards ecosystem-based fisheries management: Options for parameterizing multi-species biological reference points. *Deep Sea Research Part II: Topical Studies in Oceanography*, 134, 350–359. <https://doi.org/10.1016/j.dsr2.2015.08.002>
- Möllmann, C., & Diekmann, R. (2012). Marine Ecosystem Regime Shifts Induced by Climate and Overfishing. In *Advances in Ecological Research* (Vol. 47, pp. 303–347). Elsevier. <https://doi.org/10.1016/B978-0-12-398315-2.00004-1>
- Möllmann, C., Folke, C., Edwards, M., & Conversi, A. (2015). Marine regime shifts around the globe: Theory, drivers and impacts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1659), 20130260. <https://doi.org/10.1098/rstb.2013.0260>
- Morris, D. J., Speirs, D. C., Cameron, A. I., & Heath, M. R. (2014). Global sensitivity analysis of an end-to-end marine ecosystem model of the North Sea: Factors affecting the biomass of fish and benthos. *Ecological Modelling*, 273, 251–263. <https://doi.org/10.1016/j.ecolmodel.2013.11.019>
- Mousing, E., Planque, B., Arneberg, P., Bjørndal, V., Keulder-Stenevik, F., Liebig, P., & Langøy, H. (in prep.). *Weight vs occurrence for assessing major prey group diet composition for pelagic fish in the Norwegian Sea*.
- Mullon, C., Fréon, P., Cury, P., Shannon, L., & Roy, C. (2009). A minimal model of the variability of marine ecosystems. *Fish and Fisheries*, 10(2), 115–131. <https://doi.org/10.1111/j.1467-2979.2008.00296.x>
- Myers, R. A., & Quinn II, T. J. (2002). Estimating and testing non-additivity in fishing mortality: Implications for detecting a fisheries collapse. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(4), 597–601. <https://doi.org/10.1139/f02-048>



NAMMCO – North Atlantic Marine Mammal Commission (2021) Retrieved from <https://nammco.no/topics/catch-database/> on

Nichols, J. D., Kendall, W. L., & Boomer, G. S. (2019). Accumulating evidence in ecology: Once is not enough. *Ecology and Evolution*, 9(24), 13991–14004. <https://doi.org/10.1002/ece3.5836>

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., Müller-Karulis, B., Neumann, T., & Meier, M. (2013). Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Global Change Biology*, 19(11), 3327–3342. <https://doi.org/10.1111/gcb.12309>

Nye, J. A., Gamble, R. J., & Link, J. S. (2013). The relative impact of warming and removing top predators on the Northeast US large marine biotic community. *Ecological Modelling*, 264, 157–168. <https://doi.org/10.1016/j.ecolmodel.2012.08.019>

O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, 104(4), 1266–1271. <https://doi.org/10.1073/pnas.0603422104>

Okamoto, D. K., Schmitt, R. J., & Holbrook, S. J. (2016). Stochastic density effects on adult fish survival and implications for population fluctuations. *Ecology Letters*, 19(2), 153–162. <https://doi.org/10.1111/ele.12547>

Olafsdottir, A. H., Slotte, A., Jacobsen, J. A., Oskarsson, G. J., Utne, K. R., & Nøttestad, L. (2016). Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: Effects of mackerel stock size and herring (*Clupea harengus*) stock size. *ICES Journal of Marine Science*, 73(4), 1255–1265. <https://doi.org/10.1093/icesjms/fsv142>

Olsen, E. M., Melle, W., Kaartvedt, S., Holst, J. C., & Mork, K. A. (2007). Spatially structured interactions between a migratory pelagic predator, the Norwegian spring-spawning herring *Clupea harengus* L., and its zooplankton prey. *Journal of Fish Biology*, 70(3), 799–815. <https://doi.org/10.1111/j.1095-8649.2007.01342.x>

Onarheim, I. H., & Ártun, M. (2017). Toward an ice-free Barents Sea. *Geophysical Research Letters*, 44(16), 8387–8395. <https://doi.org/10.1002/2017GL074304>

Onarheim, I. H., Eldevik, T., Smedsrud, L. H., & Stroeve, J. C. (2018). Seasonal and Regional Manifestation of Arctic Sea Ice Loss. *Journal of Climate*, 31(12), 4917–4932. <https://doi.org/10.1175/JCLI-D-17-0427.1>

Ortega-Cisneros, K., Cochrane, K. L., Fulton, E. A., Gorton, R., & Popova, E. (2018). Evaluating the effects of climate change in the southern Benguela upwelling system using the Atlantis modelling framework. *Fisheries Oceanography*, 27(5), 489–503. <https://doi.org/10.1111/fog.12268>

Ortuño Crespo, G., & Dunn, D. C. (2017). A review of the impacts of fisheries on open-ocean ecosystems. *ICES Journal of Marine Science*, 74(9), 2283–2297. <https://doi.org/10.1093/icesjms/fsx084>

Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P. E., Nascimento, M. C., Blanchet, M.-

A., Ellingsen, I. H., Jørgensen, L. L., & Blanchet, H. (2021). Overexploitation, Recovery, and Warming of the Barents Sea Ecosystem During 1950–2013. *Frontiers in Marine Science*, 8, 1291. <https://doi.org/10.3389/fmars.2021.732637>

Péron, G. (2013). Compensation and additivity of anthropogenic mortality: Life-history effects and review of methods. *Journal of Animal Ecology*, 82(2), 408–417. <https://doi.org/10.1111/1365-2656.12014>

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., & Planque, B. (2010). Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *Journal of Marine Systems*, 79(3), 427–435. <https://doi.org/10.1016/j.jmarsys.2008.12.017>

Perryman, H. A., Hansen, C., Howell, D., & Olsen, E. M. (2021). A Review of Applications Evaluating Fisheries Management Scenarios through Marine Ecosystem Models. *Reviews in Fisheries Science & Aquaculture*, 29(4), 800–835. <https://doi.org/10.1080/23308249.2021.1884642>

Petchey, O. L., Pontarp, M., Massie, T. M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G. M., Altermatt, F., Matthews, B., Levine, J. M., Childs, D. Z., McGill, B. J., Schaeppman, M. E., Schmid, B., Spaak, P., Beckerman, A. P., Pennekamp, F., & Pearse, I. S. (2015). The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters*, 18(7), 597–611. <https://doi.org/10.1111/ele.12443>

Piggott, J. J., Townsend, C. R., & Matthaei, C. D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, 5(7), 1538–1547. <https://doi.org/10.1002/ece3.1465>

Pimm, S. L., & Redfearn, A. (1988). The variability of population densities. *Nature*, 334(6183), 613–614. <https://doi.org/10.1038/334613a0>

Planque, B., & Arneberg, P. (2018). Principal component analyses for integrated ecosystem assessments may primarily reflect methodological artefacts. *ICES Journal of Marine Science*, 75(3), 1021–1028. <https://doi.org/10.1093/icesjms/fsx223>

Planque, B., Lindstrøm, U., & Subbey, S. (2014). Non-Deterministic Modelling of Food-Web Dynamics. *PLoS ONE*, 9(10), e108243. <https://doi.org/10.1371/journal.pone.0108243>

Planque, B., & Mullon, C. (2020). Modelling chance and necessity in natural systems. *ICES Journal of Marine Science*, 77(4), 1573–1588. <https://doi.org/10.1093/icesjms/fsz173>

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), 919–925. <https://doi.org/10.1038/nclimate1958>

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman, D. S., & Sydeman, W. J. (2016). Responses of Marine Organisms to Climate Change across Oceans. *Frontiers in Marine Science*, 3. <https://doi.org/10.3389/fmars.2016.00062>

Polovina, J. J. (1984). Model of a coral reef ecosystem. *Coral Reefs*, 3(1), 1–11.

<https://doi.org/10.1007/BF00306135>

Poulsen, B. (2010). The variability of fisheries and fish populations prior to industrialized fishing: An appraisal of the historical evidence. *Journal of Marine Systems*, 79(3), 327–332. <https://doi.org/10.1016/j.jmarsys.2008.12.011>

Powers, S. M., & Hampton, S. E. (2019). Open science, reproducibility, and transparency in ecology. *Ecological Applications*, 29(1), e01822. <https://doi.org/10.1002/eap.1822>

Prokopchuk, I., & Sentyabov, E. (2006). Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES Journal of Marine Science*, 63(1), 117–127. <https://doi.org/10.1016/j.icesjms.2005.08.005>

Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., & Haddon, M. (2016). Management strategy evaluation: Best practices. *Fish and Fisheries*, 17(2), 303–334. <https://doi.org/10.1111/faf.12104>

Quetglas, A., Ordines, F., Hidalgo, M., Monserrat, S., Ruiz, S., Amores, Á., Moranta, J., & Massutí, E. (2013). Synchronous combined effects of fishing and climate within a demersal community. *ICES Journal of Marine Science*, 70(2), 319–328. <https://doi.org/10.1093/icesjms/fss181>

Regan, H. M., Colyvan, M., & Burgman, M. A. (2002). A Taxonomy and Treatment of Uncertainty for Ecology and Conservation Biology. *Ecological Applications*, 12(2), 618–628. [https://doi.org/10.1890/1051-0761\(2002\)012\[0618:ATATOU\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0618:ATATOU]2.0.CO;2)

Rouyer, T., Sadykov, A., Ohlberger, J., & Stenseth, N. C. (2012). Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecology Letters*, 15(7), 658–665. <https://doi.org/10.1111/j.1461-0248.2012.01781.x>

Seabra, R., Wethey, D. S., Santos, A. M., & Lima, F. P. (2015). Understanding complex biogeographic responses to climate change. *Scientific Reports*, 5(1), 12930. <https://doi.org/10.1038/srep12930>

Sears, R., & Perrin, W. F. (2018). Blue Whale: *Balaenoptera musculus*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals (Third Edition)* (pp. 110–114). Academic Press. <https://doi.org/10.1016/B978-0-12-804327-1.00070-4>

Shannon, L. J., Coll, M., Yemane, D., Jouffre, D., Neira, S., Bertrand, A., Diaz, E., & Shin, Y.-J. (2010). Comparing data-based indicators across upwelling and comparable systems for communicating ecosystem states and trends. *ICES Journal of Marine Science*, 67(4), 807–832. <https://doi.org/10.1093/icesjms/fsp270>

Shelton, A. O., & Mangel, M. (2011). Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences*, 108(17), 7075–7080. <https://doi.org/10.1073/pnas.1100334108>

Shin, Y.-J., & Cury, P. (2001). Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquatic Living Resources*, 14(2), 65–80. [https://doi.org/10.1016/S0990-7440\(01\)01106-8](https://doi.org/10.1016/S0990-7440(01)01106-8)

Shin, Y.-J., Houle, J. E., Akoglu, E., Blanchard, J. L., Bundy, A., Coll, M., Demarcq, H., Fu, C., Fulton, E. A., Heymans, J. J., Salihoglu, B., Shannon, L., Sporcic, M., & Velez, L. (2018).

The specificity of marine ecological indicators to fishing in the face of environmental change: A multi-model evaluation. *Ecological Indicators*, 89, 317–326. <https://doi.org/10.1016/j.ecolind.2018.01.010>

Shoemaker, L. G., Sullivan, L. L., Donohue, I., Cabral, J. S., Williams, R. J., Mayfield, M. M., Chase, J. M., Chu, C., Harpole, W. S., Huth, A., HilleRisLambers, J., James, A. R. M., Kraft, N. J. B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., ... Abbott, K. C. (2020). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, 101(2), e02922. <https://doi.org/10.1002/ecy.2922>

Skern-Mauritzen, M., Olsen, E., & Huse, G. (2018). Opportunities for advancing ecosystem-based management in a rapidly changing, high latitude ecosystem. *ICES Journal of Marine Science*, 75(7), 2425–2433. <https://doi.org/10.1093/icesjms/fsy150>

Stige, L. C., Dalpadado, P., Orlova, E., Boulay, A.-C., Durant, J. M., Ottersen, G., & Stenseth, N. C. (2014). Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in the Barents Sea. *Progress in Oceanography*, 120, 243–253. <https://doi.org/10.1016/j.pocean.2013.09.006>

Stige, L. C., Eriksen, E., Dalpadado, P., & Ono, K. (2019). Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. *ICES Journal of Marine Science*, 76(Supplement\_1), i24–i36. <https://doi.org/10.1093/icesjms/fsz063>

Stow, C. A., Jolliff, J., McGillicuddy, D. J., Doney, S. C., Allen, J. I., Friedrichs, M. A. M., Rose, K. A., & Wallhead, P. (2009). Skill assessment for coupled biological/physical models of marine systems. *Journal of Marine Systems*, 76(1), 4–15. <https://doi.org/10.1016/j.jmarsys.2008.03.011>

Szabó, P. (2010). Why history matters in ecology: An interdisciplinary perspective. *Environmental Conservation*, 37(4), 380–387. <https://doi.org/10.1017/S0376892910000718>

Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A., & Hilborn, R. (2015). Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, 16(4), 633–648. <https://doi.org/10.1111/faf.12083>

Taylor, L. R. (1961). Aggregation, Variance and the Mean. *Nature*, 189(4766), 732–735. <https://doi.org/10.1038/189732a0>

Timmermans, M.-L., & Ladd, C. (2019). Sea Surface Temperature. In *Arctic Report Card 2019* (J. Richter-Menge, M. L. Druckenmiller, and M. Jeffries, Eds.). <http://www.arctic.noaa.gov/Report-Card>

Toresen, R., & Østvedt, O. J. (2000). Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries*, 1(3), 231–256. <https://doi.org/10.1111/j.1467-2979.2000.00022.x>

Travers, M., Shin, Y.-J., Shannon, L., & Cury, P. (2011). Simulating and testing the sensitivity of ecosystem-based indicators to fishing in the southern Benguela ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*. <https://doi.org/10.1139/f06-003>

- Trenkel, V. M., Huse, G., MacKenzie, Brian R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñi, N., Grégoire, F., Hátún, H., Jansen, T., Jacobsen, J. A., Lehodey, P., Lutcavage, M., Mariani, P., Melvin, G. D., Neilson, J. D., Nøttestad, L., Óskarsson, G. J., Payne, M. R., ... Speirs, D. C. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Progress in Oceanography*, *129*, 219–243. <https://doi.org/10.1016/j.pocean.2014.04.030>
- Utne, K. R., Huse, G., Ottersen, G., Refsgaard, J. C., Zabavnikov, V., Jacobsen, J. A., Óskarsson, G. J., & Nøttestad, L. (2012). Horizontal distribution and overlap of planktivorous fish stocks in the Norwegian Sea during summers 1995–2006. *Marine Biology Research*, *8*(5–6), 420–441. <https://doi.org/10.1080/17451000.2011.640937>
- Uusi-Heikkilä, S., Perälä, T., & Kuparinen, A. (2021). Fishing triggers trophic cascade in terms of variation, not abundance in an allometric trophic network model. *Canadian Journal of Fisheries and Aquatic Sciences*. <https://doi.org/10.1139/cjfas-2021-0146>
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., & Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change*, *109*(1), 5. <https://doi.org/10.1007/s10584-011-0148-z>
- Vasseur, D. A., & McCann, K. S. (2005). A Mechanistic Approach for Modeling Temperature-Dependent Consumer-Resource Dynamics. *The American Naturalist*, *166*(2), 184–198. <https://doi.org/10.1086/431285>
- Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., Kraft, N. J. B., Letaw, A. D., Macdonald, A. A. M., Maclean, J. E., Myers-Smith, I. H., Norris, A. R., & Xue, X. (2014). Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, *123*(12), 1420–1430. <https://doi.org/10.1111/oik.01493>
- Wakelin, S. L., Holt, J., Blackford, J. C., Allen, J. I., Butenschön, M., & Artioli, Y. (2012). Modeling the carbon fluxes of the northwest European continental shelf: Validation and budgets. *Journal of Geophysical Research: Oceans*, *117*(C5), C05020. <https://doi.org/10.1029/2011JC007402>
- Walters, C., & Christensen, V. (2019). Effect of non-additivity in mortality rates on predictions of potential yield of forage fishes. *Ecological Modelling*, *410*, 108776. <https://doi.org/10.1016/j.ecolmodel.2019.108776>
- Walters, C. J. (1986). *Adaptive management of renewable resources* (Wayne M. Getz). Macmillan Publishers Ltd.
- Walters, C. J., Christensen, V., & Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, *7*(2), 139–172. <https://doi.org/10.1023/A:1018479526149>
- Walters, C. J., Pauly, D., & Christensen, V. (1999). Ecospace: Prediction of Mesoscale Spatial Patterns in Trophic Relationships of Exploited Ecosystems, with Emphasis on the Impacts of Marine Protected Areas. *Ecosystems*, *2*(6), 539–554. <https://doi.org/10.1007/s100219900101>
- Ward, P., & Myers, R. A. (2005). Shifts in Open-Ocean Fish Communities Coinciding with the Commencement of Commercial Fishing. *Ecology*, *86*(4), 835–847. <https://doi.org/10.1890/03-0746>

Westgate, M. J., Likens, G. E., & Lindenmayer, D. B. (2013). Adaptive management of biological systems: A review. *Biological Conservation*, *158*, 128–139. <https://doi.org/10.1016/j.biocon.2012.08.016>

Yaragina, N. A., & Dolgov, A. V. (2009). Ecosystem structure and resilience—A comparison between the Norwegian and the Barents Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *56*(21–22), 2141–2153. <https://doi.org/10.1016/j.dsr2.2008.11.025>

Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, *139*(6), 1151–1175. <https://doi.org/10.1086/285380>

# Paper I

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## MULTIPLE CONFIGURATIONS AND FLUCTUATING TROPHIC CONTROL IN THE BARENTS SEA FOOD-WEB

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## RESEARCH ARTICLE

# Multiple configurations and fluctuating trophic control in the Barents Sea food-web

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## Abstract

The Barents Sea is a subarctic shelf sea which has experienced major changes during the past decades. From ecological time-series, three different food-web configurations, reflecting successive shifts of dominance of pelagic fish, demersal fish, and zooplankton, as well as varying trophic control have been identified in the last decades. This covers a relatively short time-period as available ecological time-series are often relatively short. As we lack information for prior time-periods, we use a chance and necessity model to investigate if there are other possible configurations of the Barents Sea food-web than those observed in the ecological time-series, and if this food-web is characterized by a persistent trophic control. We perform food-web simulations using the Non-Deterministic Network Dynamic model (NDND) for the Barents Sea, identify food-web configurations and compare those to historical reconstructions of food-web dynamics. Biomass configurations fall into four major types and three trophic pathways. Reconstructed data match one of the major biomass configurations but is characterized by a different trophic pathway than most of the simulated configurations. The simulated biomass displays fluctuations between bottom-up and top-down trophic control over time rather than persistent trophic control. Our results show that the configurations we have reconstructed are strongly overlapping with our simulated configurations, though they represent only a subset of the possible configurations of the Barents Sea food-web.

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## Introduction

Marine ecosystems have complex structures, functions, and dynamics. They include a diversity of species, comprise various habitats, and often display non-linear feedback mechanisms [1–3]. Interactions emerging at higher levels of the system can result from interactions and processes occurring at lower levels and vice versa [1]. Marine ecosystems are dynamic and constantly undergo structural and functional changes [4–7], evolving through different states or “configurations”. A number of ecological studies focus on how external pressures may explain the differences between configurations of a same ecosystem at different time-periods [5,7,8]. However, changes in ecosystem configurations can also result from the internal dynamics emerging from its functioning or from external, stochastic events [9].

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The historical range of variability informs us on how an ecosystem varied in the past. It can be used as a reference for the variability of an ecosystem to improve the assessment and the prediction of future changes in its dynamics [10]. Available ecological time-series used to estimate the historical range of variability of marine ecosystems are often relatively short, typically less than 50 years [11,12]. Furthermore, ecological time-series are not available for all trophic groups (e.g. benthos, marine mammals, birds) and the lifespan of some species exceeds 50 years. Consequently, it is difficult to make inference about the past and future variability of marine ecosystems without making assumptions that can result in large uncertainties [11,13]. Yet, it is expected that ecosystem variability increases with the length of the study period [14,15], and that the baselines used for the assessment of fish abundances have shifted since 1950 [16,17]. To better anticipate possible changes in future marine ecosystem dynamics, one must explore the variability of the system dynamics on a timescale longer than the 50 years for which data are available. In some instances, these dynamics can be reconstructed using paleontological or archeological data (e.g. [18]). An alternative approach is to use numerical models to simulate dynamics over multidecadal time-periods.

Numerical food-web models, which represent one specific type of ecosystem models, integrate available data to simulate the dynamics of food-webs [19]. These models focus on trophic interactions between a subset of species or functional groups in the ecosystem. In the search of more realism, food-web models have become more complex by adding more parameters and variables for which data are not always available [20] thus increasing both the structural and parameter uncertainties. Despite this increase in complexity, these models are too constrained and are not able to reproduce the observed variability patterns in the ecosystem [6,21].

An alternative modelling approach, proposed by Mullan and collaborators [22], addresses specifically the issue of ecosystem stochastic variability. The Non-Deterministic Network Dynamic model (NDND) is a mass-balanced stochastic food-web model based on the principles of chance and necessity [23]. Chance implies that any event is possible as long as it complies with a number of basic biological and physical constraints ensuring that the ecosystem sustains itself over time. As such, the NDND model has been designed to reproduce the high variability of natural systems by exploring their “state-space”. It thereby allows us to explore many possible food-web configurations (i.e. distribution of biomass among the species, trophic controls between the compartments) and the temporal variability in these configurations. A more recent study [24] showed that the NDND model was able to reproduce the variability patterns of several ecosystem properties (e.g. stability, trophic control, density dependence, etc.) observed in the Barents Sea food-web during the last three decades.

The Barents Sea is a subarctic shelf sea which has experienced major changes in species composition and dynamics during the past decades [7,8,25]. Available ecological time-series of the Barents Sea species revealed successive changes in food-web configurations reflecting shifts of dominance between pelagic fish, demersal fish [8], and zooplankton [25]. A past modelling study identified two distinct trophic pathways in the Barents Sea food-web based on an Eco-path model [26]: one pelagic and one benthic. Yaragina and Dolgov [27] suggested a wasp-waist control of the Barents Sea food-web where pelagic fish is assumed to exert a top-down control on zooplankton and a bottom-up control on its predators, whereas, Johannesen and collaborators [8] identified fluctuating trophic control between the species of the Barents Sea food-web. However, there is a need to define a baseline for the variability of the Barents Sea ecosystem to assess if the recent changes in its dynamics may reflect its stochastic variability or if they were induced by variations in anthropogenic drivers.

In this study, we investigate the variability of the Barents Sea food-web configurations emerging from random trophic interactions and how they differ from the configurations observed during the past three decades. To this end, we perform food-web simulations using

the NDND model for the Barents Sea food-web and analyze the biomass configurations and trophic pathways of these simulated food-webs and compare past vs. simulated food-web configurations. Furthermore, we investigate if the previously reported trophic control (top-down or bottom-up) of the Barents Sea food-web are persistent features of the Barents Sea food-web.

## Material and methods

### A. NDND model parametrization

The NDND model is a stochastic mass-balanced food-web model in which the food-web topology (i.e. who eats who) is fixed but the predation rates are indeterminate [22–24]. In the NDND model, the dynamics of the different trophospecies (hereafter named species) result from biomass exchanges between species whose values are sampled randomly (chance), given a set of biological and physical constraints (necessity). Trophic flows define mechanistically the biomass at the next time-step according to the master equation of the model (see supplementary materials S1 in [S1 File](#)). Estimated biomass values will then constrain the values of the trophic flows for the next time-step, and so on. Five constraints are defined for the NDND model: (1) the food intake of a predator is limited due to satiation, (2) the increase of biomass per time-step is limited, as well as (3) the decrease of biomass per time-step, (4) a trophic flow between two species cannot be negative, and (5) the biomass of species must stay above a threshold value referred to as the refuge biomass. The mathematical formulation of the NDND model is detailed in supplementary material S1 in [S1 File](#).

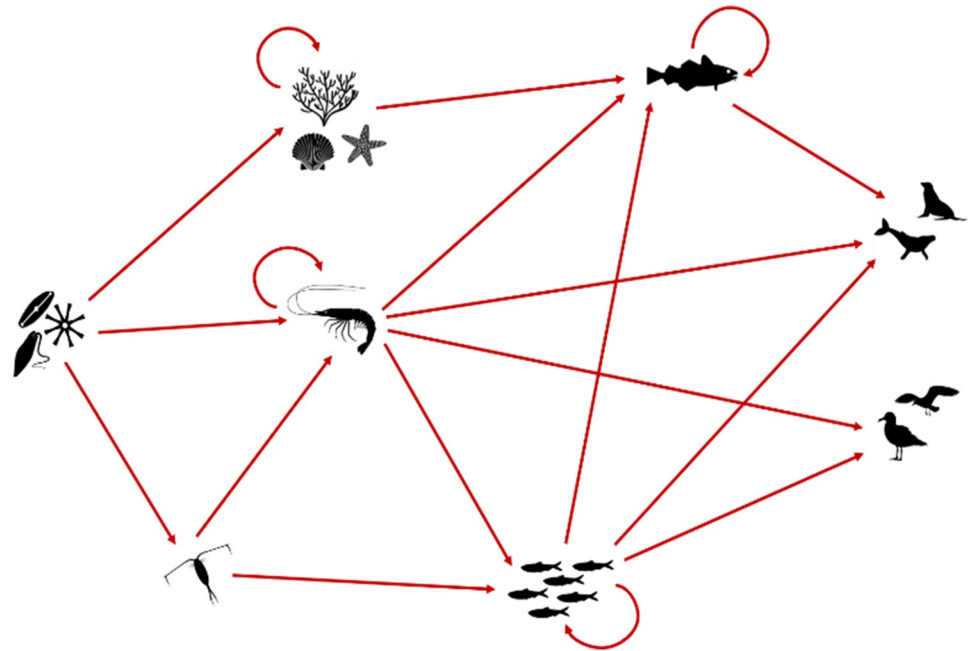
In the present study, we used the food-web topology from Lindstrøm *et al.* [24] comprising eight species (phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, mammals, and birds) and 18 trophic links ([Fig 1](#)). The values of the inertia parameter were adjusted to account for asynchronous growth rates of different species within species groups. Parameter values are presented in [Table 1](#).

Harvesting of pelagic and demersal fish is explicitly included. In contrast to Lindstrøm *et al.* [24], who modelled fish catches as a constant fraction of biomass, we express fishing using a harvest control rule (HCR) that resemble the fishing regulations that operate in the Barents Sea [28]. To apply the HCR to the NDND model, we make the following assumptions: (1) we assume the ratio catch/stock to be equivalent in biomass and numbers, (2) the fishing mortality is estimated based on the total stock biomass instead of the spawning stock biomass, and (3) as capelin and cod are the major species of the pelagic and demersal fish groups, we use the parameter values from these two species to construct the HCR for the pelagic and demersal fish groups respectively.

The HCR is defined as follows:

1. when the stock biomass is smaller than the trigger biomass ( $B_{lim}$ ), then the catch is set to 0,
2. when the stock biomass is greater than  $B_{lim}$  and lower than the target biomass ( $B_{mp}$ ), the catch increases linearly with the total stock biomass,
3. when the stock biomass is larger than  $B_{mp}$  then, the caught biomass is estimated using the Baranov equation [29,30].

Parameter values of  $F_{mp}$ ,  $B_{mp}$  and  $B_{lim}$  are set according to [28] and the natural mortality rates ( $M$ ) are set according to [31]. Parameter values of the HCR are presented in [Table 2](#).



**Fig 1. Schematic of the simplified Barents Sea food-web.** Species are represented by icons, from the left to the right: Phytoplankton, herbivorous and omnivorous zooplankton, benthos, pelagic and demersal fish, mammals, and birds. Trophic links are represented by red arrows. Circular arrows correspond to cannibalistic interactions.

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**Table 1. Parameter input for the simulation with the NDND model.**

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Initial Biomass ( $B_0$ , tons·km <sup>-2</sup> )	25	23	12.9	66	0.36	1.18	0.34	0.007
Import ( $I$ , tons·km <sup>-2</sup> )	1000	8	2	0	0	0	0	0
Export ( $E$ , tons·km <sup>-2</sup> )	0	0	0	0	0	0	0	0
Assimilation efficiency ( $\gamma$ )	1	1	1	0.94	0.9	0.93	1	0.84
Digestibility ( $\kappa$ )	0.65	0.9	0.9	0.6	0.9	0.85	-	-
Other losses ( $\mu$ )	6.74	8.4	5.5	1.5	2.85	1.65	5.5	60
Inertia ( $\rho$ )	12.94	7.58	3.1	0.74	0.9	0.25	0.11	0.81
Satiation ( $\sigma$ )	-	128	42	25.2	13.5	5.5	10.9	123
Refuge biomass ( $\beta$ , tons·km <sup>-2</sup> )	0.25	0.23	0.13	0.66	0.025	0.023	0.0034	0.0001

Assimilation efficiency and digestibility are ratio and do not have units. Other losses, inertia and satiation do not have units but represent ratios over a 1-year time-period.

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**Table 2. Harvesting control rule input parameter values.**

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Fishing mortality rate ( $F_{mp}$ )	-	-	-	-	0.05	0.4	-	-
Target biomass ( $B_{mp}$ , tons·km <sup>-2</sup> )	-	-	-	-	0.125	0.475	-	-
Trigger biomass ( $B_{lim}$ , tons·km <sup>-2</sup> )	-	-	-	-	0.125	0.25	-	-
Natural mortality ( $M$ )	-	-	-	-	0.85	0.2	-	-

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## B. Simulations

All simulations and statistical analysis are performed using R (v.3.6.2) [32]. A summary of all data transformations and statistical analysis methods used in this study is given in supplementary material S2 in [S1 File](#).

The sampling algorithm used in this study is the Complex Polytope Gibbs Sampling algorithm (cpgs) available in the RCaN package [33].

To ensure an extensive exploration of the “state-space” of the system, we generated 1000 trajectories of 500 years each. Possible configurations of the food-web can be defined based on the distribution of biomass in the different trophospecies or based on the distribution of trophic flows. To ensure that the simulated biomasses used for statistical analysis were independent from the initial biomasses at the start of the simulations, we removed a burn-in period of 121 years, leaving us with 1000 time-series of 379 years (biomass) and 378 years (flows) each. The method used to estimate the burn-in period is described in supplementary material S3 in [S1 File](#). Finally, biomass data were log<sub>10</sub> transformed to remove the scale difference between species. For the same purpose but, as some flows are close to zero, the flow data were log<sub>10</sub>(x + 0.001) transformed.

In the NDND model, phytoplankton biomass time-series reflect the remaining primary production after consumption by predator rather than the actual standing stock of algae or bacteria. These time-series were therefore not included in the analysis.

In addition to the NDND simulations, we used reconstructed trajectories of the Barents Sea food-web for the period 1988–2019 estimated from a Chance and Necessity model (CaN) for the Barents Sea [34]. In essence, NDND and CaN trajectories result from the same dynamical process but while the NDND trajectories are only constrained by ecological and biological limits, the CaN trajectories are also constrained by historical time-series of abundance and food consumption. Fishing in the CaN model is reconstructed as a non-trophic flow that is constrained by historical landing time-series for omnivorous zooplankton, pelagic fish, demersal fish, benthos, and marine mammals. The CaN model outputs provide an ensemble of biomass and trophic flow reconstructions for the whole food-web using available data series from a subset of species groups only. CaN model outputs are hereafter referred to as “reconstructed data”. The details of the CaN model setup are provided in Supplementary material S4 in [S1 File](#).

## C. Statistical analysis

A main goal of this study is to explore possible food-web configurations in the Barents Sea food-web and compare those to previously observed configurations. We define food-web configurations as either 1) the relative distribution of biomass among species in the food-web or 2) the relative distribution of trophic flows. Because the configurations are multivariate, a space reduction method such as principal component analysis (PCA) is useful to summarize the configurations.

Principal component analysis (PCA) has been widely used to identify ecosystem configurations [8,25,35]. PCA is best suited for cross-sectional studies, but as pointed out by Planque and Arneberg [36], the patterns emerging from PCA performed on multivariate autocorrelated time-series can be spurious. In such situations, an alternative statistical approach should be considered. Dynamical principal component analysis (dPCA) is a statistical method aiming at performing a PCA accounting for temporal autocorrelation [37,38]. In dPCA, time-lagged data are included in the analysis in addition to the original observational series. The number of lags to be considered can be defined by estimating partial autocorrelation (see method in Supplementary material S5 in [S1 File](#)). In the present case, the biomass dataset was lagged by 1

year, and trophic flow dataset was lagged by 3 years. Original and lagged datasets were merged in single data tables (378000\*14 for biomass data table and 375000\*72 for trophic flow data table). PCA was performed on the new matrix using the *ade4* package [39]. To compare the results of the NDND simulations against reconstructed food-web configurations, we projected the reconstructed data for the reference period 1986–2019 into the PCA space.

To identify the nature of trophic controls, we used correlation measures between species following the approach in Johannesen *et al.* [8]. Negative correlations and positive correlations are interpreted as top-down and bottom-up control, respectively. To identify persistent patterns of trophic control in the food-web, we then grouped biomass trajectories based on the similarity of their correlation patterns. Correlation patterns refer to the partial Pearson correlation matrix for each simulation. Partial correlation measures the direct correlation between two variables while accounting for the indirect correlation between the same two groups [40]. The correlation matrix is calculated from the lagged biomass data table (i.e. the data table containing the original observational series and the time-lagged series) and therefore includes instantaneous correlations but also lagged correlations (e.g. prey in years  $t$  with predator in year  $t+1$ , and vice versa). A complete linkage hierarchical clustering was performed on all simulations using the Euclidean distance between correlation matrices as the distance measure. The relevant number of clusters was set visually based on the dendrograms, and average correlation matrices were presented for each cluster. This analysis identified trophic controls over centennial time scales.

To explore the possibility of transient correlations at shorter time scales and to compare trophic control in simulated biomass trajectories with trophic control found based on observed data, we removed the last 19 simulated years from each time-series and derived a set of shorter time-series of 40 years each. A similar cluster analysis was performed on these shorter time-series.

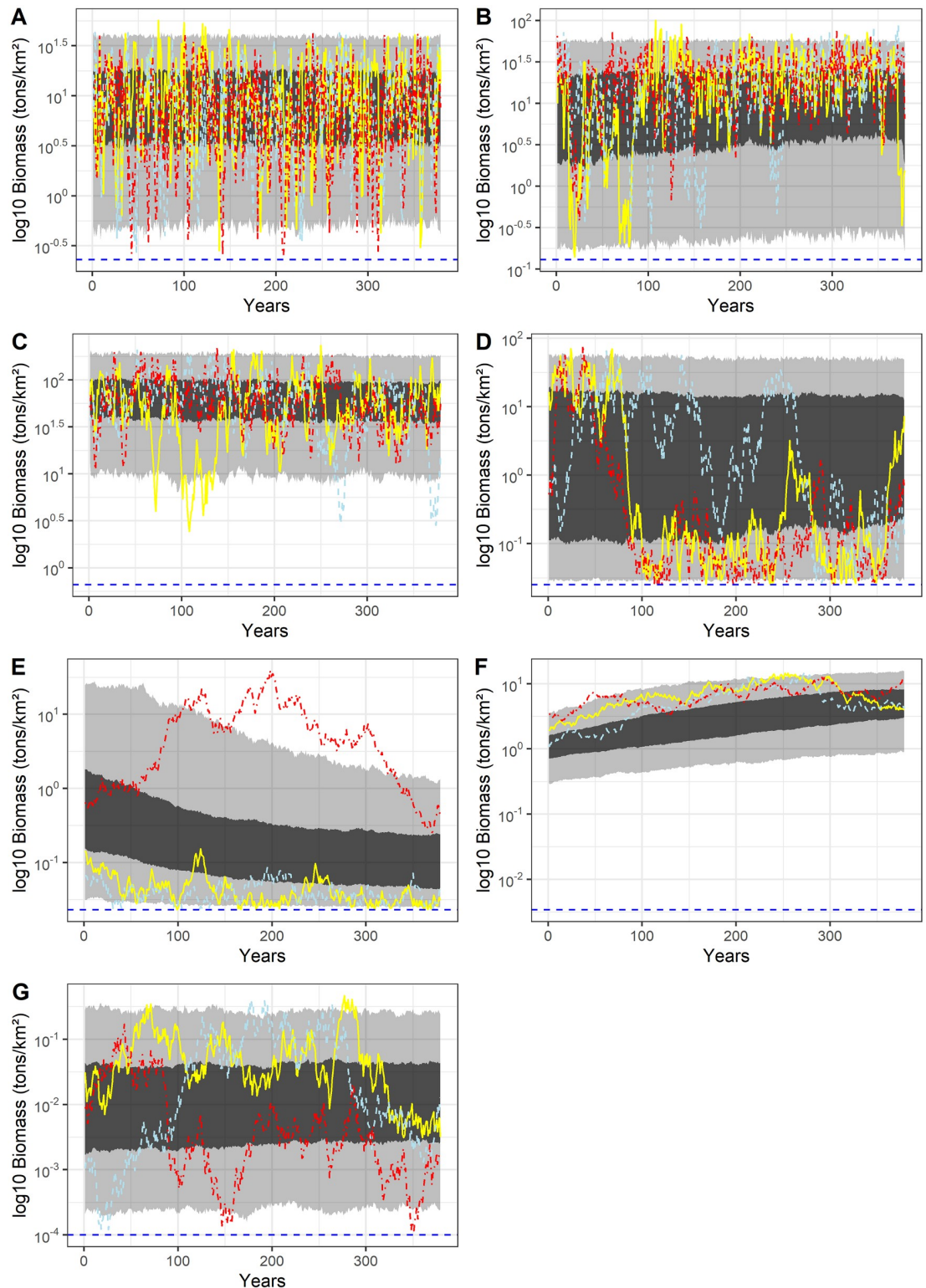
Finally, to explore the variability of trophic control at decadal time scales, we performed a 15-year centered sliding window marginal correlation analysis on the short biomass time-series (40 years). The same analysis was conducted on the reconstructed data. The results of this analysis were then compared to the results of Lindstrøm *et al.* [24] and Johannesen *et al.* [8].

## Results

### A. Simulation outputs

Simulated time-series of individual species displayed high variability within and between simulations (Fig 2). Life history and biological traits of individual species led to inter-specific variability of biomass dynamics (Fig 2).

Not surprisingly, the herbivorous and omnivorous zooplankton biomass displayed more rapid short-term and long-term changes than the other trophospecies: the simulated biomass of herbivorous and omnivorous zooplankton varied by two and three orders of magnitude, respectively. Benthos biomass varied by more than one order of magnitude. In the benthos group, the individual trajectories were more autocorrelated than for herbivorous and omnivorous zooplankton, and no long-term variability was observed. As omnivorous zooplankton, pelagic fish displayed biomass varying up to three orders of magnitude, but pelagic fish showed smaller short-term variability than omnivorous zooplankton leading to fewer shifts between configurations with higher pelagic fish biomass and configurations with lower pelagic fish biomass. Compared to previous trophospecies, demersal fish biomass displayed higher autocorrelation even though biomass could vary up to three orders of magnitude. The mammals biomass showed the lowest short-term and long-term variability of all trophospecies. Birds

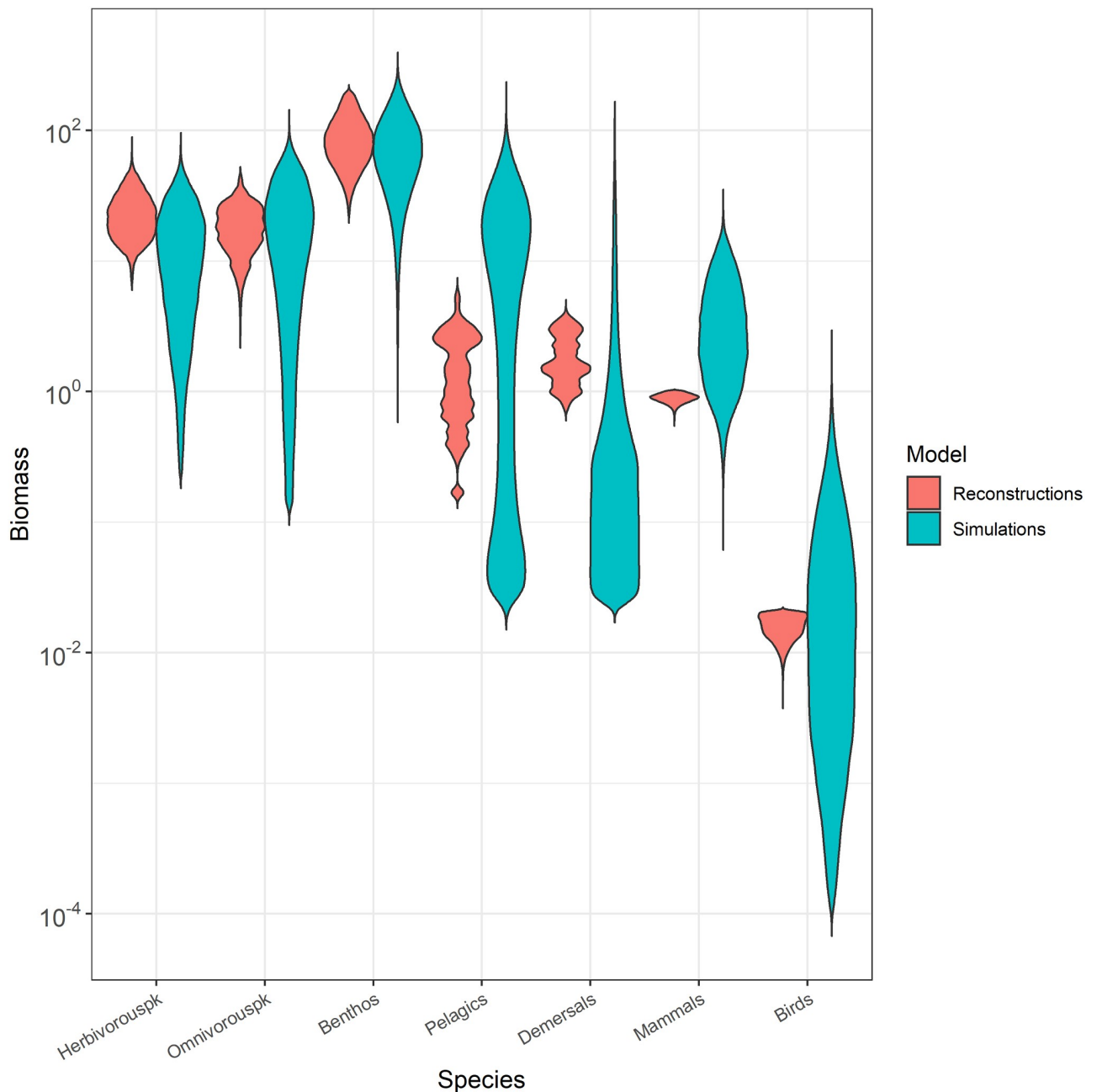


**Fig 2. Biomass time-series ( $\log_{10}$ , tons.km<sup>-2</sup>) of Herbivorous zooplankton (A), omnivorous zooplankton (B), benthos (C), pelagic (D) and demersal fish (E), mammals (F) and birds (G). The colored lines (red-dashed-dotted, yellow-plain, and light blue-dashed) represent three randomly selected simulations. The dark blue dotted line represents the refuge biomass constraint. The light and dark grey areas contain 95% and 50% of all the simulated data, respectively.**

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biomass displayed higher variability on long-term scale with variations by approximately three orders of magnitude, but with limited year-to-year variations.

The CaN model reconstructs trajectories by including historical observations. Although observation data are not available for all the trophic groups specified in the model, the CaN model can provide a range of plausible biomass trajectories for each species, based on existing observations. As expected, the reconstructed data biomass envelopes of each trophospecies were smaller than those of simulated biomass and were included in the range of simulated biomass (Fig 3). For herbivorous and omnivorous zooplankton, benthos and birds, the



**Fig 3. Density distributions of biomass (tons.km<sup>-2</sup>) in the NDND simulations (blue-right) and the CaN reconstructed biomass (red-left).** Biomass values are log<sub>10</sub> transformed.

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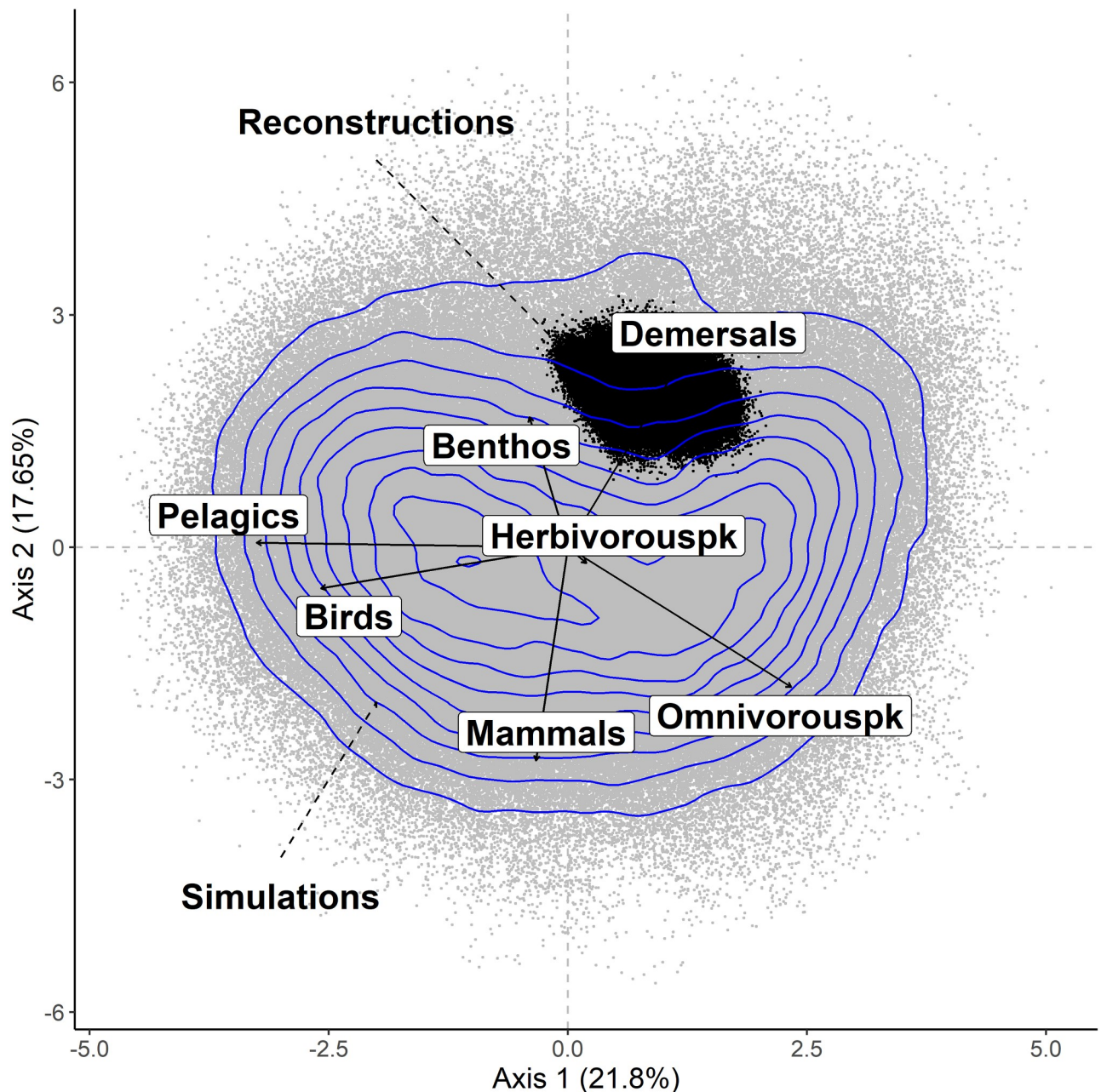
reconstructed data matched most of the simulated biomass as they overlapped with the densest part of the distributions. For pelagic and demersal fish and mammals, reconstructed data did not match the most frequent simulated biomass. The distribution of biomass for pelagic fish in the NDND model was bimodal with two “states” centered around high ( $\sim 30 \text{ t.km}^{-2}$ ) and a low ( $\sim 0.03 \text{ t.km}^{-2}$ ) biomass whereas the reconstructed data pointed toward intermediate levels ( $\sim 1 \text{ t.km}^{-2}$ ). In the reconstructed data, demersal fish biomass were generally higher than most of the NDND simulated demersal biomass. On the contrary, the reconstructed mammal biomass was on average lower than the mammal biomass simulated with the NDND.

## B. Biomass configurations

The two first axes of the dPCA performed on simulated biomass explained 39.45% of variance (Fig 4). The projection of simulated (NDND) and reconstructed (CaN) biomass showed that reconstructed biomass overlapped with the simulation space (Fig 4). The reconstructed biomass configurations were included within the space of the simulated configurations, which was consistent with the biomass distributions from individual species (Fig 4). Biplot of the dPCA on simulated biomass highlighted two configurations of biomass. The first was aligned with the first axis of the dPCA and represented an opposition between pelagic fish, bird and omnivorous zooplankton biomass with pelagic fish and bird biomass being strongly positively correlated. The second was aligned with the second axis of the dPCA and reflected the opposition between marine mammals, demersal fish and benthos with benthos and demersal fish positively correlated. Interestingly, the reconstructed data displayed higher biomass of demersal fish and benthos, and low biomass of mammals and omnivorous zooplankton. In other words, past configurations of the Barents Sea food-web were dominated by demersal fish and benthos.

## C. Trophic pathways

The two first axis of the dPCA performed on the simulated flows explained 39.3% of variance (Fig 5). Complete overlap between simulated flows (NDND) and reconstructed flows (CaN) was observed (Fig 5A). Simulated flows formed three configurations of flows. The first configuration corresponded to the case where flows entering and exiting the pelagic fish group towards mammals and birds were high (Fig 5B). The second configuration was characterized by high flow rates between phytoplankton, omnivorous zooplankton, and mammals. The third configuration reflected to cases where flows entering and exiting the demersal fish group were high. In other words, the first main configuration corresponded to a pelagic trophic pathway, the second one described a short pathway from plankton to mammals and the third one reflected a benthic-demersal pathway. In the second configuration, both fish groups are completely bypassed by mammals feeding directly on omnivorous zooplankton. The density plots indicated that the pelagic and plankton-mammals pathway occurred more often than the benthic-demersal pathway in the simulated flows. Reconstructed flows were characterized by a benthic-demersal pathway as flows entering and exiting the demersal fish group were higher in the reconstructed data (Fig 5B). The pelagic fish-demersal fish flow was not included within any configuration. We assume that it is because the flow is part of the pelagic and the benthic-demersal pathways. In the benthic-demersal pathway, the pelagic-demersal flow is an income of biomass for the demersal fish, whereas in the pelagic pathway, it corresponds to removed biomass from the pelagic species.

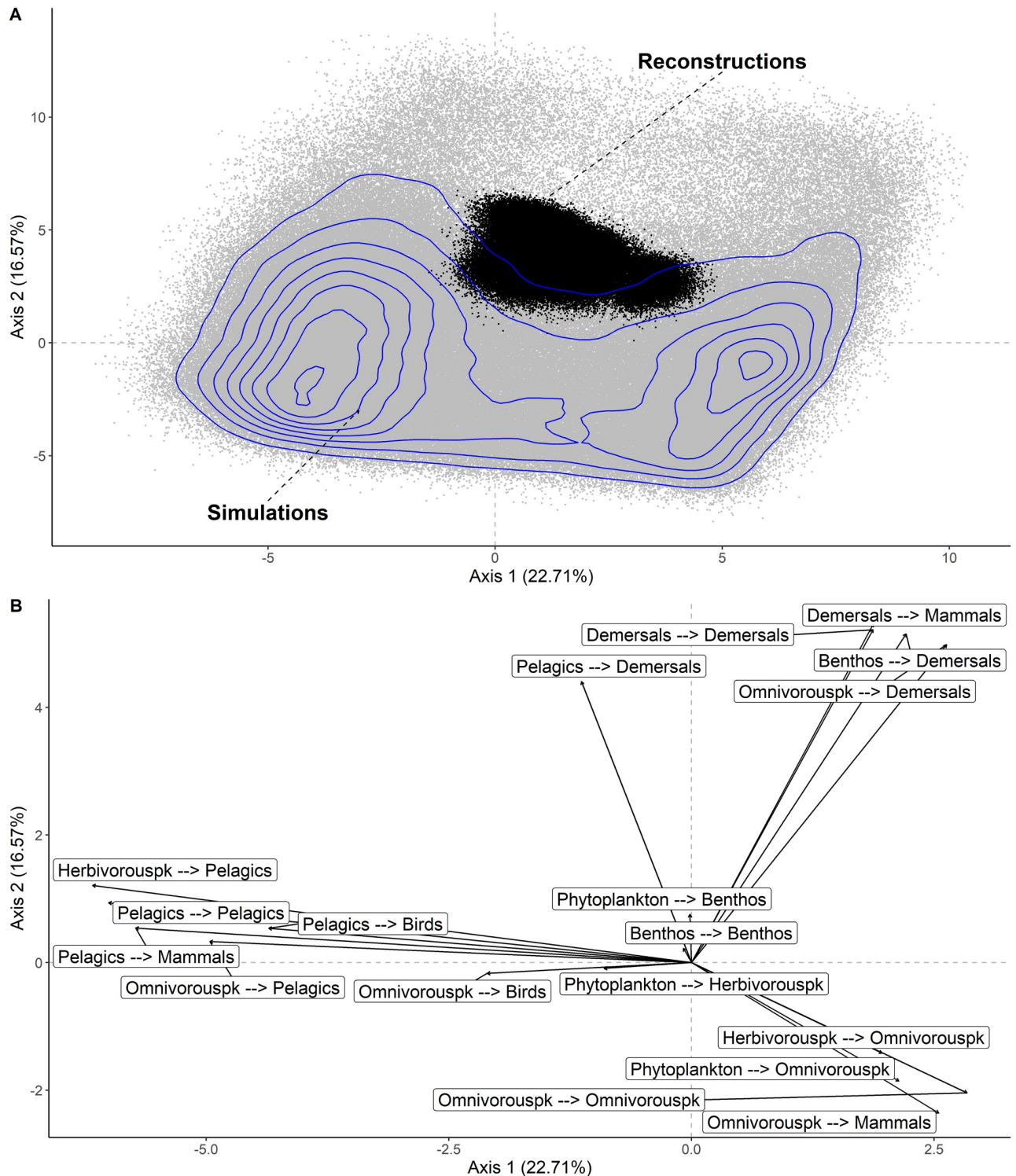


**Fig 4. Biplot of the dynamical principal component analysis (dPCA) performed on the simulated biomass time-series with the NDND, showing individual (grey points) and the projection of the original variables (arrows). The projections of the reconstructed data configurations in the dPCA space are shown as black point. Blue lines show the contours of the density of observations in the simulated data only. The percentage of variance explained is reported on each axis.**

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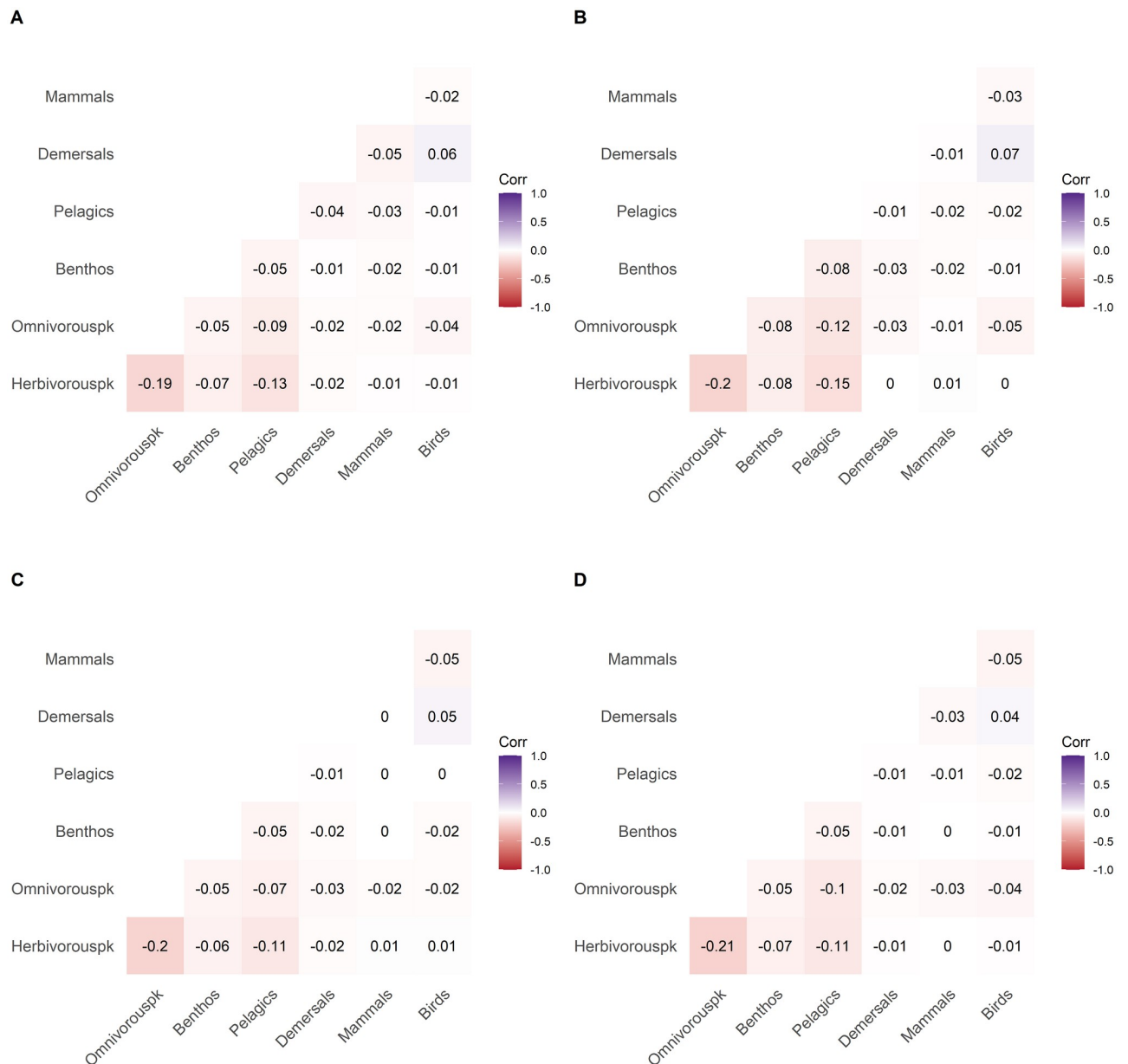
#### D. Trophic control

Distances between partial correlation matrices of long time-series (379 years) revealed small distances between the single partial correlation matrices indicating that partial correlation matrices of single time-series were similar. The maximum measured distance was slightly below 0.06 (see Supplementary materials S6 in [S1 File](#)). We cut the dendrogram in four



**Fig 5. Dynamical principal component analysis (dPCA) on fluxes generated by the NDND and CaN models and displayed as scatter plot (A) and projection of initial variables (B).** Each individual point represents a simulated flow configuration at time step  $t$  (grey points). The projection of reconstructed data is represented as black points. Blue lines show the contours of the density of observations in the simulated data only. The percentage of variance explained is reported on each axis.

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**Fig 6. Correlation plots of mean partial correlation matrices of clusters 1 (A), 2 (B), 3 (C) and 4 (D) defined in the hierarchical clustering.** Values in the plot correspond to mean Pearson partial correlation values between trophospecies. Red and blue colors indicate negative and positive correlations between two trophospecies, respectively. Negative and positive correlation represent bottom-up and top-down control, respectively.

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clusters. The number of time-series in each cluster was uneven ( $n_1 = 135$ ,  $n_2 = 274$ ,  $n_3 = 311$ , and  $n_4 = 280$ ).

The four clusters displayed few correlation patterns, i.e. the mean partial correlation of each cluster displayed no correlation pattern, and very little difference was identified between clusters (Fig 6). Most of the correlation values were between -0.21 and 0.07. Top-down control of herbivorous zooplankton by omnivorous zooplankton was present in all four clusters but correlation values were relatively low (between -0.21 and -0.19). Top-down control of pelagic fish on herbivorous zooplankton was found for all four clusters but again correlation values were

weak (-0.13, -0.15, -0.11 and -0.11 respectively) indicating weak trophic control. The absence of strong correlation values indicates that no long-term persistent trophic control can be highlighted.

The distances between 9000 partial correlation matrices of short biomass time-series (40 years) were higher than those between longer time-series. The maximum distance measured was 0.6 (see Supplementary materials S6 in [S1 File](#)). Thus, there were important differences between partial correlation matrices of single short time-series. We cut the dendrogram in three clusters. As for longer time-series, the number of time-series within the clusters was uneven ( $n_1 = 4786$ ,  $n_2 = 3577$  and  $n_3 = 627$ ). Surprisingly, like long time-series (379 years), we observed almost no difference in correlation values between the clusters ([Fig 7](#)). Top-down control of herbivorous zooplankton by omnivorous zooplankton was found but the correlation values were relatively low (-0.21, -0.19 and -0.18 for each cluster respectively). Clusters 1 and 2 ([Fig 7A & 7B](#)) displayed higher correlation value between pelagic fish and herbivorous zooplankton than cluster 3 (-0.1 and -0.11 respectively). Cluster 3 ([Fig 7C](#)) was also characterized by negative correlation between mammals and benthos (-0.12). This interaction is indirect as no direct trophic link is defined between benthos and marine mammals. Furthermore, the correlation value was relatively low. Apart from the few correlation patterns mentioned above, no other significant correlation values were found indicating that for shorter time-periods (40 years) as for long time-series (379 years), no persistent trophic control was found.

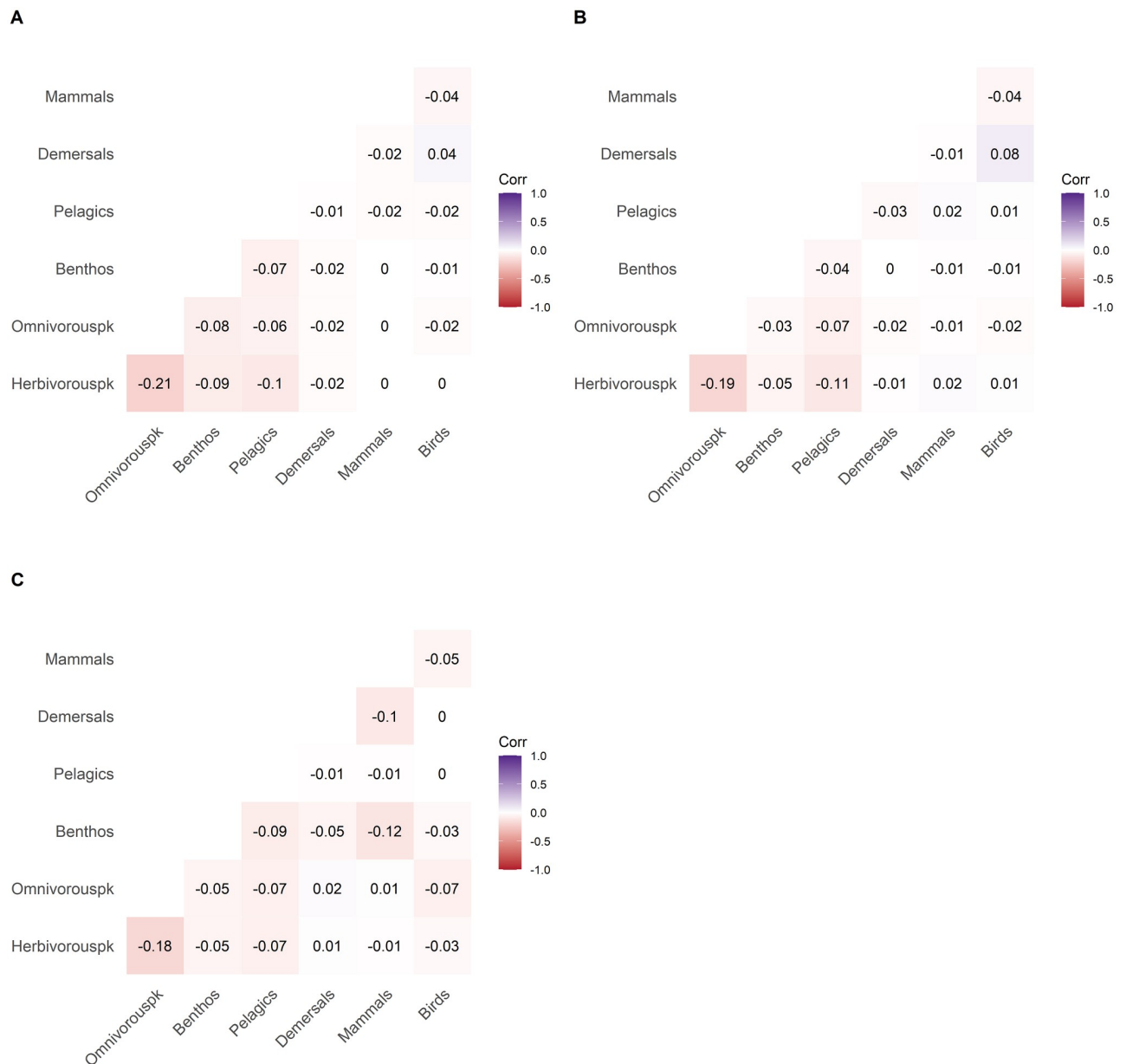
The absence of correlation can result from two factors: (1) Either the correlation between two species stays close to 0, or (2) trophic control is variable within the same time-series, and higher and lower correlation values compensate each other leading to low correlation values. Estimating correlations on a sliding window, allows us to display the dynamics of trophic control within the same time-series. Correlation time-series displayed no trend ([Fig 8A and 8C](#)). 50% and 95% envelopes were centered around a correlation of 0. When time-series were considered separately, interdecadal shifts of trophic control were visible. Correlation between demersal and pelagic fish were found between -0.8 and 0.9 whereas correlations between pelagic fish and omnivorous zooplankton were found between -0.8 and 0.8 ([Fig 8A and 8C](#)).

Time-series of correlation between demersal and pelagic fish from reconstructed data ranged from -0.8 to 0.8 whereas correlations between pelagic fish and omnivorous zooplankton in the reconstructed data ranged from -0.75 to 0.5 ([Fig 8B and 8D](#)). Thus, reconstructed data were included in the NDND simulation range for demersal vs pelagic correlations. Reconstructed data also displayed variations of trophic control as observed in the NDND simulations, but the length of time-series was smaller for reconstructed data making difficult to observe possible cycles.

## Discussion

Studying the historical range of variability is essential to define a baseline for the variability of the Barents Sea ecosystem that can be used to design successful management policies [10]. However, past studies focusing on the variability of the Barents Sea food-web based on ecological time-series often define this baseline based on short time-periods representing only a fraction of the possible variability of the ecosystem. Thus, we explored the possible range of stochastic variability of the Barents Sea food-web using the NDND model. The primary aim of this study was to identify possible configurations of the Barents Sea food-web and to confront them to historical data. Our study shows that the range of possible food-web configurations is larger than the range observed during the last three decades.

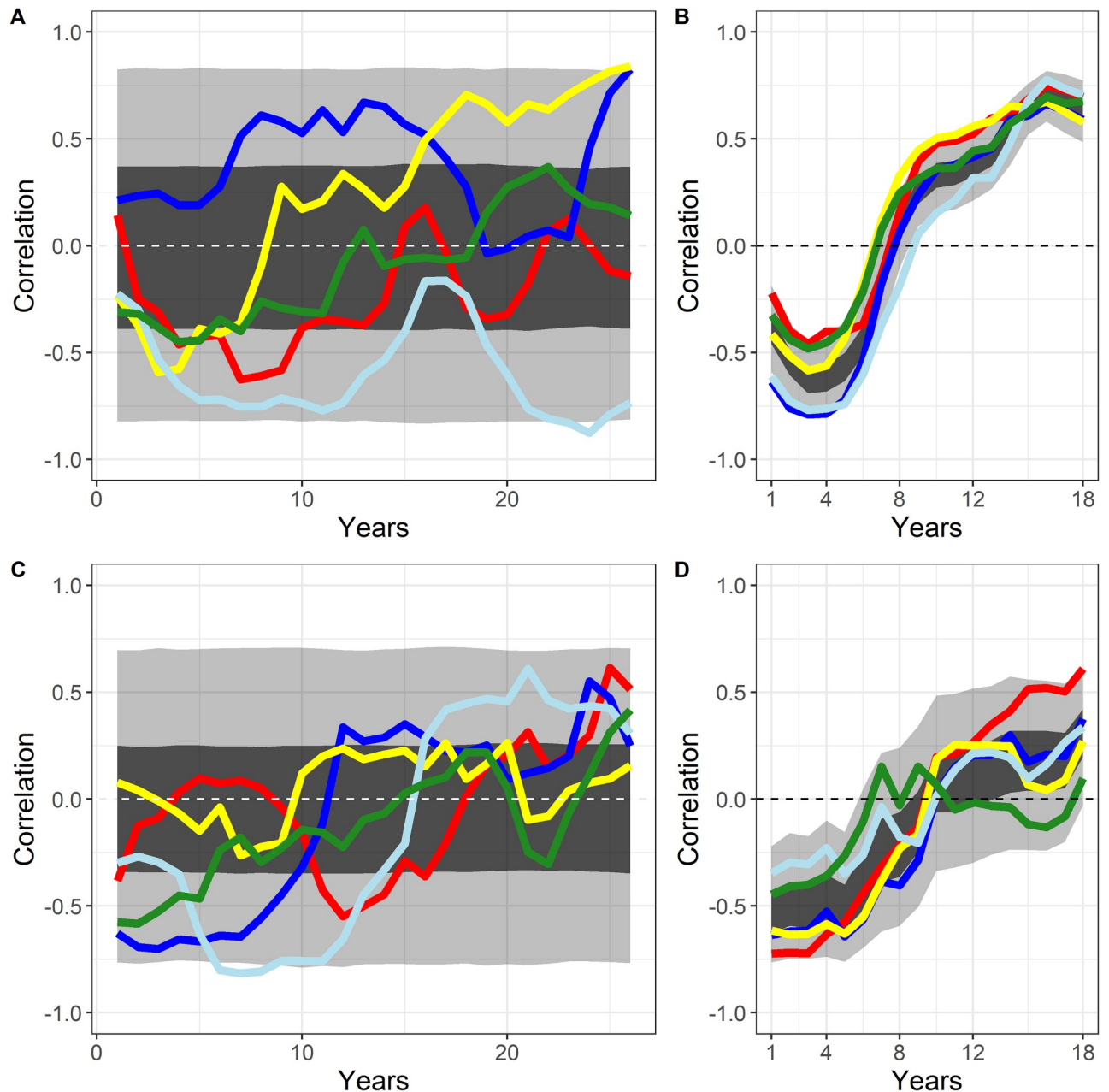
Our analysis revealed four major configurations in the simulated biomass, which represent two types of opposition of biomass. The first opposed pelagic fish and birds to omnivorous



**Fig 7. Correlation plots of mean partial correlation matrices for clusters identified in the hierarchical clustering performed on short time-series (A-C for clusters 1–3 respectively).** Values in the plot correspond to mean Pearson partial correlation values between trophospecies. Red and blue colors indicate negative and positive correlations between two trophospecies, respectively. Negative and positive correlation represent bottom-up and top-down control, respectively.

<https://doi.org/10.1371/journal.pone.0254015.g007>

zooplankton, whereas the second opposed demersal fish and benthos to marine mammals. The projection of reconstructed data in the dPCA space (Fig 4) indicated that the current state of the Barents Sea ecosystem corresponds to a configuration dominated by demersal fish and benthos. Reconstructed data displayed higher demersal fish biomass and lower mammals biomass than the majority of simulated biomass in the NDND simulations (Fig 3). These results are consistent with the hypothesized competition between mammals and demersal fish in the Barents Sea [41] and with the lower levels of estimated marine mammals abundance during the last three decades in the Barents Sea [42]. The simulated pelagic fish biomass displayed a



**Fig 8. Correlation estimated on a 15-year centered sliding window between demersal vs pelagic in the NDND simulations (A) and CaN simulations (B), and between pelagic vs. omnivorous zooplankton in the NDND simulations (C) and CaN simulations (D).** The white/black dotted line indicates when the correlation is null, the black envelope contains 50% of measured correlations, the grey envelope constrains 95% of all measured correlations. Colored lines correspond to correlation values of five randomly selected short time-series (40 years).

<https://doi.org/10.1371/journal.pone.0254015.g008>

bimodal distribution with many high and low values of biomass, and few intermediate biomass values (Fig 3). Reconstructed data for pelagic fish biomass corresponded to the intermediate situation. A possible interpretation is that pelagic fish populations are in a transition phase between two states and could possibly substantially decrease or increase in the future, towards the levels observed in the simulations.

Past studies described three configurations of the Barents Sea food-web based on observed data for the last five decades [8,25], which are believed to have resulted from collapses of pelagic fish stocks, predation of pelagic fish by demersal fish, and management policies applied for pelagic and demersal fish groups. Our analysis pointed to four contrasted configurations that are partly consistent with the ones described in previous studies. Marine mammal-dominated configurations have not been reported in previous studies. In past dynamics of the Barents Sea, omnivorous zooplankton biomass increased when the pelagic fish biomass collapsed [25,27]. Our results are consistent with this observation as the configuration with low pelagic fish biomass was also characterized by high omnivorous zooplankton biomass. The pelagic fish-dominated configuration we define in this study is also characterized by a higher biomass of birds. This result is in line with previous studies showing that bird population size is linked to the biomass of pelagic fish in the Barents Sea, with observed declines in the population size of birds at times of pelagic fish stock collapses [43].

Our results show that there are three different trophic pathways of biomass in the NDND simulations. The pelagic and planktonic pathways appear to be the most common even though, our results suggest that the benthic-demersal pathway is also possible. Interestingly, the trophic pathway found in reconstructed data corresponded to the benthic-demersal trophic pathway. Trophic pathways in the simulated data emphasize the key role of pelagic fish for transferring energy from lower trophic levels to top-predators [27,44,45]. However, the pelagic fish species can be bypassed by the mammals feeding directly on omnivorous zooplankton in the NDND simulations. We assume that this pathway of energy corresponds to configurations of the food-web where biomass of pelagic fish is low and not sufficient to maintain the biomass of mammals. The benthic-demersal trophic pathway we identified is in line with trophic pathways identified using an Ecopath modelling approach [26]. Even though we found a complete overlap between simulated and reconstructed flows, reconstructed flows corresponded to configurations occurring less frequently than the pelagic and planktonic trophic pathways in the simulated flows. This indicates that according to the assumptions we have made, the dominant pathway of the Barents Sea food-web during the last three decades did not correspond to the dominant pathways identified in the simulations. An external factor, not accounted for in our study, might be forcing the Barents Sea food-web into the benthic-demersal pathway (i.e. the values of the trophic flows involving the demersal fish are higher in the reconstructions than in the simulations).

Previous studies exploring trophic relationships in the Barents Sea [46,47] have suggested that zooplankton species could be controlled by pelagic fish. However, a more recent study suggested bottom up-control of pelagic fish by zooplankton combined with top-down control of zooplankton by pelagic fish [48]. A study of demersal fish colonizing the northern part of the Barents Sea and the associated rapid decline in stomach fullness also suggested a top-down control [49]. In contrast to these studies, we found no persistent trophic control in the Barents Sea food-web neither over centennial (Fig 6) nor over decadal time scales (Fig 7). Rather, trophic controls tend to fluctuate on inter-decadal time scales and are highly variable between time-series (Fig 8). This variability of trophic control is found for most of the trophic interactions (see Supplementary material S7 in S1 File). Previously, in the Barents Sea food-web, trophic control shifted between top-down, bottom-up and wasp-waist processes [8,27]. The analysis of the NDND simulations suggests that this pattern of interannual variability in trophic control [8,24] is to be expected, even in situations in which trophic flows are varying at random.

The difference in the range of variability between our reconstructions and our simulations ensues from the differences in the constraints between the CaN model and the NDND model.



The CaN model and the NDND model are based on the same modelling principles: chance and necessity. Yet, the CaN model is more constrained than the NDND model since it integrates past observations to constrain the food-web trajectories [34]. Thus, we could expect the range of variability of the CaN reconstructed food-web configurations to be smaller than the range of variability of the NDND simulated food-web configurations.

The NDND model considers all configurations derived from a small number of biological and physical constraints. Hence, just as we argue that large deterministic models are too constrained and thus are not able to generate the natural variability of food-webs, it is fair to consider that the NDND simulations are under-determinate and that their variability could be greater than the real range of variability of the food-web.

In the NDND model, the dynamics of the Barents Sea food-web is driven by trophic flows [22,23]. At any time-step, the flows are drawn randomly (within the model constraints) and their values determine the species biomass at the next time step. This in turn modifies the constraints and thereby affects the drawing of the trophic flows at the following time step. The overlap between simulated and reconstructed food-web configurations is primarily driven by chance. It indicates that the reconstructed food-web configurations are part of a wider set of configurations that reflect the possible range of stochastic variability of Barents Sea food-web. Although exploring the range of historical variability is essential to define a baseline for the variability of marine ecosystems for management purposes [10], it is a challenge to measure it. In management policies, stochastic variability is described as a source of uncertainty in ecosystem models [50]. The model we use in this study explores the possible range of stochastic variability of the Barents Sea food-web instead of considering it as a source of uncertainty. Our findings can be useful to management as it provides a baseline for the variability of the Barents Sea food-web which can be used to assess the future changes in the dynamics of the ecosystem.

## Conclusion

This study shows that the diversity of possible biomass configurations and trophic pathways in the Barents Sea food-web extends beyond what has been observed during the last three decades. We found that reconstructed biomass configurations as well as reconstructed trophic pathways are strongly overlapping with our simulations though they only represent a subset of possible situations. Our simulations indicate that the Barents Sea food-web is dominated by pelagic and planktonic pathways. Our analyses suggest four major types of biomass configurations, characterized by opposite patterns in the abundance of pelagic fish and omnivorous zooplankton on one side and demersal fish and marine mammals on the other. We found no evidence for persistent trophic control in the Barents Sea food-web over centennial and multi-decadal scales throughout the food-web but revealed fluctuating top-down and bottom-up controls over interdecadal time scales.

## Supporting information

**S1 File. Revised supplementary information.**  
(DOCX)

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**Writing – original draft:** Elliot Sivel.

**Writing – review & editing:** Benjamin Planque, Ulf Lindstrøm, Nigel G. Yoccoz.

## References

1. Levin SA. Ecosystems and the Biosphere as Complex Adaptive Systems. *Ecosystems*. 1998; 1(5): 431–436. <https://doi.org/10.1007/s100219900037>
2. Levin SA. Self-organization and the emergence of complexity in ecological systems. *Bioscience*. 2005; 55(12): 1075–1079. [https://doi.org/10.1641/0006-3568\(2005\)055\[1075:SATEOC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[1075:SATEOC]2.0.CO;2)
3. Levin S, Xepapadeas T, Crépin A-S, Norberg J, de Zeeuw A, Folke C, et al. Social-ecological systems as complex adaptive systems: modeling and policy implications. *Environment and Development Economics*. 2013; 18(2): 111–132. <https://doi.org/10.1017/S1355770X12000460>
4. Calvo E, Simó R, Coma R, Ribes M, Pascual J, Sabatés A, et al. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Climate Research*. 2011; 50(1): 1–29. <https://doi.org/10.3354/cr01040>
5. Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*. 2015; 282(1814): 20151546. <https://doi.org/10.1098/rspb.2015.1546> PMID: 26336179
6. Niiranen S, Yletyinen J, Tomczak MT, Blenckner T, Hjerne O, MacKenzie BR, et al. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. *Global Change Biology*. 2013; 19: 3327–3342. <https://doi.org/10.1111/gcb.12309> PMID: 23818413
7. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*. 2015; 5(7): 673–677. <https://doi.org/10.1038/nclimate2647>
8. Johannesen E, Ingvaldsen RB, Bogstad B, Dalpadado P, Eriksen E, Gjørseter H, et al. Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES Journal of Marine Science*. 2012; 69(5): 880–889. <https://doi.org/10.1093/icesjms/fss046>
9. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. Catastrophic shifts in ecosystems. *Nature*. 2001; 413(6856): 591–596. <https://doi.org/10.1038/35098000> PMID: 11595939
10. Landres PB, Morgan P, Swanson FJ. Overview of the Use of Natural Variability Concepts in Managing Ecological Systems. *Ecological Applications*. 1999; 9(4): 1179–1188. [https://doi.org/10.1890/1051-0761\(1999\)009\[1179:OOTUON\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1179:OOTUON]2.0.CO;2)
11. Lotze HK, Worm B. Historical baselines for large marine animals. *Trends in Ecology & Evolution*. 2009; 24(5): 254–262. <https://doi.org/10.1016/j.tree.2008.12.004> PMID: 19251340
12. Evans K, Brown JN, Sen Gupta A, Nicol SJ, Hoyle S, Matear R, et al. When 1+1 can be >2: Uncertainties compound when simulating climate, fisheries and marine ecosystems. *Deep Sea Research Part II: Topical Studies in Oceanography*. 2015; 113: 312–322. <https://doi.org/10.1016/j.dsr2.2014.04.006>
13. Longhurst AR. *Mismanagement of marine fisheries*. Cambridge, UK; New York: Cambridge University Press; 2010.
14. Lawton JH. More time means more variation. *Nature*. 1988; 334(6183): 563–563. <https://doi.org/10.1038/334563a0>
15. Pimm SL, Redfearn A. The variability of population densities. *Nature*. 1988; 334(3183): 613–614. <https://doi.org/10.1038/334613a0>
16. Myers RA, Worm B. Rapid worldwide depletion of predatory fish communities. *Nature*. 2003(6937); 423: 280–283. <https://doi.org/10.1038/nature01610> PMID: 12748640

17. Baum JK, Myers RA. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters*. 2004; 7(2): 135–145. <https://doi.org/10.1111/j.1461-0248.2003.00564.x>
18. Baumgartner TR, Soutar A, Ferreira-Bartrina V. Reconstruction of the history of the Pacific sardine and northern anchovy populations over the past two millenia from sediments of the Santa Barbara basin, California. *California Cooperative Oceanic Fisheries Investigation Reports*. 1992; 33: 24–40.
19. Christensen V, Walters CJ. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*. 2004; 172(2): 109–139. <https://doi.org/10.1016/j.ecolmodel.2003.09.003>
20. Fulton EA, Blanchard JL, Melbourne-Thomas J, Plagányi ÉE, Tulloch VJD. Where the Ecological Gaps Remain, a Modelers' Perspective. *Frontiers in Ecology and Evolution*. 2019; 7:424. <https://doi.org/10.3389/fevo.2019.00424>
21. Möllmann C, Folke C, Edwards M, Conversi A. Marine regime shifts around the globe: theory, drivers and impacts. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2015; 370(1659): 20130260. <https://doi.org/10.1098/rstb.2013.0260>
22. Mullon C, Fréon P, Cury P, Shannon L, Roy C. A minimal model of the variability of marine ecosystems. *Fish and Fisheries*. 2009; 10(2): 115–131. <https://doi.org/10.1111/j.1467-2979.2008.00296.x>
23. Planque B, Lindstrøm U, Subbey S. Non-Deterministic Modelling of Food-Web Dynamics. *Chiaradia A*, editor. *PLoS ONE*. 2014; 9(10): e108243. <https://doi.org/10.1371/journal.pone.0108243> PMID: 25299245
24. Lindstrøm U, Planque B, Subbey S. Multiple Patterns of Food Web Dynamics Revealed by a Minimal Non-deterministic Model. *Ecosystems*. 2017; 20(1): 163–182. <https://doi.org/10.1007/s10021-016-0022-y>
25. Eriksen E, Skjoldal HR, Gjøsæter H, Primicerio R. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progress in Oceanography*. 2017; 151: 206–226. <https://doi.org/10.1016/j.pocean.2016.12.009>
26. Megrey BA, Aydin KY. A macrodescriptor perspective of ecological attributes for the Bering and Barents Seas. *Deep Sea Research Part II: Topical Studies in Oceanography*. 2009; 56(21): 2132–2140. <https://doi.org/10.1016/j.dsr2.2008.11.024>
27. Yaragina NA, Dolgov AV. Ecosystem structure and resilience—A comparison between the Norwegian and the Barents Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*. 2009; 56(21–22): 2141–2153. <https://doi.org/10.1016/j.dsr2.2008.11.025>
28. Gullestad P, Aglen A, Bjordal Å, Blom G, Johansen S, Krog J, et al. Changing attitudes 1970–2012: evolution of the Norwegian management framework to prevent overfishing and to secure long-term sustainability. *ICES Journal of Marine Science*. 2014; 71(2): 173–182. <https://doi.org/10.1093/icesjms/fst094>
29. Baranov FI. On the question of the biological basis of fisheries. *Izvestiya*. 1918; 1: 81–128.
30. Branch TA. Differences in predicted catch composition between two widely used catch equation formulations. *Canadian Journal of Fisheries and Aquatic Sciences*. 2009; 66(1): 126–132. <https://doi.org/10.1139/F08-196>
31. ICES. Arctic Fisheries Working Group 2020 Report. 2020 (AFWG). ICES Scientific Reports. 2:52. 577 pp.
32. R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing; 2019. <https://www.R-project.org/>.
33. Drouineau H, Planque B, Mullon C. RCaN: a package to fit Chance and Necessity model. 2021. bioRxiv:2021.2006.2009.447734.
34. Planque B, Mullon C. Modelling chance and necessity in natural systems. *ICES Journal of Marine Science*. 2020; 77(4): 1573–1588. <https://doi.org/10.1093/icesjms/fsz173>
35. Möllmann C, Diekmann R, Müller-Karulis B, Kornilovs G, Plikshs M, Axe P. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biology*. 2009; 15(6): 1377–1393. <https://doi.org/10.1111/j.1365-2486.2008.01814.x>
36. Planque B, Arneberg P. Principal component analyses for integrated ecosystem assessments may primarily reflect methodological artefacts. *ICES Journal of Marine Science*. 2018; 75(3): 1021–1028. <https://doi.org/10.1093/icesjms/fsx223>
37. Ku W, Storer RH, Georgakis C. Disturbance detection and isolation by dynamic principal component analysis. *Chemometrics and Intelligent Laboratory Systems*. 1995; 30(1): 179–196. [https://doi.org/10.1016/0169-7439\(95\)00076-3](https://doi.org/10.1016/0169-7439(95)00076-3)
38. De Ketelaere B, Hubert M, Schmitt E. Overview of PCA-Based Statistical Process-Monitoring Methods for Time-Dependent, High-Dimensional Data. *Journal of Quality Technology*. 2015; 47(4): 318–335. <https://doi.org/10.1080/00224065.2015.11918137>

39. Dray S, Dufour A-B. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*. 2007; 22(4). <https://doi.org/10.18637/jss.v022.i04>
40. Legendre L, Legendre P. *Ecologie numérique*. Paris; Québec: Masson: Presses de l'Université du Québec; 1984.
41. Bogstad B, Gjøsæter H, Haug T, Lindstrøm U. A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Frontiers in Ecology and Evolution*. 2015; 3. <https://doi.org/10.3389/fevo.2015.00029>
42. Stenson GB, Haug T, Hammill MO. Harp Seals: Monitors of Change in Differing Ecosystems. *Frontiers in Marine Science*. 2020; 7. <https://doi.org/10.3389/fmars.2020.569258>
43. Gjøsæter H, Bogstad B, Tjelmeland S. Ecosystem effects of the three capelin stock collapses in the Barents Sea. *Marine Biology Research*. 2009; 5(1): 40–53. <https://doi.org/10.1080/17451000802454866>
44. Hop H, Gjøsæter H. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*. 2013; 9(9): 878–894. <https://doi.org/10.1080/17451000.2013.775458>
45. Lynam CP, Llope M, Möllmann C, Helaouët P, Bayliss-Brown GA, Stenseth NC. Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences*. 2017; 114(8): 1952–1957. <https://doi.org/10.1073/pnas.1621037114> PMID: 28167770
46. Stige LC, Dalpadado P, Orlova E, Boulay A-C, Durant JM, Ottersen G, et al. Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in the Barents Sea. *Progress in Oceanography*. 2014; 120: 243–253. <https://doi.org/10.1016/j.pocean.2013.09.006>
47. Dalpadado P, Arrigo KR, Hjøllø SS, Rey F, Ingvaldsen RB, Sperfeld E, et al. Productivity in the Barents Sea—Response to Recent Climate Variability. *PLoS ONE*. 2014; 9(5): e95273. <https://doi.org/10.1371/journal.pone.0095273> PMID: 24788513
48. Stige LC, Eriksen E, Dalpadado P, Ono K. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. *ICES Journal of Marine Science*. 2019; 76(Supplement\_1): i24–i36. <https://doi.org/10.1093/icesjms/fsz063>
49. Johannesen E, Yoccoz NG, Tveraa T, Shackell NL, Ellingsen KE, Dolgov AV, et al. Resource-driven colonization by cod in a high Arctic food web. *Ecology and Evolution*. 2020; 10(24): 14272–14281. <https://doi.org/10.1002/ece3.7025> PMID: 33391714
50. Link JS, Ihde TF, Harvey CJ, Gaichas SK, Field JC, Brodziak JKT, et al. Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management. *Progress in Oceanography*. 2012; 102: 102–114. <https://doi.org/10.1016/j.pocean.2012.03.008>

# Paper II

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## COMBINED EFFECTS OF TEMPERATURE AND FISHING MORTALITY ON THE BARENTS SEA ECOSYSTEM STABILITY

**Sivel E., Planque B., Lindstrøm U., Yoccoz N.G.**

(subm.) Fisheries Oceanography



1 **Combined effects of temperature and fishing mortality on the Barents Sea ecosystem**  
2 **stability**

3

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20 **Data Availability Statement**

21 The data and codes used to simulate output time-series are available on the online repository  
22 <https://github.com/ElliotSivel/NDNDScenarios>. Output time-series are available on request  
23 from the corresponding author. The data are not publicly available to the large size of data  
24 files.

25 **Abstract**

26 Temporal variability in abundance and composition of species in marine ecosystems results  
27 from a combination of internal processes, external drivers, and stochasticity. One way to  
28 explore the temporal variability in an ecosystem is through temporal stability, measured using  
29 the inverse of the coefficient of variation for biomass of single species. The effect of  
30 temperature and fisheries on the variability of the Barents Sea food-web is still poorly  
31 understood. To address this question, we simulate the possible dynamics of Barents Sea food-  
32 web under different temperature and fishery scenarios using a simple food-web model  
33 (NDND; Non-Deterministic Network Dynamic). The NDND model, which is based on Chance  
34 and Necessity (CaN), defines the state-space of the ecosystem using its structural constraints  
35 (necessity) and explores it stochastically (chance). The effects of temperature and fisheries  
36 on stability are explored both separately and combined. The simulation results suggest that  
37 increasing temperature has a negative effect on species biomass and increasing fisheries  
38 triggers compensatory dynamics of fish species. There is a major intra-scenario variability in  
39 temporal stability while individual scenarios of temperature and fisheries display a weak  
40 negative impact and no effect on stability, respectively. However, Combined scenarios  
41 indicate that fisheries amplify the effects of temperature on stability while increasing  
42 temperature leads to a shift from synergistic to antagonistic effects between these two  
43 drivers.

44 Keywords: Simulation modelling, Non-deterministic modelling, Chance and Necessity,  
45 Cumulative impacts, Climate change, Fishing mortality, Temporal variability,

46



## 47 **Introduction**

48 Stability is an essential ecosystem feature that has relevance for conservation and  
49 management of resources in terrestrial and aquatic ecosystems (Donohue et al. 2016). Early  
50 works have investigated how species diversity and complexity influence stability (May 1972;  
51 Ives and Carpenter 2007; Pimm 1984; Rooney and McCann 2012). Ecosystem stability is  
52 generally expected to increase with diversity (Tilman, Reich, and Knops 2006; Campbell,  
53 Murphy, and Romanuk 2011) and complexity (May 1972; McCann 2000; Mougi and Kondoh  
54 2016). In contrast, a more recent study showed that species richness explained a relative  
55 small fraction of the variability in population or community abundances (Houlahan et al.  
56 2018). Also, Jacquet et al. (2016) found no association between indicators of food-web  
57 complexity and stability.

58 Ecological stability is a multidimensional concept and encompasses many definitions (Grimm  
59 and Wissel 1997; Donohue et al. 2013; Kéfi et al. 2019). Some definitions of ecological stability  
60 (e.g., resilience, persistence, reliability, or resistance) quantify the response of ecosystems to  
61 perturbations (Donohue et al. 2013; Van Meerbeek, Jucker, and Svenning 2021). This  
62 approach often focuses on the asymptotical behavior of the ecosystem (i.e., the long-term  
63 dynamics of the ecosystem after the perturbation). However, the asymptotical state of  
64 ecosystems is rarely observed in nature (Morozov et al. 2020), leading to an emphasis on  
65 transient dynamics, i.e., short-term dynamics different from the asymptotical behavior  
66 (Hastings 2004; Frank et al. 2011; Dunn, Samhouri, and Baskett 2021). Stochasticity may  
67 promote the occurrence of transient dynamics (Hastings et al. 2021).

68 Rather than to focus on response to perturbation, one can focus on temporal variability as an  
69 indicator of ecological stability (MacArthur 1955). Tilman (1999) proposed a measure of  
70 temporal stability, referred to as constancy (Orians 1975), that is the inverse of the variability  
71 of a variable (e.g., species biomass), often with reference to a specific value, such as the mean  
72 biomass. The inverse of the coefficient of variation is such a measure. It can be applied in a  
73 non-equilibrium context, and it can be generalized at the whole ecosystem scale (Lehman and  
74 Tilman 2000; Hillebrand et al. 2018).

75 Temporal stability of a food-web or species can be calculated from ecological time-series,  
76 informing us about the past dynamics. Unfortunately, using ecological time-series has its  
77 limitations. First, ecological time-series are often relatively short, typically less than 50 years

78 (Lotze and Worm 2009; Evans et al. 2015). Second, ecological time-series are not available for  
79 all species of the ecosystems (e.g., benthos and mammals). Consequently, the variability of  
80 ecological time-series only represents a fraction of the possible variability of marine  
81 ecosystems (Sivel et al. 2021). An alternative to investigate the ecosystem variability is to use  
82 numerical models to simulate ecosystem dynamics over multiple decades.

83 In this study we used the Non-Deterministic Network Dynamic (NDND) model to simulate  
84 possible food-web trajectories. The NDND model is a mass-balanced stochastic food-web  
85 model (i.e., it simulates species dynamics based on their trophic interactions) based on the  
86 principles of chance and necessity (Planque, Lindstrøm, and Subbey 2014). In chance and  
87 necessity modelling, chance reflects the indeterminacy of ecosystem processes and necessity  
88 corresponds to the physical and biological constraints of the system (Mullon et al. 2009;  
89 Planque et al. 2014; Planque and Mullon 2020). In other terms, one considers that possible  
90 events are not pre-determined, but occur randomly (chance) within a set of physical and  
91 biological constraints of the system (necessity). The NDND model was designed to reproduce  
92 the high variability of natural systems by exploring their "state-space". Lindstrøm et al. (2017)  
93 used the model to explore the Barents Sea food-web dynamics and concluded that the model  
94 was able to reproduce multiple emergent food-web patterns, including the temporal stability,  
95 observed the past 30 years.

96 The Barents Sea (Figure 1a) is a sub-arctic shelf sea which have experienced significant  
97 warming (ca. 1°C increase in surface temperature) the past four decades (Timmermans and  
98 Ladd 2019). It resulted in an increase in primary production and a stabilization of the  
99 mesozooplankton biomass (Dalpadado et al. 2020). While, higher temperatures are expected  
100 to increase metabolic rates of organisms in marine ecosystems (O'Connor et al. 2007; Carozza,  
101 Bianchi, and Galbraith 2019), there is no clear consensus on the effect of higher metabolic  
102 rates on the temporal stability of ecosystems. Vasseur & McCann (2005) highlighted a  
103 destabilizing effect of temperature-induced increase of metabolic rates on biomass densities  
104 in simple consumer-resource systems whereas Fussmann et al. (2014) suggested the opposite  
105 for ecosystems. Furthermore, although fisheries are strongly regulated in the Barents Sea,  
106 they still represent an important disturbance of ecosystem dynamics (ICES 2020a). Beside the  
107 decrease of population sizes of harvested species stocks, fishing may also lead to increased  
108 variability of harvested species (Hsieh et al. 2006).

109 Anthropogenic activities are expected to increase in the future (Hoegh-Guldberg and Bruno  
110 2010). Thus, their impact on ecosystems needs to be quantified properly to better inform  
111 management and to anticipate possible future changes in ecosystem structure and  
112 functioning. Past studies have assessed the effect of anthropogenic drivers on the ecosystem.  
113 They have pointed out that the effects of anthropogenic drivers should not be treated  
114 separately (e.g., Shannon et al., 2010; Jarre et al., 2015). Although the impact of  
115 anthropogenic drivers of marine ecosystems are well documented, their combined effects  
116 with climate change are still debated in the literature. Single species modelling studies  
117 highlighted synergistic effects between climate change and fisheries on species biomass in  
118 different ecosystems (Hidalgo et al. 2011; Fuller, Brush, and Pinsky 2015; Koul et al. 2021). At  
119 the ecosystem scale, a recent multi-model study suggested additive effects of temperature  
120 and fisheries on species mean biomass as they found no major alteration of the effects of  
121 climate change when harvesting was accounted for in their models (Lotze et al. 2019).  
122 Another model study using the end-to-end ecosystem model Atlantis suggested that  
123 combined effects of temperature and fishing on biomass were variable for individual species  
124 of the Southern Benguela upwelling ecosystem (Ortega-Cisneros et al. 2018).

125 Perry et al. (2010) and Planque et al. (2010) suggested that climate variability and fisheries  
126 have synergistic effects on the ecosystem variability due to an increase in the sensitivity of  
127 marine ecosystems to climate variability. Barents Sea dynamics displayed large fluctuations  
128 during the past five decades as the result of a combination of harvesting and ecological  
129 processes (Hjermann, Ottersen, and Stenseth 2004; Koen-Alonso, Lindstrøm, and Cuff 2021).  
130 Fisheries led the cod stock to decline in the 1980's before recovering only recently due to  
131 appropriate management policies (Lilly, Nakken, and Brattey 2013), while a combination of  
132 harvesting and predation triggered large fluctuations of the capelin stock on an interdecadal  
133 timescale since 1980 (Hjermann et al. 2004). As anthropogenic activities are expected to  
134 increase in intensity over the next decades, it is essential to understand how combined effects  
135 of climate change and fisheries affects the biomass variability of the Barents Sea ecosystem.

136 In this study, we explore the combined impacts of climate change and fisheries on the  
137 temporal stability of the Barents Sea food-web. We performed simulations of food-web  
138 dynamics for scenarios of climate change (temperature) and fisheries (fishing mortality) using  
139 the NDND model for the Barents Sea. We estimated the temporal stability of the food-web

140 for each simulation to assess the impact of climate change and fisheries on the food-web  
141 independently, and to test for additive, synergistic or antagonistic effects of both drivers on  
142 the temporal stability of the Barents Sea food-web.

## 143 **Material and Methods**

### 144 A. The Non-Deterministic Network Dynamics model (NDND)

145 The NDND model is a stochastic mass-balanced food-web model in which trophic interactions  
146 are indeterminate (Mullon et al. 2009; Planque et al. 2014; Lindstrøm et al. 2017). In the  
147 NDND model, variations in biomass result from transfers of biomass between the  
148 trophospecies (hereafter named species). The values of trophic flows are randomly sampled  
149 (chance) given a set of simple physical and biological constraints (necessity). There are five  
150 constraints implemented in the NDND model: 1) satiation constrains the food intake of a  
151 predator, inertia constrains the maximum 2) increase and 3) decrease of species biomass at  
152 each time-step, 4) the trophic flows must be positive, and 5) species biomass must be higher  
153 than a threshold value referred to as the refuge biomass.

154 In the present study, we used the simplified food-web topology of the Barents Sea, defined  
155 by Lindstrøm et al. (2017). It comprises eight trophospecies (phytoplankton, herbivorous  
156 zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, marine  
157 mammals, and birds), 18 trophic links, and 4 flows towards fisheries (Figure 1b).

158 We used the parametrization of the NDND model specified by Sivel et al. (2021) as the  
159 reference scenario (Table 1). We updated the initial biomass of the herbivorous zooplankton,  
160 omnivorous zooplankton, pelagic fish, and demersal fish groups with the biomass data from  
161 the working group on integrated assessment of the Barents Sea (WGIBAR) for the year 2018  
162 (ICES 2020b). For phytoplankton, benthos, marine mammals, and birds, biomass data were  
163 not available. Thus, we kept initial biomass values estimated by Lindstrøm et al. (2017).

164 As in Sivel et al. (2021), we have expressed harvesting of fish species (i.e., pelagic and  
165 demersal fish) using harvest control rules (HCR) which resemble current fishing regulations in  
166 the Barents Sea (Gullestad et al. 2014). In this study, we added harvesting of benthos, and  
167 marine mammals. Harvesting of benthos corresponds to harvesting of Northern shrimp  
168 (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*). Harvesting of marine mammals  
169 represents harvesting of harp seal (*Pagophilus groenlandicus*) and minke whale

170 (*Balaenoptera acutorostrata*). Given that catches of Northern shrimp and snow crab  
 171 represent only a small fraction of the total harvested benthos biomass, and that no HCR was  
 172 defined for minke whales (Howell and Bogstad 2010), we implemented harvesting of benthos  
 173 and marine mammals as a constant catch ( $C$ ) at each time-step, over the entire simulation.  
 174 Total catches for snow crab were not available for the year 2018, thus we implemented the  
 175 total catches of benthos for the year 2017. The aggregated total catches of Northern shrimp  
 176 and snow crab in 2017 was  $0.026 \text{ tons}\cdot\text{km}^{-2}$  (Hjelset, Hvingel, and Sundet 2018; NAFO/ICES  
 177 2020). Annual catches of marine mammals are expressed in number of hunted individuals. To  
 178 estimate the catch of marine mammals in biomass (i.e., in  $\text{tons}\cdot\text{km}^{-2}$ ), we applied conversion  
 179 factors of 0.15 and 5  $\text{tons}\cdot\text{ind}^{-1}$  for harp seals and minke whales, respectively. For harp seals,  
 180 we excluded the pups (i.e., all individuals younger than one year) from the total count of  
 181 hunted individuals. In 2019, 568 harp seals and 429 minke whales were caught, leading to a  
 182 total catch of  $0.0014 \text{ tons}\cdot\text{km}^{-2}$  (NAMMCO – North Atlantic Marine Mammal Commission,  
 183 2021). The initial harvesting parameters used for our simulations are presented in Table 2.  
 184 For all harvested species, we assumed fisheries to be compensatory (i.e., losses due to  
 185 harvesting are compensated by predation rates).

#### 186 B. Estimation of temporal stability

187 The NDND model simulates multiple biomass trajectories for the species of the Barents Sea  
 188 food-web. Temporal stability of individual species ( $S_i$ ) corresponds to the inverse of the  
 189 coefficient of variation (Lehman and Tilman 2000):

$$S_i = \frac{\overline{B}_i}{sd(B_i)} \quad \text{Eq. 1}$$

190 Where  $\overline{B}_i$  is the mean biomass for species  $i$  and  $sd(B_i)$  is the standard deviation of biomass of  
 191 species  $i$ . Lehman and Tilman (2000) suggested a generalized formulation of temporal stability  
 192 for the whole food-web ( $S$ ):

$$S = \frac{\sum_i \overline{B}_i}{\sqrt{\sum_i \text{var } B_i + \sum_{i,j} \text{cov } B_{i,j}}} \quad \text{Eq. 1}$$

193 Where the numerator is the sum of mean species biomasses ( $\overline{B}_i$ ),  $\text{var } B_i$  is the variance of  
 194 biomass of species  $i$  and  $\text{cov } B_{i,j}$  is the covariance estimated from the biomass time-series of  
 195 species  $i$  and  $j$  (i.e. the sum of all terms of the species covariance matrix).

### 196 C. Scenarios of temperature and fishing mortality

197 To assess the effect of climate change and fisheries on the stability of the Barents Sea food-  
198 web, we used predefined scenarios of changes in temperature and fisheries catches.

199 The four temperature change scenarios were as follows: 1) decrease by one degree, 2) no  
200 temperature variation, 3) increase by one degree, and 4) increase by two degrees. The effects  
201 of temperature on physiological parameters were applied only for ectotherms (i.e., all species  
202 except marine mammals and birds). Conventionally, the impact of temperature variations on  
203 the values of metabolic rates is expressed as  $Q_{10}$ , which represent the temperature  
204 dependency of metabolic rates across a temperature range of  $10^{\circ}\text{C}$  (Gillooly et al. 2001). In  
205 the Metabolic Theory of Ecology (MTE, Gillooly et al. 2001; Brown et al. 2004) the metabolic  
206 rates are expressed in terms of body size and temperature. According to the MTE, we  
207 estimated that a one degree increase in temperature leads to a 10% increase in metabolic  
208 rates (supplementary materials). This applies to metabolic losses ( $\mu$ ), inertia ( $\rho$ ), and satiation  
209 ( $\sigma$ ), which are expected to be temperature dependent (Brown et al. 2004; Vasseur and  
210 McCann 2005).

211 Fisheries scenarios explored variations in fishing mortality. We considered four fishing  
212 mortality scenarios: 1) a 50% decrease in fishing mortality, 2) no change (reference level), 3)  
213 a 25% increase in fishing mortality and 4) a 50% increase in fishing mortality. We implemented  
214 the variation in fishing mortality by modifying the fishing mortality rate ( $F_{mp}$ ) for pelagic and  
215 demersal fish, and the annual catches ( $C$ ) for benthos and marine mammals.

### 216 D. Simulations

217 Simulations and statistical analysis were performed using R (v.4.1.0) (R Core Team 2021). The  
218 sampling algorithm used in the NDND model is the Complex Polytope Gibbs Sampling  
219 algorithm (cpgs) from the RCaN package (Drouineau, Planque, and Mullon 2021).

220 To explore exhaustively the possible trajectories of the Barents Sea food-web, we generated  
221 1000 biomass trajectories of 230 years for each scenario. We removed the 200 first years as  
222 a burn-in period to ensure that the simulated biomass used for estimating the temporal  
223 stability is independent from the initial biomass. Temporal stabilities were thus estimated for  
224 time-series of 30y. This is comparable to the length of many existing observational time-series  
225 for the Barents Sea ecosystem.

226 The simulated trajectories of phytoplankton correspond to the remaining biomass that has  
227 not been consumed at the previous time step and the import of phytoplankton into the  
228 Barents Sea. Thus, they do not reflect the dynamics of phytoplankton, and we removed  
229 phytoplankton from the analysis.

#### 230 E. Analysis of temperature and fishing mortality effects

231 We estimated temporal stability for individual species and the whole food-web using Eqs. 1  
232 and 2, respectively. We analyzed the effect of variations in temperature and fishing mortality  
233 on temporal stability using violin plots to visualize changes in temporal stability across  
234 scenarios. Given that temporal stability is measured as the ratio between mean biomass and  
235 biomass variability, changes in stability can possibly arise from changes in mean biomass. We  
236 investigated the dependency of temporal stability to the mean biomass for the whole food-  
237 web and the species. For this purpose, we plotted temporal stability against mean biomass.  
238 To eliminate the scale difference between biomass variations at different mean biomass  
239 levels (Fisher 1937), we plotted mean biomass on the log<sub>10</sub>-scale.

240 To identify the nature of combined effects of variations of temperature and fishing mortality  
241 on temporal stability, we compared the anomalies between the measured median temporal  
242 stability in all scenarios and the median temporal stability in the reference scenario to the  
243 expected anomalies for additive effects (see Figure S2 in supplementary materials). Piggott et  
244 al. (2015) redefined the terms of antagonism and synergism as deviations from an additive  
245 effect prediction. The authors emphasized the importance of the direction of the effect of  
246 stressors and define five directional interaction classes: additive, synergistic (+ and -), and  
247 antagonistic (+ and -). Here, we defined the combined effects of temperature and fisheries on  
248 stability as follows:

- 249 • No deviation from the additive expectation corresponds to additive effects of  
250 temperature and fishing.
- 251 • A deviation greater in absolute term than the additive effect indicates synergism while  
252 a smaller deviation indicates antagonism between temperature and fisheries.

## 253 Results

### 254 A. Impact of temperature and fishing mortality on biomass

255 Simulated biomass of each species covered a large range of values (Figure 2). While lower

256 trophic levels biomass varied by one order of magnitude, marine mammals biomass varied by  
257 two orders of magnitude. Additionally, fish and birds biomass varied up to four orders of  
258 magnitude. Interestingly, the total biomass of the food-web only varied by a factor of three.  
259 Simulated biomass of each species and of the whole food-web revealed that changes in  
260 temperature and fishing mortality influenced biomass (Figure 2). Higher temperature had a  
261 negative effect on the biomass of all species (Figure 2A). Yet, demersal fish displayed lower  
262 biomass in the scenario with lower temperature ( $-1^{\circ}\text{C}$ ). Pelagic fish biomass decreased by a  
263 factor of 5 between the scenario with the lowest temperature ( $-1^{\circ}\text{C}$ ) and the one with the  
264 highest temperature ( $+2^{\circ}\text{C}$ ) while birds biomass displayed a decline in biomass by a factor of  
265 3. For other species (zooplankton, benthos and mammals) and for the food-web as a whole,  
266 the decrease in biomass associated with increasing temperature did not exceed 20%.

267 Increasing fishing mortality affected pelagic fish, demersal fish, and birds' biomasses (Figure  
268 2B). Globally, fishing led to a redistribution of the biomass between these three species but  
269 did not significantly affect the total biomass of the food-web. Pelagic and demersal fish  
270 biomass displayed opposed responses to higher fishing mortality. Between the scenarios with  
271 the lowest ( $-50\%$ ) and the highest fishing mortality ( $+50\%$ ), pelagic fish biomass increased by  
272 a factor of 3 whereas demersal fish biomass decreased by the same factor. Birds displayed an  
273 increase in biomass of 50% between the three scenarios with the lowest fishing mortality (i.e.,  
274  $-50\%$ , no variation, and  $+25\%$ ). In the scenario with the highest fishing mortality ( $+50\%$ ), birds'  
275 biomass was at the same level as in the scenario with an increase of 25% in fishing mortality.  
276 Zooplankton species, benthos, and marine mammals' biomasses did not display any response  
277 to variations in fishing mortality.

## 278 B. Impact of temperature and fishing mortality on temporal stability

279 We estimated temporal stability from simulations for relatively short time periods (30 years)  
280 and observed a large range of temporal stability values for all species in all scenarios of  
281 temperature and fishing mortality (Figure 3). For example, the ranges of estimated stabilities  
282 for demersal fish covered one order of magnitude. This level of uncertainty remained similar  
283 across temperature and fishing scenarios. Median stability varied between temperature  
284 scenarios (Figure 3A) but displayed little variations between fishing scenarios (Figure 3B).  
285 Temporal stability declined in response to higher temperatures for benthos, pelagic fish,  
286 demersal fish species, and the whole Barents Sea food-web. Yet, changes in median stability



287 as a response to changes in temperature were small compared to the variability of stability  
288 estimates. We found the largest decrease in stability between the coldest and the warmest  
289 scenario for demersal fish (30%). For other species, the temporal stability between the coldest  
290 and the warmest scenario did not decrease by more than 10%.

#### 291 C. Effect of biomass variations on temporal stability

292 Given equation 1, observed changes in stability, can result from changes in the standard  
293 deviation of biomass and from the mean biomass. We investigated the dependency of  
294 stability estimates to the values of mean biomass of individual species and the whole food-  
295 web. For herbivorous zooplankton, omnivorous zooplankton, and benthos, stability increased  
296 with higher mean biomass (Figure 4). Pelagic fish stability decreased in response to increasing  
297 mean biomass when mean biomass was low ( $< 0.01 \text{ tons}\cdot\text{km}^{-2}$ ), while it remained constant  
298 for intermediate values of mean biomass (between  $0.01 \text{ tons}\cdot\text{km}^{-2}$  and  $0.1 \text{ tons}\cdot\text{km}^{-2}$ ), and it  
299 increased when mean biomass was high ( $> 0.1 \text{ tons}\cdot\text{km}^{-2}$ ). For demersal fish, stability  
300 decreased gradually with increasing mean biomass. For marine mammals, birds, and the  
301 whole food-web, we found no relationship between stability and mean biomass.

#### 302 D. Combined effect of fisheries and temperature on temporal stability

303 Variations in temperature were the largest driver of changes in temporal stability (Figure 5),  
304 and these changes were only observed for harvested species. The largest response was  
305 observed for demersal fish. For herbivorous zooplankton, and birds there were no visible  
306 effect of temperature and fishing on stability. Increased fishing mortality had a positive  
307 impact on demersal fish and marine mammals' stabilities regardless of the temperature  
308 scenario. Omnivorous zooplankton displayed antagonistic effects of temperature and fishing,  
309 but we found no increase in stability anomalies in response to increased temperature and  
310 harvesting. Benthos and pelagic fish showed small differences in stability anomalies indicating  
311 mostly additive effects of temperature and fishing. In the higher temperature scenario ( $+2^\circ\text{C}$ ),  
312 the response of stability to cumulated temperature and fishing pressures were lower than the  
313 addition of responses to individual pressures, indicative of antagonistic interactions.  
314 Demersal fish exhibited larger combined effects on stability than the additive ones in the  
315 scenarios with lower temperature indicating synergistic effects on stability. Contrarily, we  
316 found antagonistic effects of temperature and fishing on demersal fish stability in warmer  
317 temperature scenarios. Marine mammals displayed strong antagonistic effects of

318 temperature and fishing mortality on stability, given that the expected anomalies were larger  
319 than the measured ones.

320 Stability of the whole food-web displayed a similar pattern as the harvested species.  
321 Temperature and fishing had synergistic effects in scenarios of colder temperature and low  
322 harvesting. As for demersal fish, in scenarios of low fisheries and warmer temperatures, we  
323 found antagonistic effects. In scenarios of higher harvesting, the nature of combined effects  
324 was opposed to the scenario of low harvesting. In scenarios of colder temperature and higher  
325 fisheries combined effects were antagonistic while they were synergistic in scenarios of  
326 warmer temperature and higher fisheries.

## 327 **Discussion**

328 In this study, we explored the combined effects of temperature and fisheries on the temporal  
329 stability of the Barents Sea food-web. Temperature negatively affected the species and food-  
330 web biomass, while fisheries redistributed biomass among individual species without  
331 affecting the total biomass of the food-web. Individual drivers had weak effects on stability.  
332 However, we found amplified effects of temperature for harvested species. Also, we observed  
333 synergistic effects of temperature and fisheries in response to colder temperature scenarios  
334 and antagonistic effects in warmer temperature scenarios.

### 335 A. Effects of temperature and fishing mortality on biomass

336 Globally, increasing temperature had a negative effect on the biomass and stability of the  
337 Barents Sea food-web. The observed biomass decreases in response to increasing  
338 temperature, for all but one species (demersal fish), goes against observations of increasing  
339 zooplankton biomass in response to warmer temperature in the Barents Sea (Dalpadado et  
340 al. 2020). Furthermore, recent modelling studies suggested that increasing temperatures in  
341 polar marine ecosystems should lead to a significant biomass increase at the horizon 2100  
342 (Bryndum-Buchholz et al. 2019; Lotze et al. 2019). Lotze et al. (2019) also highlighted that  
343 biomass decreases were higher in higher trophic levels due to trophic amplification. Our  
344 results do not fully support this statement because the biomass of demersal fish and marine  
345 mammals did not decline in response to higher temperatures as much as the zooplankton  
346 species. In our simulations, demersal fish biomass decreased for the coldest temperature  
347 scenario. The analysis of the trophic flows showed that, for this scenario, the food intake by

348 demersal fish was reduced (supplementary materials Figure S4). This was caused by reduced  
349 feeding capacity at lower temperature which was not compensated by changes in other  
350 temperature dependent processes (i.e., inertia and metabolic losses).

351 Fisheries affected the biomass of pelagic fish, demersal fish, and birds. The decline of  
352 demersal fish biomass in direct response to increased fishery mortality triggered an increase  
353 in pelagic fish and birds' biomass suggesting that predatory effects outweigh harvesting  
354 effects on pelagic fish. This is to some extent in line with a previous study (Lindstrøm et al.  
355 2009), which showed that reduced abundance of cod from harvesting led to increased  
356 abundance of capelin, whereas reduced harvesting on capelin had minor impact on its own  
357 dynamics and on the dynamics of cod and herring. This is further confirmed in the study by  
358 Myers and Worm (2003), which provides multiple examples of compensatory dynamics  
359 between pelagic and demersal fish in marine ecosystems due to released predation on pelagic  
360 fish and competition. Using a simple end-to-end model, Heath et al. (2021) presented similar  
361 conclusions for the North Sea ecosystem, which are consistent with our results. The ensuing  
362 birds' biomass increase in our simulation can be explained by the increase of food availability  
363 due to higher pelagic fish biomass. However, we see that the biomass of birds is also limited  
364 by satiation as their biomass do not increase for higher fisheries although pelagic fish biomass  
365 does.

366 Interestingly, the biomass of zooplankton species, benthos, and marine mammals was not  
367 affected by variations in the biomass of other species. The relative stability of marine  
368 mammals' biomass in response to decreasing demersal fish biomass reflects the shift in the  
369 diet of marine mammals from demersal fish to pelagic fish (supplementary materials Figure  
370 S3 & S4). We assume that the lack of response of zooplankton species to variations in upper  
371 trophic levels resulted from the decoupling of zooplankton and pelagic fish dynamics. This is  
372 thought to have occurred in the past when primary production was high (Dalpadado et al.  
373 2020). When conducting model reconstructions of the past dynamics of the Barents Sea food-  
374 web, with a parametrization similar to the current study, Planque & Mullon (2020) observed  
375 that assumed that zooplankton dynamics could be reconstructed with substantially lower  
376 primary production, which suggested that the assumed primary production in the model was  
377 likely too high. In this study, we can interpret the decoupling of zooplankton and pelagic fish  
378 dynamics as a result of too high import of phytoplankton biomass, which is a proxy for primary

379 production in the NDND model. Another possible explanation is that we have underestimated  
380 some trophic flows in our simulations. For example, a recent study highlighted that feeding  
381 rates of baleen whales on krill (i.e., omnivorous zooplankton) estimated from metabolic rates  
382 were underestimated by at least a factor of three (Savoca et al. 2021). Allowing marine  
383 mammals to feed more on omnivorous zooplankton in the model could have significantly  
384 reduce the omnivorous zooplankton biomass and affect the trophic dynamics of other species  
385 feeding on omnivorous zooplankton.

386 In the NDND model, fishing mortality is implemented as a fully compensatory process i.e., the  
387 sum of the different sources of mortalities (predation, fisheries catch, and other losses) is  
388 bounded by inertia. An alternative formulation is to consider individual mortality sources as  
389 being additive, and not jointly-bounded. Full compensation of fishing mortality by other  
390 sources of mortality has not been observed in natural systems (Froese et al. 2016). It has been  
391 argued that the degree of fisheries compensation is expected to be on a continuum between  
392 compensatory and additive (Myers and Quinn II 2002; Péron 2013). Further investigations are  
393 required to better assess the degree of fisheries compensation in the Barents Sea, and to  
394 verify that the current conclusions are robust in the case of mortalities being partially additive  
395 and partially compensatory.

#### 396 B. Effects of temperature and fishing mortality on stability

397 In our simulations, increased temperature led to increased metabolic rates which rendered  
398 the system more dissipative. Increased temperature also relaxed the inertia and satiation  
399 constraints which in turn increased the range of possible biomass variations and the  
400 maximum food intake. Consequently, we expected higher temperature to destabilize the  
401 Barents Sea food-web and its species by increasing biomass variability. However, our results  
402 only partly support these expectations as only benthos and fish species temporal stability  
403 were affected by increased temperature. It indicates that the changes in biomass variability  
404 could be compensated by changes in mean biomass, or by trophic feedbacks within the food-  
405 web.

406 We expected increased fishing mortality to increase the variability of harvested species (Hsieh  
407 et al. 2006). Yet, we found minimal effects of fisheries on stability. The limited response of  
408 marine mammals' stability can result from low annual catch relative to the total marine  
409 mammals' biomass. The absence of effects of harvesting on pelagic and demersal fish stability

410 indicates that mean biomass and biomass variance covary (supplementary materials Figure  
411 S6 & S7). In other words, biomass variations for both fish species are compensated by  
412 variations in biomass standard deviation.

413 Pelagic fish displayed three distinct relationships between stability and mean biomass. We  
414 interpret these relationships as being primarily a result of the model structure, which sets  
415 hard minimum and maximum limits to the biomass of small pelagics. The refuge biomass  
416 prevents biomass to decrease below a threshold value. When the biomass tends towards this  
417 value, predators continue feeding on this species while its biomass cannot decrease further,  
418 which leads to decreasing variability. As temporal stability measures the biomass variability  
419 in relation to mean biomass, the lower variability corresponds to higher stability. A  
420 comparable effect is visible for extremely high values of biomass. In this case, a plausible  
421 explanation is that a combination of inertia and satiation that limits biomass increase while  
422 higher biomass allows higher predation on pelagic fish. It results in an increase in stability  
423 with increasing biomass. Consequently, given the absence of relationship between stability  
424 and mean biomass at intermediate levels of mean biomass, we assume that if the structural  
425 constrains of the NDND model were modified, the relationship between mean biomass and  
426 temporal stability for pelagic fish could be similar to the one observed for demersal fish.

427 Individual effects of temperature and fisheries on the stability of the whole food-web were  
428 minimal. Our results suggest “mean-variance rescaling” (Cottingham, Brown, and Lennon  
429 2001), which implies that increasing mean biomass result in increased biomass variance.  
430 Mean-variance rescaling relationships are expected to increase stability (Grman et al. 2010).  
431 On the contrary, synchrony in species dynamics is expected to have a destabilizing effect on  
432 the food-web and its species (Loreau and de Mazancourt 2008). Thus, a possible explanation  
433 for the absence of temperature effects on stability is that mean-variance rescaling and  
434 synchrony compensate each other which maintain stability at similar levels in all temperature  
435 scenarios. In our simulations, pelagic and demersal fish displayed opposite responses to  
436 increased fisheries while the stability of the whole food-web remained constant for different  
437 levels of harvesting rates. Asynchrony leads to negative covariance which result to increase  
438 the food-web’s stability (Loreau and de Mazancourt 2008). Again, the combination of mean-  
439 variance rescaling effect with the stabilizing effect of species asynchrony is a possible  
440 explanation for the absence of response of food-web level stability to increased harvesting

441 rates.

442 Species that were not harvested in our simulations (i.e., herbivorous zooplankton,  
443 omnivorous zooplankton, and birds) displayed minimal combined effects of temperature and  
444 harvesting on estimated stabilities. Increasing temperature had a negative effect on benthos,  
445 pelagic fish, and demersal fish stabilities. We assume that increasing temperature did not  
446 affect marine mammals because temperature did not affect their metabolic rates in our  
447 study. Demersal fish displayed the strongest response to increasing temperature among all  
448 harvested species. It suggests that more intense harvesting amplifies the effects of increasing  
449 temperature on stability. This result is in line with the expectations that harvesting increases  
450 the variability of exploited species (Hsieh et al. 2006). Yet, it also shows that the harvesting  
451 rate also plays a role in the sensitivity of the food-web dynamics to temperature changes.

452 For benthos and fish species, we found that in colder scenarios, combined effects were  
453 synergistic while they were antagonistic in warmer temperature scenarios. These findings are  
454 not in line with the existing literature. Nye et al. (2013) suggested that the combined effects  
455 of temperature and harvesting on the US continental shelf were mostly additive but that in  
456 some cases, strong synergistic effects were identifiable. Another study using the Atlantis  
457 model for the Benguela upwelling ecosystem high-light antagonistic, additive, and synergistic  
458 effects of temperature and fisheries (Ortega-Cisneros et al. 2018). However, their findings  
459 suggest that the nature of the combined effects of temperature and fishing were dependent  
460 on the species while our results suggest that they depend on the temperature scenario.

461 The combined effects of temperature and fisheries on the whole food-web displayed a similar  
462 pattern to the combined effects on harvested species (i.e., negative effect of temperature  
463 and positive effect of fisheries). However, the shifts in the nature of the combined effects in  
464 response to increased fishing mortality indicate that the effect of fisheries on stability is lower  
465 than expected if combined effects were additive. Furthermore, we consider that the negative  
466 effect of temperature on stability also reduces the effect of fisheries on stability. Indeed,  
467 individual effects of harvesting on stability is larger than the combined effects of temperature  
468 and harvesting in the crossed scenarios.

### 469 C. Limitations

470 In this study, we have estimated the temporal stability over time-periods of 30 years, a

471 duration that is in line with many observational time-series in the Barents Sea. Pimm &  
472 Redfearn (1988) suggested that variability increase with the length of time-series. The NDND  
473 model can be used to simulate longer time-series, and when this is done, temporal stability  
474 declines with increasing length of available time-series (Supplementary material Figure S1).  
475 This is consistent with Pimm & Redfearn (1988) proposition. Our results are therefore valid  
476 for 30y time series, but additional simulations would be required to verify that the conclusions  
477 hold for longer time periods.

478 We aimed at assessing the effect of climate change on the temporal stability of the Barents  
479 Sea food-web using temperature variations as a proxy for climate change. We have  
480 implemented the effect of temperature on the metabolic rates of the concerned species.  
481 However, we have not considered other aspects of climate change in our analysis, such as  
482 climate driven changes in primary production. We maintained a constant import of  
483 phytoplankton (i.e. proxy for primary production in the NDND model) in our simulations. Past  
484 observations displayed an increase in primary production in response to higher temperatures  
485 (Dalpadado et al. 2020). However, this increase is also closely related to the decrease of sea  
486 ice cover, which does not necessarily imply an increase of productivity per spatial unit. In  
487 addition, a modelling study suggested that increasing temperature would reduce primary  
488 production in the Barents Sea (Holt et al. 2016). In this context, as we did for temperature  
489 and fishing mortality, we assume that the effect of increased and decreased primary  
490 production on the Barents Sea food-web needs to be further investigated to anticipate for  
491 both cases.

## 492 **Conclusion**

493 In this study, we found that climate and fisheries affected the biomass of individual species in  
494 the Barents Sea while the biomass of the entire food-web was not significantly altered.  
495 Temperature increases generally led to reduced species biomass, while variations in  
496 harvesting rates led to compensatory dynamics between fish species. Counter-intuitively,  
497 climate and fisheries didn't strongly affect the stability of the food-web. We also found that  
498 the effect of fisheries on stability was negligible compared to the effect of temperature.  
499 However, increased fishing amplified the effects of climate variations. Finally, we found that  
500 combined effects of climate and fisheries shifted from synergism to antagonism with  
501 increasing temperature.

502 **Conflict of interest**

503 None.

504 **Authors contribution**

505 ES wrote the manuscript along with BP, UF, and NY. All authors conceived the presented idea.

506 ES analyzed model outputs. All authors discussed results and contributed to the final  
507 manuscript.

508 **References**

509 Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West.  
510 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85(7):1771–89. doi:  
511 10.1890/03-9000.

512 Bryndum-Buchholz, Andrea, Derek P. Tittensor, Julia L. Blanchard, William W. L. Cheung,  
513 Marta Coll, Eric D. Galbraith, Simon Jennings, Olivier Maury, and Heike K. Lotze. 2019.  
514 "Twenty-First-Century Climate Change Impacts on Marine Animal Biomass and  
515 Ecosystem Structure across Ocean Basins." *Global Change Biology* 25(2):459–72. doi:  
516 10.1111/gcb.14512.

517 Campbell, Veronik, Grace Murphy, and Tamara N. Romanuk. 2011. "Experimental Design and  
518 the Outcome and Interpretation of Diversity–Stability Relations." *Oikos* 120(3):399–  
519 408. doi: 10.1111/j.1600-0706.2010.18768.x.

520 Carozza, David A., Daniele Bianchi, and Eric D. Galbraith. 2019. "Metabolic Impacts of Climate  
521 Change on Marine Ecosystems: Implications for Fish Communities and Fisheries."  
522 *Global Ecology and Biogeography* 28(2):158–69. doi: 10.1111/geb.12832.

523 Cottingham, K. I., B. I. Brown, and J. t. Lennon. 2001. "Biodiversity May Regulate the Temporal  
524 Variability of Ecological Systems." *Ecology Letters* 4(1):72–85. doi: 10.1046/j.1461-  
525 0248.2001.00189.x.

526 Dalpadado, Padmini, Kevin R. Arrigo, Gert L. van Dijken, Hein Rune Skjoldal, Espen Bagøien,  
527 Andrey V. Dolgov, Irina P. Prokopchuk, and Erik Sperfeld. 2020. "Climate Effects on  
528 Temporal and Spatial Dynamics of Phytoplankton and Zooplankton in the Barents  
529 Sea." *Progress in Oceanography* 185:102320. doi: 10.1016/j.pocean.2020.102320.

530 Donohue, Ian, Helmut Hillebrand, José M. Montoya, Owen L. Petchey, Stuart L. Pimm, Mike  
531 S. Fowler, Kevin Healy, Andrew L. Jackson, Miguel Lurgi, Deirdre McClean, Nessa E.  
532 O'Connor, Eoin J. O'Gorman, and Qiang Yang. 2016. "Navigating the Complexity of  
533 Ecological Stability." *Ecology Letters* 19(9):1172–85. doi: 10.1111/ele.12648.

534 Donohue, Ian, Owen L. Petchey, José M. Montoya, Andrew L. Jackson, Luke McNally, Mafalda  
535 Viana, Kevin Healy, Miguel Lurgi, Nessa E. O'Connor, and Mark C. Emmerson. 2013.  
536 "On the Dimensionality of Ecological Stability." *Ecology Letters* 16(4):421–29. doi:  
537 <https://doi.org/10.1111/ele.12086>.



- 538 Drouineau, Hilaire, Benjamin Planque, and Christian Mullon. 2021. *RCaN : A Software for*  
539 *Chance and Necessity Modelling*. preprint. Ecology. doi: 10.1101/2021.06.09.447734.
- 540 Dunn, Robert P., Jameal F. Samhour, and Marissa L. Baskett. 2021. "Transient Dynamics  
541 during Kelp Forest Recovery from Fishing across Multiple Trophic Levels." *Ecological*  
542 *Applications* 31(6):e02367. doi: 10.1002/eap.2367.
- 543 Evans, Karen, Jaclyn N. Brown, Alex Sen Gupta, Simon J. Nicol, Simon Hoyle, Richard Matear,  
544 and Haritz Arrizabalaga. 2015. "When 1+1 Can Be >2: Uncertainties Compound When  
545 Simulating Climate, Fisheries and Marine Ecosystems." *Deep Sea Research Part II:*  
546 *Topical Studies in Oceanography* 113:312–22. doi: 10.1016/j.dsr2.2014.04.006.
- 547 Fisher, Ronald Aylmer. 1937. "The Relation between Variability and Abundance Shown by the  
548 Measurements of the Eggs of British Nesting Birds." *Proceedings of the Royal Society*  
549 *of London. Series B - Biological Sciences* 122(826):1–26. doi: 10.1098/rspb.1937.0006.
- 550 Frank, Kenneth T., Brian Petrie, Jonathan A. D. Fisher, and William C. Leggett. 2011. "Transient  
551 Dynamics of an Altered Large Marine Ecosystem." *Nature* 477(7362):86–89. doi:  
552 10.1038/nature10285.
- 553 Froese, Rainer, Carl Walters, Daniel Pauly, Henning Winker, Olaf L. F. Weyl, Nazli Demirel,  
554 Athanassios C. Tsikliras, and Sidney J. Holt. 2016. "A Critique of the Balanced  
555 Harvesting Approach to Fishing." *ICES Journal of Marine Science* 73(6):1640–50. doi:  
556 10.1093/icesjms/fsv122.
- 557 Fuller, Emma, Eleanor Brush, and Malin L. Pinsky. 2015. "The Persistence of Populations  
558 Facing Climate Shifts and Harvest." *Ecosphere* 6(9):art153. doi: 10.1890/ES14-  
559 00533.1.
- 560 Fussmann, Katarina E., Florian Schwarzmüller, Ulrich Brose, Alexandre Jousset, and Björn C.  
561 Rall. 2014. "Ecological Stability in Response to Warming." *Nature Climate Change*  
562 4(3):206–10. doi: 10.1038/nclimate2134.
- 563 Gillooly, James F., James H. Brown, Geoffrey B. West, Van M. Savage, and Eric L. Charnov.  
564 2001. "Effects of Size and Temperature on Metabolic Rate." *Science* 293(5538):2248–  
565 51. doi: 10.1126/science.1061967.
- 566 Grimm, V., and Christian Wissel. 1997. "Babel, or the Ecological Stability Discussions: An  
567 Inventory and Analysis of Terminology and a Guide for Avoiding Confusion." *Oecologia*  
568 109(3):323–34. doi: 10.1007/s004420050090.
- 569 Grman, Emily, Jennifer A. Lau, Donald R. Schoolmaster, and Katherine L. Gross. 2010.  
570 "Mechanisms Contributing to Stability in Ecosystem Function Depend on the  
571 Environmental Context." *Ecology Letters* 13(11):1400–1410. doi:  
572 <https://doi.org/10.1111/j.1461-0248.2010.01533.x>.
- 573 Gullestad, Peter, Asgeir Aglen, Åsmund Bjordal, Geir Blom, Sverre Johansen, Jørn Krog, Ole  
574 Arve Misund, and Ingolf Røttingen. 2014. "Changing Attitudes 1970–2012: Evolution  
575 of the Norwegian Management Framework to Prevent Overfishing and to Secure

- 576 Long-Term Sustainability." *ICES Journal of Marine Science* 71(2):173–82. doi:  
577 10.1093/icesjms/fst094.
- 578 Hastings, Alan. 2004. "Transients: The Key to Long-Term Ecological Understanding?" *Trends*  
579 *in Ecology & Evolution* 19(1):39–45. doi: 10.1016/j.tree.2003.09.007.
- 580 Hastings, Alan, Karen C. Abbott, Kim Cuddington, Tessa B. Francis, Ying-Cheng Lai, Andrew  
581 Morozov, Sergei Petrovskii, and Mary Lou Zeeman. 2021. "Effects of Stochasticity on  
582 the Length and Behaviour of Ecological Transients." *Journal of The Royal Society*  
583 *Interface* 18(180):20210257. doi: 10.1098/rsif.2021.0257.
- 584 Heath, Michael R., Douglas C. Speirs, Ian Thurlbeck, and Robert J. Wilson. 2021. "StrathE2E2:  
585 An r Package for Modelling the Dynamics of Marine Food Webs and Fisheries."  
586 *Methods in Ecology and Evolution* 12(2):280–87. doi: 10.1111/2041-210X.13510.
- 587 Hidalgo, M., T. Rouyer, J. C. Molinero, E. Massutí, J. Moranta, B. Guijarro, and N. Chr Stenseth.  
588 2011. "Synergistic Effects of Fishing-Induced Demographic Changes and Climate  
589 Variation on Fish Population Dynamics." *Marine Ecology Progress Series* 426:1–12. doi:  
590 10.3354/meps09077.
- 591 Hillebrand, Helmut, Silke Langenheder, Karen Lebret, Eva Lindström, Örjan Östman, and  
592 Maren Striebel. 2018. "Decomposing Multiple Dimensions of Stability in Global  
593 Change Experiments." *Ecology Letters* 21(1):21–30. doi:  
594 <https://doi.org/10.1111/ele.12867>.
- 595 Hjelset, Ann Merete, Carsten Hvingel, and Jan H. Sundet. 2018. *Snøkrabbe på norsk sokkel i*  
596 *Barentshavet - Bestandsvurdering og kvoterådgivning 2019*. Tromsø:  
597 Havforskningsinstituttet.
- 598 Hjermann, D. O., G. Ottersen, and N. Chr. Stenseth. 2004. "Competition among Fishermen  
599 and Fish Causes the Collapse of Barents Sea Capelin." *Proceedings of the National*  
600 *Academy of Sciences* 101(32):11679–84. doi: 10.1073/pnas.0402904101.
- 601 Hoegh-Guldberg, O., and J. F. Bruno. 2010. "The Impact of Climate Change on the World's  
602 Marine Ecosystems." *Science* 328(5985):1523–28. doi: 10.1126/science.1189930.
- 603 Holt, Jason, Corinna Schrum, Heather Cannaby, Ute Daewel, Icarus Allen, Yuri Artioli, Laurent  
604 Bopp, Momme Butenschon, Bettina A. Fach, James Harle, Dhanya Pushpadas, Baris  
605 Salihoglu, and Sarah Wakelin. 2016. "Potential Impacts of Climate Change on the  
606 Primary Production of Regional Seas: A Comparative Analysis of Five European Seas."  
607 *Progress in Oceanography* 140:91–115. doi: 10.1016/j.pocean.2015.11.004.
- 608 Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, C. S. Findlay, S. D. Fuhlendorf, P.  
609 Legendre, E. H. Muldavin, D. Noble, R. Russell, R. D. Stevens, T. J. Willis, and S. M.  
610 Wondzell. 2018. "Negative Relationships between Species Richness and Temporal  
611 Variability Are Common but Weak in Natural Systems." *Ecology* 99(11):2592–2604.  
612 doi: 10.1002/ecy.2514.

- 613 Howell, Daniel, and Bjarte Bogstad. 2010. "A Combined Gadget/FLR Model for Management  
614 Strategy Evaluations of the Barents Sea Fisheries." *ICES Journal of Marine Science*  
615 67(9):1998–2004. doi: 10.1093/icesjms/fsq135.
- 616 Hsieh, Chih-hao, Christian S. Reiss, John R. Hunter, John R. Beddington, Robert M. May, and  
617 George Sugihara. 2006. "Fishing Elevates Variability in the Abundance of Exploited  
618 Species." *Nature* 443(7113):859–62. doi: 10.1038/nature05232.
- 619 ICES. 2020a. "Arctic Fisheries Working Group 2020 Report." doi: 10.17895/ICES.PUB.6050.
- 620 ICES. 2020b. "Working Group on the Integrated Assessments of the Barents Sea (WGIBAR)."  
621 *ICES Scientific Reports* 2(30):206. doi: 10.17895/ICES.PUB.5998.
- 622 Ives, Anthony R., and Stephen R. Carpenter. 2007. "Stability and Diversity of Ecosystems."  
623 *Science* 317(5834):58–62. doi: 10.1126/science.1133258.
- 624 Jacquet, Claire, Charlotte Moritz, Lyne Morissette, Pierre Legagneux, François Massol,  
625 Philippe Archambault, and Dominique Gravel. 2016. "No Complexity–Stability  
626 Relationship in Empirical Ecosystems." *Nature Communications* 7(1):12573. doi:  
627 10.1038/ncomms12573.
- 628 Jarre, Astrid, Laurence Hutchings, Stephen P. Kirkman, Anja Kreiner, Pedro C. M. Tchipalanga,  
629 Paulus Kainge, Uatjavi Uanivi, Anja K. van der Plas, Laura K. Blamey, Janet C. Coetzee,  
630 Tarron Lamont, Toufiek Samaai, Hans M. Verheye, Dawit G. Yemane, Bjoern E.  
631 Axelsen, Marek Ostrowski, Erling K. Stenevik, and Harald Loeng. 2015. "Synthesis:  
632 Climate Effects on Biodiversity, Abundance and Distribution of Marine Organisms in  
633 the Benguela." *Fisheries Oceanography* 24(S1):122–49. doi: 10.1111/fog.12086.
- 634 Kéfi, Sonia, Virginia Domínguez-García, Ian Donohue, Colin Fontaine, Elisa Thébault, and  
635 Vasilis Dakos. 2019. "Advancing Our Understanding of Ecological Stability." *Ecology*  
636 *Letters* 22(9):1349–56. doi: 10.1111/ele.13340.
- 637 Koen-Alonso, Mariano, Ulf Lindstrøm, and Andrew Cuff. 2021. "Comparative Modeling of  
638 Cod-Capelin Dynamics in the Newfoundland-Labrador Shelves and Barents Sea  
639 Ecosystems." *Frontiers in Marine Science* 8:139. doi: 10.3389/fmars.2021.579946.
- 640 Koul, Vimal, Camilla Sguotti, Marius Årthun, Sebastian Brune, André Düsterhus, Bjarte  
641 Bogstad, Geir Ottersen, Johanna Baehr, and Corinna Schrum. 2021. "Skilful Prediction  
642 of Cod Stocks in the North and Barents Sea a Decade in Advance." *Communications*  
643 *Earth & Environment* 2(1):1–10. doi: 10.1038/s43247-021-00207-6.
- 644 Lehman, Clarence L., and David Tilman. 2000. "Biodiversity, Stability, and Productivity in  
645 Competitive Communities." *The American Naturalist* 156(5):534–52. doi:  
646 10.1086/303402.
- 647 Lilly, George R., Odd Nakken, and John Bratley. 2013. "A Review of the Contributions of  
648 Fisheries and Climate Variability to Contrasting Dynamics in Two Arcto-Boreal Atlantic  
649 Cod (*Gadus Morhua*) Stocks: Persistent High Productivity in the Barents Sea and

- 650 Collapse on the Newfoundland and Labrador Shelf." *Progress in Oceanography*  
651 114:106–25. doi: 10.1016/j.pocean.2013.05.008.
- 652 Lindstrøm, Ulf, Benjamin Planque, and Sam Subbey. 2017. "Multiple Patterns of Food Web  
653 Dynamics Revealed by a Minimal Non-Deterministic Model." *Ecosystems* 20(1):163–  
654 82. doi: 10.1007/s10021-016-0022-y.
- 655 Lindstrøm, Ulf, Sophie Smout, Daniel Howell, and Bjarte Bogstad. 2009. "Modelling Multi-  
656 Species Interactions in the Barents Sea Ecosystem with Special Emphasis on Minke  
657 Whales and Their Interactions with Cod, Herring and Capelin." *Deep Sea Research Part*  
658 *II: Topical Studies in Oceanography* 56(21):2068–79. doi: 10.1016/j.dsr2.2008.11.017.
- 659 Loreau, Michel, and Claire de Mazancourt. 2008. "Species Synchrony and Its Drivers: Neutral  
660 and Nonneutral Community Dynamics in Fluctuating Environments." *The American*  
661 *Naturalist* 172(2):E48–66. doi: 10.1086/589746.
- 662 Lotze, Heike K., Derek P. Tittensor, Andrea Bryndum-Buchholz, Tyler D. Eddy, William W. L.  
663 Cheung, Eric D. Galbraith, Manuel Barange, Nicolas Barrier, Daniele Bianchi, Julia L.  
664 Blanchard, Laurent Bopp, Matthias Büchner, Catherine M. Bulman, David A. Carozza,  
665 Villy Christensen, Marta Coll, John P. Dunne, Elizabeth A. Fulton, Simon Jennings,  
666 Miranda C. Jones, Steve Mackinson, Olivier Maury, Susa Niiranen, Ricardo Oliveros-  
667 Ramos, Tilla Roy, José A. Fernandes, Jacob Schewe, Yunne-Jai Shin, Tiago A. M. Silva,  
668 Jeroen Steenbeek, Charles A. Stock, Philippe Verley, Jan Volkholz, Nicola D. Walker,  
669 and Boris Worm. 2019. "Global Ensemble Projections Reveal Trophic Amplification of  
670 Ocean Biomass Declines with Climate Change." *Proceedings of the National Academy*  
671 *of Sciences* 116(26):12907–12. doi: 10.1073/pnas.1900194116.
- 672 Lotze, Heike K., and Boris Worm. 2009. "Historical Baselines for Large Marine Animals." *Trends*  
673 *in Ecology & Evolution* 24(5):254–62. doi: 10.1016/j.tree.2008.12.004.
- 674 MacArthur, Robert. 1955. "Fluctuations of Animal Populations and a Measure of Community  
675 Stability." *Ecology* 36(3):533–36. doi: 10.2307/1929601.
- 676 May, Robert M. 1972. "Will a Large Complex System Be Stable?" *Nature* 238(5364):413–14.  
677 doi: 10.1038/238413a0.
- 678 McCann, Kevin Shear. 2000. "The Diversity–Stability Debate." *Nature* 405(6783):228–33. doi:  
679 10.1038/35012234.
- 680 Morozov, Andrew, Karen Abbott, Kim Cuddington, Tessa Francis, Gabriel Gellner, Alan  
681 Hastings, Ying-Cheng Lai, Sergei Petrovskii, Katherine Scranton, and Mary Lou Zeeman.  
682 2020. "Long Transients in Ecology: Theory and Applications." *Physics of Life Reviews*  
683 32:1–40. doi: 10.1016/j.plrev.2019.09.004.
- 684 Mougi, A., and M. Kondoh. 2016. "Food-Web Complexity, Meta-Community Complexity and  
685 Community Stability." *Scientific Reports* 6(1):24478. doi: 10.1038/srep24478.

- 686 Mullon, Christian, Pierre Fréon, Philippe Cury, Lynne Shannon, and Claude Roy. 2009. "A  
687 Minimal Model of the Variability of Marine Ecosystems." *Fish and Fisheries* 10(2):115–  
688 31. doi: 10.1111/j.1467-2979.2008.00296.x.
- 689 Myers, Ransom A., and Terrance J. Quinn II. 2002. "Estimating and Testing Non-Additivity in  
690 Fishing Mortality: Implications for Detecting a Fisheries Collapse." *Canadian Journal of*  
691 *Fisheries and Aquatic Sciences* 59(4):597–601. doi: 10.1139/f02-048.
- 692 Myers, Ransom A., and Boris Worm. 2003. "Rapid Worldwide Depletion of Predatory Fish  
693 Communities." *Nature* 423(6937):280–83. doi: 10.1038/nature01610.
- 694 NAFO/ICES. 2020. Report of the NAFO/ICES *Pandalus* Assessment Group Meeting. N7143.  
695 NAFO.
- 696 Nye, Janet A., Robert J. Gamble, and Jason S. Link. 2013. "The Relative Impact of Warming and  
697 Removing Top Predators on the Northeast US Large Marine Biotic Community." *Ecological Modelling*  
698 264:157–68. doi: 10.1016/j.ecolmodel.2012.08.019.
- 699 O'Connor, Mary I., John F. Bruno, Steven D. Gaines, Benjamin S. Halpern, Sarah E. Lester, Brian  
700 P. Kinlan, and Jack M. Weiss. 2007. "Temperature Control of Larval Dispersal and the  
701 Implications for Marine Ecology, Evolution, and Conservation." *Proceedings of the*  
702 *National Academy of Sciences* 104(4):1266–71. doi: 10.1073/pnas.0603422104.
- 703 Orians, Gordon H. 1975. "Diversity, Stability and Maturity in Natural Ecosystems." Pp. 139–50  
704 in *Unifying Concepts in Ecology: Report of the plenary sessions of the First international*  
705 *congress of ecology, The Hague, the Netherlands, September 8–14, 1974*, edited by W.  
706 H. van Dobben and R. H. Lowe-McConnell. Dordrecht: Springer Netherlands.
- 707 Ortega-Cisneros, Kelly, Kevern L. Cochrane, Elizabeth A. Fulton, Rebecca Gorton, and  
708 Ekaterina Popova. 2018. "Evaluating the Effects of Climate Change in the Southern  
709 Benguela Upwelling System Using the Atlantis Modelling Framework." *Fisheries*  
710 *Oceanography* 27(5):489–503. doi: 10.1111/fog.12268.
- 711 Péron, Guillaume. 2013. "Compensation and Additivity of Anthropogenic Mortality: Life-  
712 History Effects and Review of Methods." *Journal of Animal Ecology* 82(2):408–17. doi:  
713 10.1111/1365-2656.12014.
- 714 Perry, R. Ian, Philippe Cury, Keith Brander, Simon Jennings, Christian Möllmann, and Benjamin  
715 Planque. 2010. "Sensitivity of Marine Systems to Climate and Fishing: Concepts, Issues  
716 and Management Responses." *Journal of Marine Systems* 79(3):427–35. doi:  
717 10.1016/j.jmarsys.2008.12.017.
- 718 Piggott, Jeremy J., Colin R. Townsend, and Christoph D. Matthaei. 2015. "Reconceptualizing  
719 Synergism and Antagonism among Multiple Stressors." *Ecology and Evolution*  
720 5(7):1538–47. doi: 10.1002/ece3.1465.
- 721 Pimm, Stuart L. 1984. "The Complexity and Stability of Ecosystems." *Nature* 307(5949):321–  
722 26. doi: 10.1038/307321a0.

- 723 Pimm, Stuart L., and Andrew Redfearn. 1988. "The Variability of Population Densities." *Nature*  
724 334(6183):613–14. doi: 10.1038/334613a0.
- 725 Planque, Benjamin, Jean-Marc Fromentin, Philippe Cury, Kenneth F. Drinkwater, Simon  
726 Jennings, R. Ian Perry, and Souad Kifani. 2010. "How Does Fishing Alter Marine  
727 Populations and Ecosystems Sensitivity to Climate?" *Journal of Marine Systems*  
728 79(3):403–17. doi: 10.1016/j.jmarsys.2008.12.018.
- 729 Planque, Benjamin, Ulf Lindstrøm, and Sam Subbey. 2014. "Non-Deterministic Modelling of  
730 Food-Web Dynamics" edited by A. Chiaradia. *PLoS ONE* 9(10):e108243. doi:  
731 10.1371/journal.pone.0108243.
- 732 Planque, Benjamin, and Christian Mullan. 2020. "Modelling Chance and Necessity in Natural  
733 Systems." *ICES Journal of Marine Science* 77(4):1573–88. doi: 10.1093/icesjms/fsz173.
- 734 R Core Team. 2021. *R: A Language and Environment for Statistical Computing* [computer  
735 program]. Version 4.1.0. <https://www.R-project.org/>.
- 736 Rooney, Neil, and Kevin S. McCann. 2012. "Integrating Food Web Diversity, Structure and  
737 Stability." *Trends in Ecology & Evolution* 27(1):40–46. doi: 10.1016/j.tree.2011.09.001.
- 738 Savoca, Matthew S., Max F. Czapanskiy, Shirel R. Kahane-Rapport, William T. Gough, James A.  
739 Fahllbusch, K. C. Bierlich, Paolo S. Segre, Jacopo Di Clemente, Gwenith S. Penry, David  
740 N. Wiley, John Calambokidis, Douglas P. Nowacek, David W. Johnston, Nicholas D.  
741 Pyenson, Ari S. Friedlaender, Elliott L. Hazen, and Jeremy A. Goldbogen. 2021. "Baleen  
742 Whale Prey Consumption Based on High-Resolution Foraging Measurements." *Nature*  
743 599(7883):85–90. doi: 10.1038/s41586-021-03991-5.
- 744 Shannon, Lynne J., Marta Coll, Dawit Yemane, Didier Jouffre, Sergio Neira, Arnaud Bertrand,  
745 Erich Diaz, and Yunne-Jai Shin. 2010. "Comparing Data-Based Indicators across  
746 Upwelling and Comparable Systems for Communicating Ecosystem States and  
747 Trends." *ICES Journal of Marine Science* 67(4):807–32. doi: 10.1093/icesjms/fsp270.
- 748 Sivel, Elliot, Benjamin Planque, Ulf Lindstrøm, and Nigel G. Yoccoz. 2021. "Multiple  
749 Configurations and Fluctuating Trophic Control in the Barents Sea Food-Web." *PLOS*  
750 *ONE* 16(7):e0254015. doi: 10.1371/journal.pone.0254015.
- 751 Tilman, David. 1999. "The Ecological Consequences of Changes in Biodiversity: A Search for  
752 General Principles." *Ecology* 80(5):1455–74. doi: 10.1890/0012-  
753 9658(1999)080[1455:TECOCI]2.0.CO;2.
- 754 Tilman, David, Peter B. Reich, and Johannes M. H. Knops. 2006. "Biodiversity and Ecosystem  
755 Stability in a Decade-Long Grassland Experiment." *Nature* 441(7093):629–32. doi:  
756 10.1038/nature04742.
- 757 Timmermans, Mary-Louise, and Carol Ladd. 2019. "Sea Surface Temperature." in *Arctic Report*  
758 *Card 2019*.

759 Van Meerbeek, Koenraad, Tommaso Jucker, and Jens-Christian Svenning. 2021. "Unifying the  
 760 Concepts of Stability and Resilience in Ecology." *Journal of Ecology* 109(9):3114–32.  
 761 doi: 10.1111/1365-2745.13651.

762 Vasseur, David A., and Kevin S. McCann. 2005. "A Mechanistic Approach for Modeling  
 763 Temperature-Dependent Consumer-Resource Dynamics." *The American Naturalist*  
 764 166(2):184–98. doi: 10.1086/431285.

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766

767 **Tables**

768 *Table 1. Initial parameters input for the NDND simulations. Units are given in brackets. Assimilation*  
 769 *efficiency and digestibility are ratios and do not have units. Other losses, inertia, and satiation are*  
 770 *ratios but integrated for a 1-year time-period. Initial biomass, Import, Export, and Refuge biomass*  
 771 *correspond to total weights for a species but expressed per spatial unit. For demersal fish, Initial*  
 772 *biomass corresponds to  $2.31 \cdot 1600 = 3696$  thousand tons for the entire Barents Sea area. Refuge*  
 773 *biomass corresponds to  $0.023 \cdot 1600 = 36.8$  thousand tons for the entire Barents Sea area*

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Initial Biomass ( $B_0$ , tons·km <sup>-2</sup> )	25	25.64	3.32	66	1.02	2.31	0.34	0.007
Import ( $I$ , tons·km <sup>-2</sup> )	1000	8	2	0	0	0	0	0
Export ( $E$ , tons·km <sup>-2</sup> )	0	0	0	0	0	0	0	0
Assimilation efficiency ( $\gamma$ )	1	1	1	0.94	0.9	0.93	1	0.84
Digestibility ( $\kappa$ )	0.65	0.9	0.9	0.6	0.9	0.85	-	-
Other losses ( $\mu$ )	6.74	8.4	5.5	1.5	2.85	1.65	5.5	60
Inertia ( $\rho$ )	12.94	7.58	3.1	0.74	0.9	0.25	0.11	0.81
Satiation ( $\sigma$ )	-	128	42	25.2	13.5	5.5	10.9	123
Refuge biomass ( $\beta$ , tons·km <sup>-2</sup> )	0.25	0.23	0.13	0.66	0.025	0.023	0.0034	0.0001

774

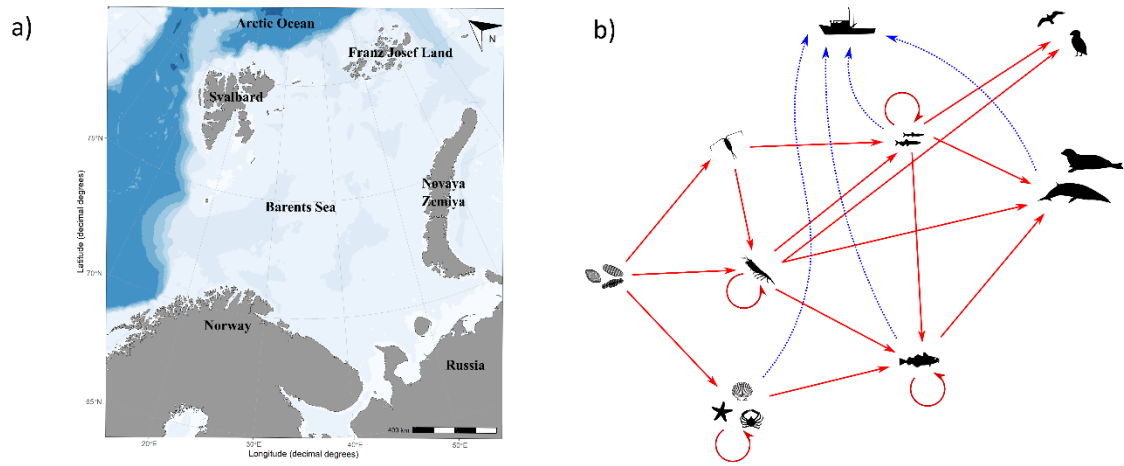
775 *Table 2. Initial harvesting parameter input for the NDND simulations. Units are given in brackets.*  
 776 *Fishing mortality ( $F_{mp}$ ) and the natural mortality ( $M$ ) do not have units because they are ratios*  
 777 *integrated for a 1-year time-period.*

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Fishing mortality rate (Fmp)	-	-	-	-	0.05	0.4	-	-
Target biomass (Bmp, tons·km <sup>-2</sup> )	-	-	-	-	0.125	0.475	-	-
Trigger biomass (Blim, tons·km <sup>-2</sup> )	-	-	-	-	0.125	0.25	-	-
Natural mortality (M)	-	-	-	-	0.85	0.2	-	-
Catches (C, tons·km <sup>-2</sup> )	-	-	-	0.026	-	-	0.0014	-

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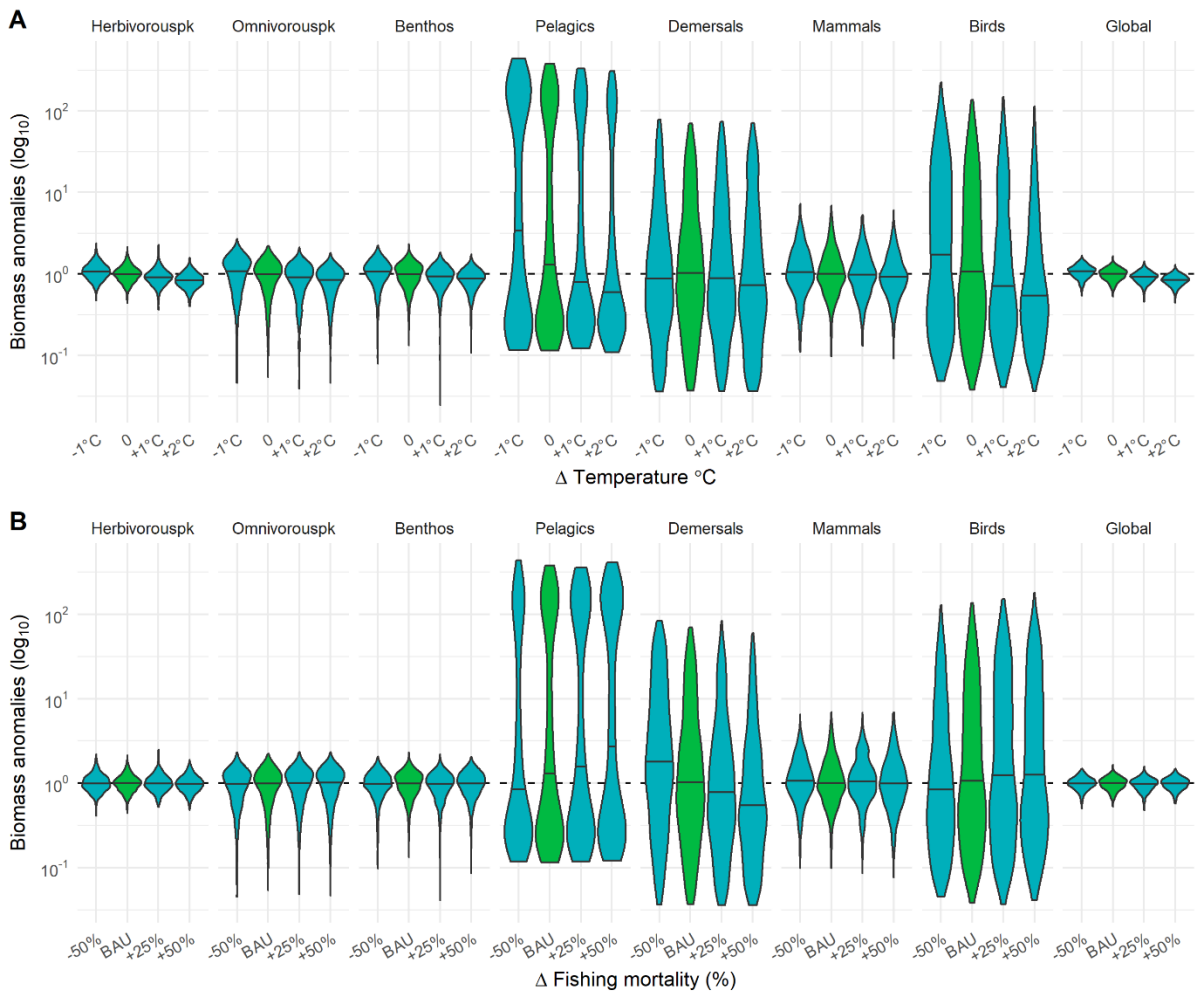




780

781 *Figure 1. The study area of the Barents Sea (a) and its simplified food-web topology (b). Icons represent*  
 782 *the eight species (phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic*  
 783 *fish, demersal fish, marine mammals, and birds). Red-full arrows represent the possible flows towards*  
 784 *other species of the food-web. Red-circular arrows represent cannibalistic interactions. Blue-dashed*  
 785 *arrows represent flows towards the fisheries.*

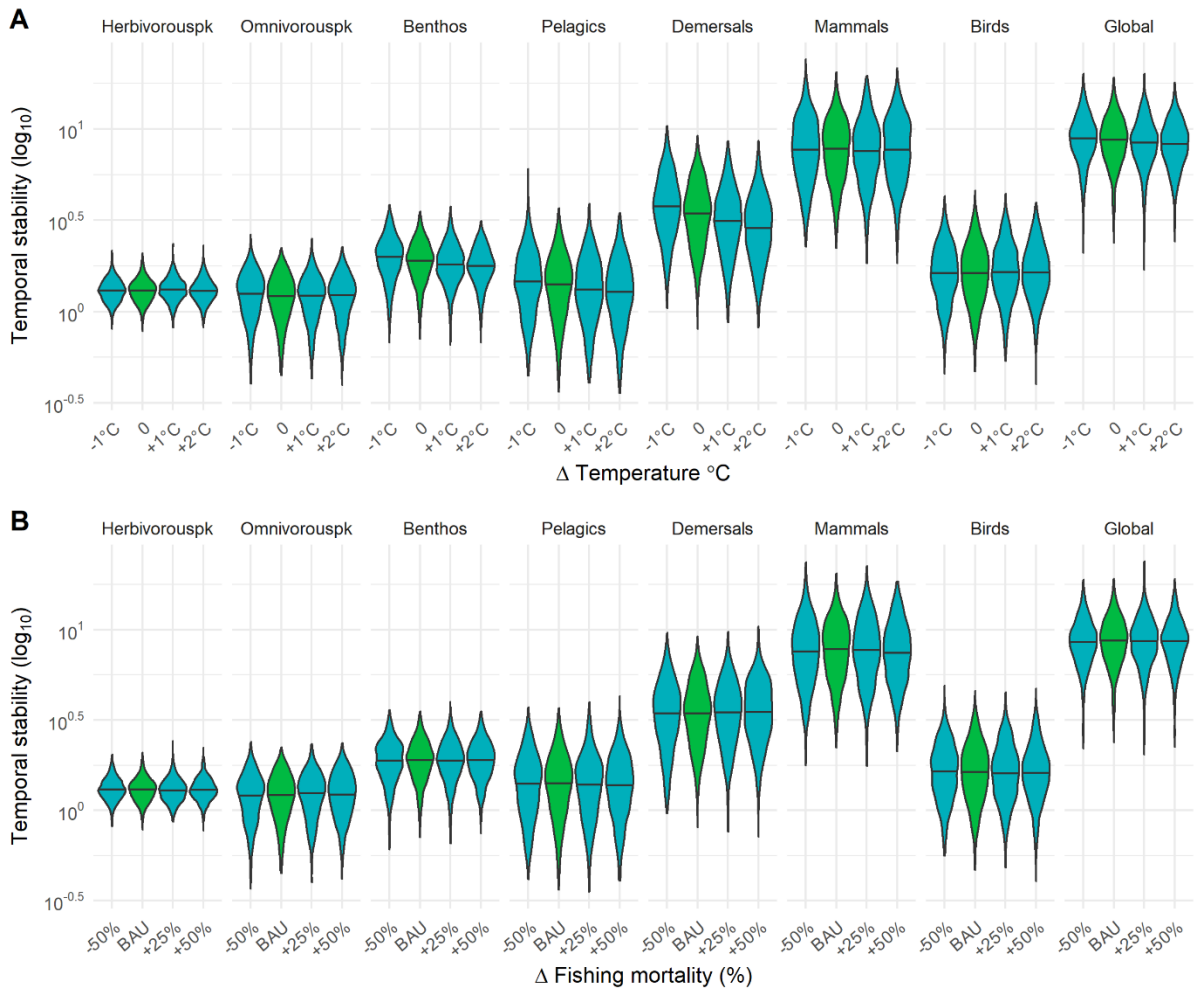
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788 *Figure 2. Effect of variations of temperature (A) and fishing mortality (B) on the simulated biomass of*  
 789 *each species and the entire Barents Sea food-web (Global). The reference scenario (i.e. no variation in*  
 790 *temperature and fishing mortality) is identified in green. The variations in biomass are expressed as*  
 791 *anomalies on the log<sub>10</sub>-scale regarding the median of the reference scenario. The black dotted line*  
 792 *indicates biomass values equal to the median biomass of the reference scenario.*

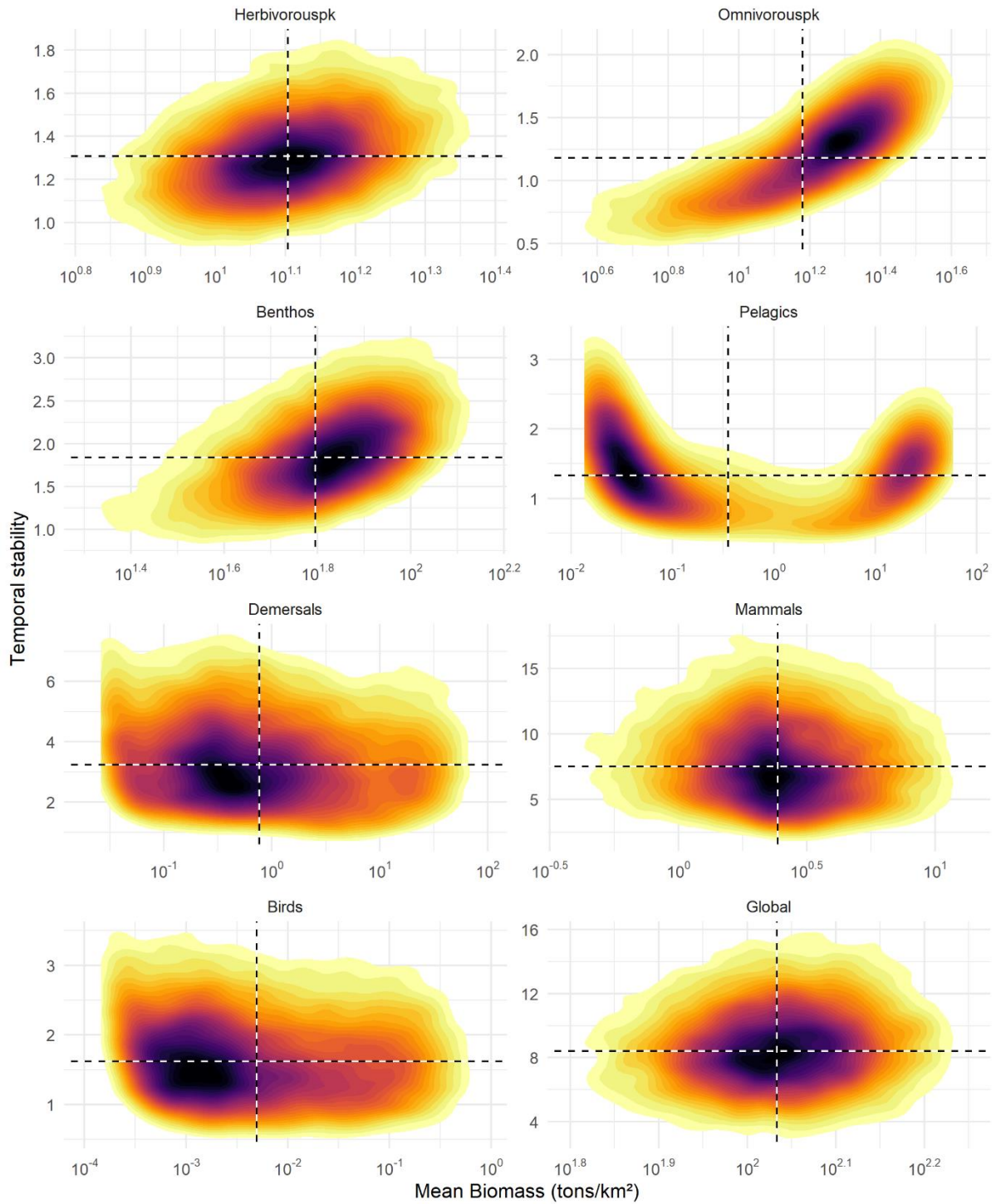
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794

795 *Figure 3. Effect of variations in temperature (A) and fishing mortality (B) on the temporal stability (on*  
 796 *a log<sub>10</sub> scale) of each species and of the entire Barents Sea food-web. Higher values indicate higher*  
 797 *stability. The black lines in the violin plot correspond to the median of the stability of each species in*  
 798 *each scenario. The reference scenario is identified in green.*

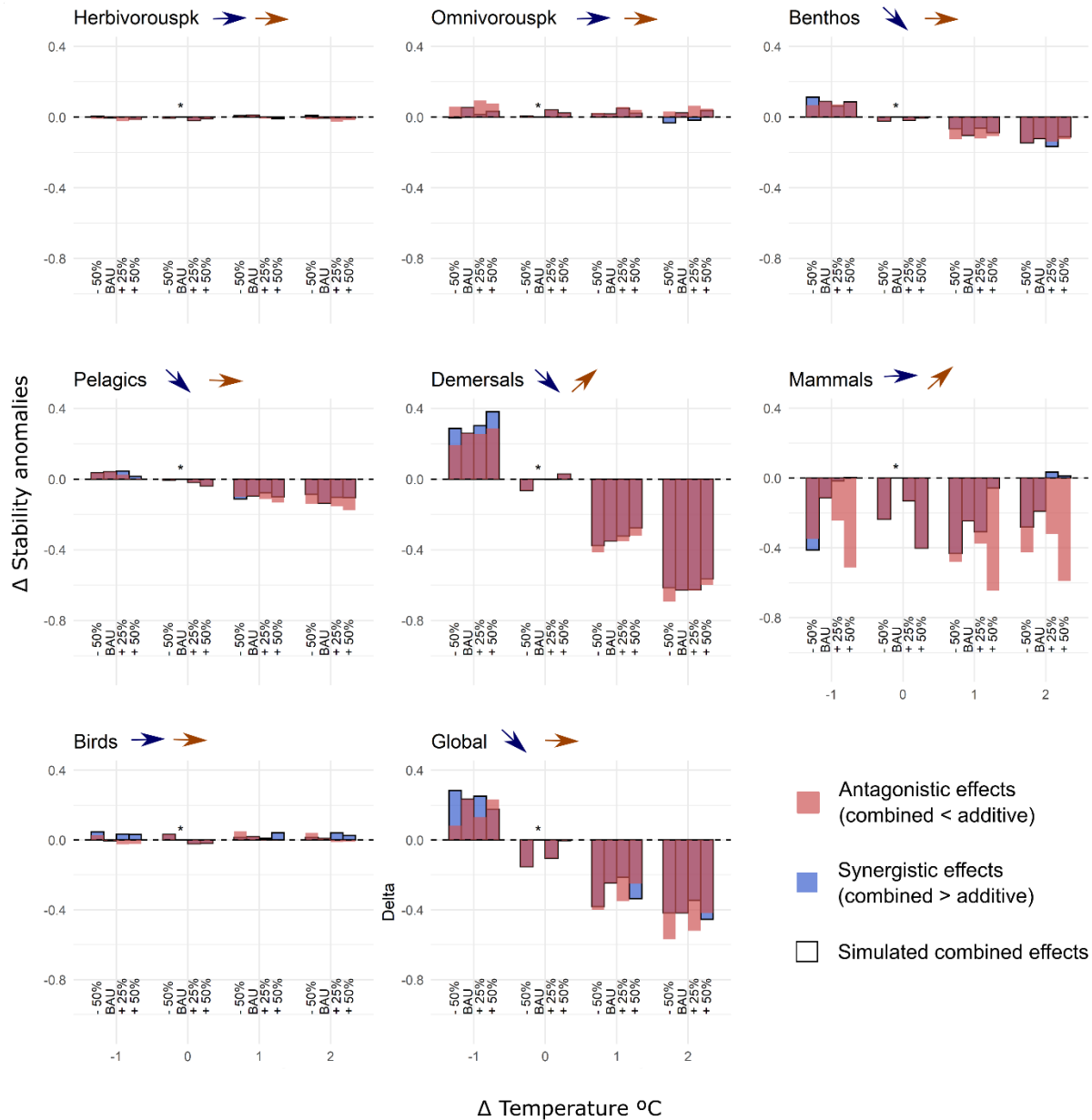
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801 *Figure 4. Density plots between mean biomass (on the log10-scale) and temporal stability for all*  
 802 *species and the whole food-web (the darker, the denser). The black/white-dashed lines represent the*  
 803 *geometric mean of the mean biomass by species and the mean temporal stability by species.*

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805

806 *Figure 5. Combined effects of temperature and fisheries the temporal stability of the Barents Sea food-*  
 807 *web and its species. Bars represent the anomalies in stability regarding the reference scenario*  
 808 *(identified by “\*”). Each bar represents a scenario of temperature and fishing mortality. Blue and black-*  
 809 *outlined bars represent the simulated combined effects of temperature and fisheries. Red bars*  
 810 *represent the additive effects of temperature and fisheries. Complete overlap indicates additive effects.*  
 811 *Larger combined effects than additive effects correspond to synergistic effects. Combined effects*  
 812 *smaller than additive effects correspond to antagonistic effects. Dark blue arrows indicate the*  
 813 *anomalies trend for scenarios of temperature. Orange arrows indicates the anomalies trend for*  
 814 *scenarios of fishing mortality. The black-dashed line corresponds to anomalies of 0 (i.e. estimated*  
 815 *stability equals stability of the reference scenario). The grey dashed lines represent the trends in*  
 816 *stability anomalies for demersal fish.*

817

# Paper III

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## A STANDARD PROTOCOL FOR DESCRIBING THE EVALUATION OF ECOLOGICAL MODELS

**Planque B., Aarflot J.M., Buttay L., Carroll J., Fransner F., Hansen C., Husson B., Langangen Ø., Lindstrøm U., Pedersen T., Primicerio R., Sivel E., Skogen M.D., Strombom E., Stige L.C., Varpe Ø., & Yoccoz N.G.**

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Title: **A standard protocol for describing the evaluation of ecological models**

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## Abstract

Numerical models of ecological systems are increasingly used by scientists to address complex environmental questions. One challenge for scientists, managers, and stakeholders is to appraise the performance of these models to answer specific questions of scientific or societal relevance, that is to perform, communicate or access transparent evaluations of ecological models. While there have been substantial developments to support standardised descriptions of ecological models, less has been done to standardise and to report model evaluation practices. We present here a general protocol designed to guide the reporting of model evaluation. The protocol is organised in three major parts: the *objective(s)* of the modelling application, the ecological *patterns* of relevance and the *evaluation* methodology proper, and is termed the OPE (objectives, patterns, evaluation) protocol. We present the 25 questions of the OPE protocol which address the many aspects of the evaluation process and then apply them to six case studies based on a diversity of ecological models. In addition to standardising and increasing the transparency of the model evaluation process, we find that going through the OPE protocol helps modellers to think more deeply about the evaluation of their models. From this last point, we suggest that it would be highly beneficial for modellers to consider the OPE early in the modelling process, in addition to using it as a reporting tool and as a reviewing tool.

## Keywords

Standardisation, best practice, ecological patterns, skill assessment, transparency.

## 1. Introduction

Scientists, managers, and stakeholders increasingly rely on numerical models of ecological systems. One challenge is to appraise the efficiency of these models to tackle complex environmental questions. Providing clear evaluations of model performance is one way to address this challenge. Models are constructed, analysed, and used by different actors, from scientists to policymakers, and these actors have different understandings and expectations from models. Assessing how good a model is at addressing specific problems is difficult when ecological modellers use a variety of model types, have different modelling cultures and practices, and use different vocabularies. This can hinder communication, transparency, reproducibility, and the general development of good practices within the modelling community. It is therefore essential to provide tools to support a collective understanding of what can be expected from a model and how a model is to be validated (Cartwright *et al.* 2016; Eker *et al.* 2018).

Transparency and reproducibility are at the core of the scientific method. However, the complexity of the tools used to observe and model ecological systems challenges reproducibility and transparency (Powers and Hampton 2019). The ongoing so-called reproducibility or replicability crisis reflects this difficulty, although the crisis has primarily been identified in the fields of psychology (Pashler and Wagenmakers 2012), clinical studies (Begley and Ioannidis 2015) and economics (Camerer *et al.* 2016). It is much less discussed in ecological research (but see Ives 2018; Nichols *et al.* 2019, 2021). It may not be possible to strictly replicate ecological observations, but transparency in workflow and data analyses can facilitate reproducibility. It is nevertheless possible to reproduce ecological model simulations, given that the relevant information is provided for that purpose. In addition to replicating a model and the associated simulations, it is equally important to be able to understand, assess and replicate how model performance was evaluated. This step is critical, given that almost every new method published are claimed to outperform existing ones, but are seldom re-evaluated (Boulesteix *et al.* 2020). Providing relevant and comprehensive information is a first step towards replicability, which needs to be complemented by appropriate communication and quality standards. How is the information communicated? Is it accessible? Is it unambiguous? Is it sufficient? A standardised protocol for reporting model evaluation procedures would address these questions and contribute to increased transparency and reproducibility of ecological models.

There have been considerable collective efforts in recent decades to develop standardized modelling practices, from model building to evaluation of model performances. A major advancement has been the development of standardised protocols such as the ODD (Overview, Design concepts, and Details, Grimm *et al.* 2006). The ODD protocol was originally developed to respond to the lack of a standard protocol for describing individual based models (IBMs). The protocol was reviewed and updated twice since its original publication (Grimm *et al.* 2010, 2020) and it is now commonly used by ecological modellers, beyond the original IBM community, to describe their models in reports and publications. The ODD protocol has been inspirational to groups of modellers with diverse focus, such as on model optimisation (ODDO, Mahévas 2019), data-mapping (ODD+2D, Laatabi *et al.* 2018), and inclusion of human decisions (ODD+D, Müller *et al.* 2013). In each case these groups have borrowed from the original ODD protocol idea and extended it for their specific purpose, thereby contributing to the harmonisation and communication of modelling practices.

A major step in the development and application of ecological models is the evaluation phase. There exists a large body of literature on how to perform model evaluation for various classes of models (e.g. Stow *et al.* 2009; Allen and Somerfield 2009; Bennett *et al.* 2013; Conn *et al.* 2018; Hipsey *et al.* 2020), but much less work has been done to standardise the reporting of model evaluations. The TRACE (TRANSPARENT and Comprehensive Ecological modelling) documentation (Grimm *et al.* 2014) is a notable exception which provides a framework for documenting the modelling process, including several aspects of model evaluation. Standardised protocols for reporting model evaluation can constitute useful tools for modellers and end-users to easily understand and compare evaluation procedures and appreciate the performance of models in relation to specific objectives. Making such tools available is therefore anticipated to benefit the scientific community and model end-users.

The issue of model validation and evaluation in environmental science has been the subject of extensive research and debate. Oreskes (1998) argued that quantitative models cannot be validated but only evaluated. In Oreskes' view, evaluation is described as “an assessment in which both positive and negative results are possible, and where the grounds on which a model is declared good enough are clearly articulated”. This assessment implies an examination of model outputs against pre-specified performance criteria. In the literature, the term *model validation* has remained pervasive (Eker *et al.* 2019) although often overlapping with the concept of evaluation as originally presented by Oreskes. In their 10-step procedure for developing and evaluating environmental models, Jakeman *et al.* (2006) introduced a stepwise

approach in which every stage is open to critical review and revision, in consort with end-users. The evaluation step is left to the end and is concerned with the model being *fit for purpose*, although the criteria for achieving this goal are not fully developed. More recently, Parker (2020) explores the meaning of a model being *adequate for purpose* for different classes of models, whether pedagogical, explanatory or pexplanatory. In the works of Jakeman and Parker, model evaluation is primarily achieved by measuring the performance of a model against pre-specified objectives, thereby following the original argument of Oreskes. This excludes the idea of a *general validity* of a model and favours the principle of an evaluation of a model for a specific objective (or a set of objectives). This mirrors George Box's notorious statement that "*all models are wrong; the practical question is how wrong do they have to be to not be useful*" (Box and Draper 1987), where *useful* implies use and therefore purpose. This also is in line with Augusiak's review of the literature on model evaluation and validation which concludes that despite little agreement on terms and underlying notions in the literature, it has repeatedly been pointed out that the evaluation of a model should depend on its *purpose* (Augusiak et al. 2014).

Evaluating that an ecological model is fit for purpose implies that the same model can (and should) be evaluated each time it is used for a new purpose. This is a rather trivial implication of the *fit for purpose* evaluation, however examples of re-evaluation of the performance of complex ecological models are scarce. Complex ecological models require extensive development efforts, and these materialise in the first publication of the model, together with a global evaluation (or validation) of the model (see e.g., Radach and Moll 2006; Link et al. 2010; Travers-Trolet et al. 2014; Pedersen et al. 2021). A fit-for-purpose approach would require that this first model evaluation be revised and reported for each new application of the model. One challenge in doing so is that the task of reporting model evaluation, which is already substantial when the model is first published, may seem daunting if it is to be repeated for every new model application. This can possibly be eased by reporting primarily on aspects of the model evaluation that are specific to each new application. An additional help can be provided by following a template in which a set of questions can guide the modeller through the reporting process.

By taking inspiration from the success and utility of the ODD protocol and the following extensions, we here present a complementary protocol for the reporting of ecological model evaluation procedures: the OPE (Objectives, Patterns, Evaluation) protocol. We discuss the rationale for the different elements of this protocol and provide a list of questions that can guide

modellers to report in OPE format. We summarise the protocol (Table 1) and provide an easy-to-use Word template to support documenting model evaluations. (Supplementary material S1). Finally, we test the protocol on six case studies taken from a collection of marine ecosystem models with which the authors are familiar. These case studies are presented in detail in the supplementary material (S2). These modelling applications pre-existed the OPE protocol. The OPE has therefore not been used to guide the model evaluations presented here, but only to report how these evaluations were performed.

## 2. Elements of the OPE protocol

The elements of the OPE protocol are divided in three sections: Objectives, Patterns and Evaluation. Each section is then divided in subsections which contain one to six questions.

### 2.1. Objectives

#### 2.1.1. Context and motivations

We recognize that many environmental models are not developed with the sole purpose of answering a single, well circumscribed question. Rather, models take time to develop and are gradually applied to a range of questions. Models of natural systems are inevitably embedded with multiple sources of uncertainty, and modellers make decisions during model construction (e.g., on which processes to include or simplify) which will affect the final outcome (Babel *et al.* 2019). There is a risk that assumptions which are reasonable for one particular model application are inadequate for another (Parker 2020; Saltelli *et al.* 2020). It is therefore essential that model suitability and performance are assessed and described for each application, and a crucial first step is describing the purpose of the specific application. In other words, to evaluate that a model is fit for purpose one must first specify the purpose. In this contribution, we refer to *model* as the generic description of the modelling tool (e.g. Ecopath, Atlantis, NorCPM1)(e.g. Ecopath with Ecosim, Polovina 1984; Christensen and Walters 2004), we use the terms *goal*, *purpose* and *purpose,ive* in an interchangeable manner to express the motivation driving the study and we refer to a model *application* when the model is applied towards a pre-defined objective or set of objectives. Central in the OPE framework is our conception that it is sensible to evaluate the same model against different patterns or data when applied for different purposes.

Describing the main objectives of the study and how modelling will contribute to reach these objectives is perhaps the most crucial step in evaluating model performance and suitability, and

it should be a key reference point throughout the evaluation process. Without a clear understanding of the purpose, it becomes difficult to communicate credibility and generate trust in the modelling work. Furthermore, it may be sensible to evaluate the same model against quite different patterns or data when applied for different purposes. Defining the aims and objectives of the model application early in the research process can save time, for instance with the realisation that objectives may depend on key processes for which the model of choice lacks functionality.

The aims and objectives of a model application should be stated in simple, clear language. We suggest using active sentences (e.g., construct, produce, test, document) and avoid vague wordings (e.g., explore, study, investigate). Beware that ambiguity in the description of the purpose of a model often leads to multiple (subjective) interpretations of whether an outcome was successful or not (Parker 2020). This hinders a reliable evaluation process. The following questions guide the reporting of objectives:

1. What are the objectives of the model application?
2. Why is the model suitable to address the objectives?
3. What would count as successful in achieving these objectives?

#### 2.1.2. Specific model setup

Optimally, the ecological model has already been fully described following a standardized protocol such as the ODD. It is possible that the original description is adequate for a new application of the model, but specific applications may also require adjustments of the model structure, parameters, or assumptions. Assumptions are particularly important to report when the model is used to perform predictions at other points in time and space (Wenger and Olden 2012; Yates et al. 2018). This is the case when the objective of the model is to produce forecasts or to predict ecosystem properties in one region based on a model developed in another. It is wise to explicitly state what lies behind the often-implicit assumption of *ceteris paribus* (everything else being equal). For example, are trophic interactions assumed to follow the same rules in different regions? Are spatial distributions or environmental conditions assumed to be unchanged in the future? When models are used for conditional forecasting, one should also report assumptions about expected changes that can affect the system studied. For example, how are possibly future changes in water temperature, fishing effort, accidental oil spill or increase in noise due to shipping represented in the model? A model can be revised to better reproduce the ecological components or processes that are relevant to a new application. It is

also possible that revised estimates of input parameters or new data on the forcing conditions of the model become available. All these updates should be reported in this section which describes any changes or additions which have been made since the original model description.

4. Are there any deviations from the original model description?
  - a. In the model assumptions,
  - b. in the model structure (e.g., addition of submodels, variables, components, modifications of spatial or temporal scales),
  - c. in the model details (e.g., changes in parameter values, functional relationships),
  - d. in the model forcing (e.g., initial conditions, boundary conditions, forcing time series and maps).

## 2.2. Patterns

### 2.2.1. Selected patterns

A *pattern* may be defined as a characteristic and clearly identifiable structure in nature, or in data extracted from nature (e.g., population cycles, animal space use, species diversity etc.), that can be attributed to a generative process (Levin 1992; Grimm et al. 1996). Thus defined, a pattern is key to ecological understanding and prediction. Ecological patterns emerge from multiple ecological processes, which operate at multiple spatial and temporal scales and levels of organization (individual, population, community, and ecosystem). Understanding the causal mechanisms responsible for pattern formation is a primary goal of ecology (Levin 1992).

Modelling complex adaptive systems (see Levin 1992), such as marine ecosystems, is challenging, but pattern-oriented modelling (POM) may facilitate the task (Grimm et al. 1996, 2005; Grimm and Railsback 2012). POM “starts with identifying a set of patterns observed at multiple scales and levels that characterize a system with respect to the particular problem being modelled” (Grimm and Railsback 2012). In other words, the selection of patterns to be used in model evaluation, depends on the objective or hypothesis of the study.

Relevant ecological patterns may be related to numbers, biomass, production, or consumption of relevant ecological entities, to dynamic behaviour at equilibrium, or to character of state transitions in perturbation studies or in systems undergoing change (e.g. Beisner et al. 2003). Other examples are spatial patterns such as spatial synchrony or traveling waves (e.g. Sherratt and Smith 2008). More complex emerging patterns (e.g., spatial structure described by a variogram, degree of spatial overlap between species) may also be candidate targets for model



evaluation. The selection of specific patterns is motivated by the objectives of the modelling application and is generally driven by the hypotheses that can explain the emergence of these patterns. It is therefore critical to report on the selection of patterns and on the justification for this selection.

5. Which ecological patterns are used for the model evaluation?
  - a. temporal patterns such as cycles, regime shift or trends, measures of temporal variability, and autocorrelation.
  - b. spatial patterns such as spatial synchrony, traveling waves, patchiness, and autocorrelation.
  - c. structural and functional patterns, such as taxonomic diversity, biomass ratios, integrated production, diet fractions, and trait distributions.
6. Why are these patterns important/essential to address the objectives?

In the following part of the OPE one must describe the data used for evaluation purposes, which can include both data from the model output and data which are independent of the model. Information on data used for model building should be provided in the model description (typically, an ODD protocol) and data used for optimization should be reported in the optimization description (e.g. in an ODDO protocol, Mahévas 2019).

#### 2.2.2. Independent data

Independent data – that is data that exists independently of the model being built – are often derived from field observations, and procedures for collecting and processing these observations should briefly be summarized in this part of the OPE. Relevant information includes i) whether the data originate from a dedicated field survey, an open database, or another model, ii) the spatial/ temporal/ taxonomic/ etc. extent and resolution of the data, iii) data representativeness, and iv) accuracy, precision, bias, or uncertainty. Data representativeness is the degree to which data can be used to represent the ecological patterns that are relevant for the objective of the study. For example, daily, weekly, or monthly time-series will have different representativeness if the ecological pattern of interest is phenology. Similarly, the representativeness of data collected at a single sampling station is also expected to vary with the spatial scale of the ecological question of concern, being more representative for small scale modelling studies centred around the sampling station than for larger scale investigations. Deriving ecological patterns (section 2.2.1) from observations can involve extensive data processing, and this should be reported here. When the same type of data can be

used for model optimisation and evaluation (as in cross validation) this should be reported in this section. In some cases, although the data is collected independently of the model being built, the model and data may not be completely independent from each other (for example, knowledge from historical data used to build the model, or input data in an Ecopath model is also expressed as an output of the model) and this should be reported. The following questions guide the collection of information about the independent data used to evaluate the model, given selected pattern(s).

7. Where do the independent data originate from?

Field survey, open database, another model, ...

8. What are the extent and resolution of the independent data?

Spatially, temporally, taxonomically, ...

9. How representative are the independent data of the ecological process?

10. Are there estimates of independent data accuracy, precision, bias, or uncertainty?

11. How are the independent data processed to represent the selected patterns and are assumptions made to derive these patterns from the data?

### 2.2.3. Model outputs

Often, only parts of the model outputs are used in a specific application and the aim of this section is to describe which outputs have been used and evaluated. In some cases, the data may be post-processed (e.g., aggregation of results by guild, geographical region, or integration in time). The purpose of post-processing can be to generate indicators of the relevant patterns (ex. species spatial distribution, biomass ratios, index of seasonality, see section 2.2.1) or to generate model outputs that are comparable with independent data (section 2.2.2). The post processing step can require new assumptions (e.g., assume that conversion rates such as C:Chla are constant in time/space/taxa). The aim of this section is to describe the selection of model outputs, the post-processing operations, and to report on quality, quantity, representativeness, uncertainties, or potential bias in the model outputs.

12. Which model outputs are used for the evaluation?

13. Have the outputs been post-processed, and how?

14. Are there estimates of model outputs accuracy, precision, bias, or uncertainty?

15. Are additional assumptions made when deriving patterns from model outputs?

## 2.3. Evaluation

### 2.3.1. Evaluation methodology

We refer here to the evaluation method applied in the context of a specific application of a model to address stated objectives (section 2.1.1). Model verification (*sensu* Grabner 2018) - the act of testing whether the model does what it is supposed to do, i.e., that it is technically functional - should precede any application of the model and is not considered here. A first model evaluation step is often to conduct *sanity checks*. These are rapid explorations of the model outputs which ensure that, even though the model is technically functional, it is not behaving poorly. Sanity checks are often non-quantitative and based on domain knowledge rather than on quantitative comparisons of observations vs. model outputs. Though these are not often reported in model evaluation procedures, they inform about key conditions that the model must satisfy to be considered useful. Examples of sanity checks can include an inspection that population sizes or biomasses are within plausible ranges, that seasonal patterns are plausible or that emerging spatial patterns are visually credible. These can be done via Fermi estimations, often referred to as ‘back of the envelope’ calculations of plausible ranges.

16. Are sanity checks conducted? If so, what is the method used?

- a. Which data and patterns are used for this?
- b. Does this apply to patterns that are not otherwise evaluated for this model application?

The core of the evaluation process is the comparison of patterns emerging from model outputs against those obtained from independent observations. This first raises the issue of the comparability between independent observations and model outputs, i.e., whether model outputs and independent data are directly comparable and whether modelled patterns are directly comparable to observed patterns. For example, are modelled biomass integrated over a large continuous geographical domain comparable with biomass field observations from a limited number of sampling sites? The second issue is the methodology used to compare ecological patterns derived from observations to those derived from the model. There can be many methodological approaches, ranging from qualitative visual comparisons to fully quantitative estimates of the model performance at reproducing observed patterns (Allen and Somerfield 2009; Bennett *et al.* 2013). The latter can include univariate or multivariate approaches, and can be based on error-based measures, information theory measures,

parametric tests, non-parametric tests, distance-based measures, combined measures (Hora and Campos 2015). This stage of the evaluation is sometimes referred to as *skill assessment*.

The choice of methods and metrics used in model skills evaluation will depend on the relevant patterns. For example, when dealing with cycles, the degree of congruence between modelled and observed cycles amplitude and frequency should be reported. When modelling state transitions, agreement in the rate of change of a trend should be reported. With ecosystem models addressing ecological stability or temporal variability, the stability measure should be reported at multiple levels of organisation (e.g., species, functional group, community etc). The quantitative criteria to evaluate the match between observed and simulated patterns must be reported. For example, if the mean of the simulations is within a certain range (e.g. 1 standard deviation) of the observed pattern, the model satisfactorily addresses the pattern (e.g. Kramer-Schadt et al. 2007). Each methodology usually comes with associated assumptions that need fulfilling for the method to be valid, and these should also be reported here.

The core issue at the end of the evaluation process is whether the model outputs can be considered satisfying for the purpose of answering the modelling objective, i.e., that the grounds on which a model is declared good enough are clearly articulated (Oreskes 1998).

17. What is the methodology used to compare ecological patterns derived from independent data with patterns derived from the model?
  - a. What is the rationale for choosing this method?
  - b. How are observational and/or model output uncertainties handled?
  - c. Does the methodology rely on specific assumptions?
18. Is there a threshold level (in the match between observed and modelled patterns) that can separate acceptable from unacceptable models?
19. How comparable are the patterns derived from the model and those derived from the independent data?

By answering the above questions, researchers should also discuss if there are patterns that cannot be well evaluated with the chosen method.

### 2.3.2. Sensitivities

We distinguish between two types of sensitivities to be reported. First, *model sensitivity* which is the result of a sensitivity analysis (SA), usually performed on model structure and parameters.

Second, *evaluation method sensitivity*, which refers to the sensitivity of the model evaluation to the choice of evaluation methodology and available observational data.

Sensitivity analysis (SA) scrutinizes how variations in model inputs influence variations in model outputs, a fundamental step in model evaluation and corroboration (EPA 2009). A diverse array of SA approaches has been developed to help cope with the various needs dictated by differing model assumptions, computational complexity, availability of relevant information (Saltelli et al. 2004; EPA 2009). Reviews and guidelines for best SA practice in the context of ecological and environmental modelling are an important aid to SA planning, implementation, and reporting (Saltelli et al. 2004, 2021; EPA 2009; Pianosi et al. 2016).

Attributes of SA methods worth considering in reporting include: independence of model linearity and additivity assumptions, ability to address interaction effects among input factors, capacity to handle differences in scale and shape of input probability distribution functions, ability to deal with differences in input spatial and temporal dimensions, and capacity to evaluate the effect of an input while all other inputs are allowed to vary as well (Frey 2002; Saltelli et al. 2004).

In this section, one should consider the sensitivity of the model outputs that are relevant to the objective of the study i.e., the modelled *patterns* (section 2.2.3). Priority should be given to reporting sensitivity analyses that were conducted specifically for the model application. Sensitivity analyses performed in earlier stages of model development can be reported if also relevant for the objective(s) of the study.

20. Has a model sensitivity analysis been performed? How?

- a. on the model structure?
- b. on the model parametrization?
- c. on other aspects of the model?

21. Which elements are the modelled patterns most sensitive to?

- a. input parameters
- b. priors and assumptions
- c. structural elements

22. How sensitive are the modelled patterns to the choice of initial conditions, boundary conditions, spatial and temporal resolution?

While there is no perfect model to address a specific ecological question, there is no perfect method either to evaluate the performance of a model (Makridakis et al. 2020). Typically, the choice of the sensitivity analyses depends on the availability of observational data with which the model can be compared, on the computational requirements to perform certain types of model evaluation, and on the availability of evaluation methodologies to the modellers. This section reports on the rationale and criteria for choosing a particular approach to evaluate the model performance, stressing when the choices are dictated by the objectives of the study as opposed to computational constraints, lack of relevant information or other considerations. For example, run times for complex simulation models impose restrictions on the parameter space, thus limiting the scope for global SA and simultaneous exploration of known sources of uncertainty, two desirable features of SA in relation to the objectives of the study. This section also reports on how sensitive the evaluation method is to the data used for evaluation (section 2.4). Could the model evaluation give significantly different results if other/new/more precise data were used? In summary, this section highlights the relevant attributes of the model evaluation, caveats, and possible limitations, clarifying the implications of the model evaluation in relation to the objectives.

23. How sensitive is the model evaluation to availability and uncertainty of the independent data?
24. How much is the model evaluation constrained by computational or theoretical limits?
25. How does the perceived performance of the model depend on the chosen evaluation methodology?

### 3. OPE template

As a practical tool, we provide in Table 1 a summary of the OPE protocol which highlight the main sections of the protocol, the 25 questions as well as guidelines on how to answer them. We also provide in supplementary material (S1), a Word template that can be used to directly input information relevant to a modelling study.

**Table 1. The 25 questions of the OPE protocol, grouped into three headings: Objectives, Patterns and Evaluation. A brief comment accompanies each question to guide the reporting. A template form is provided in appendix S1, in which reporting can be directly entered.**

#	Question	Comments	
<b>OBJECTIVES</b>	<b>CONTEXT AND MOTIVATIONS</b>	1 <b>What are the objectives of the model application?</b>	<i>Describe here the motivation and context for using the model. What is the purpose of the study? Do not describe the model, or its general objectives but focus on study-specific objectives. Use active sentences (e.g., produce, test, quantify, reconstruct dynamics) and avoid vague wordings (e.g., explore, study, investigate, understand).</i>
		2 <b>Why is the model suitable to address the objectives?</b>	<i>Provide the main rationale for why this specific model approach is suited to address the objective(s) raised in question 1. For example, is the model representing a process that is central to addressing the objectives?</i>
		3 <b>What would count as successful in achieving these objectives?</b>	<i>Explain here which criteria are used to determine if the model can address the objective or not. For example, if the objective of the model is to quantify a variable/process, is success defined based on the uncertainty around these estimated quantities?</i>
	<b>SPECIFIC MODEL SETUP</b>	4 <b>Are there any deviations from the original model description?</b>	<i>If this is the first time the model is presented, a full ODD description should be provided (Grimm et al., 2006, 2010, 2020). If the model has already been presented elsewhere, only deviations from the original description should be provided here. Models are often adjusted to address a specific ecological question/objective. It is these adjustments that should be reported here.</i>
a. <b>In the model assumptions?</b>			
b. <b>In the model structure – submodels, variables, components, scales?</b>			
c. <b>In the model details – parameter values, functional relationships</b>			
	d. <b>In the model forcing – initial conditions, boundary conditions, observation forcing, maps?</b>		

	#	Question	Comments
PATTERNS	SELECTED PATTERNS	5 <b>Which ecological patterns are used for the model evaluation?</b>	<i>The term "ecological pattern" refers to Pattern Oriented Modelling (POM, Grimm et al., 1996, 2005; Grimm and Railsback, 2012). Relevant ecological patterns can be observed at various scales and characterize the ecological system with respect to the particular problem being modelled. The patterns listed in a, b, and c are by no mean required or exhaustive, but are provided as examples of possibly relevant patterns.</i>
		<ul style="list-style-type: none"> <li>a. <b>Temporal patterns – cycles, shifts, trends, variability, autocorrelation</b></li> <li>b. <b>Spatial patterns – synchrony, travelling waves, patchiness, autocorrelation</b></li> <li>c. <b>Structural, functional patterns – diversity, biomass ratio, integrated production, diet, traits</b></li> </ul>	
		6 <b>Why are these patterns important/essential to address the objectives?</b>	<i>Explain here how the selection of ecological patterns is justified in relation to the objectives of the modelling application. Are there hypotheses that can explain the emergence of these patterns? Do not discuss how these patterns can be derived from observations or model outputs, this is addressed in questions 11-15.</i>
		7 <b>Where do the independent data originate from?</b>	<i>Independent data refers to data that exists independently from the current model being developed. These can be observational data or outputs from other models. Do not discuss outputs from the modelling study, these are addressed in questions 12-15.</i>
INDEPENDENT DATA		8 <b>What are the extent and resolution of the independent data?</b>	<i>Report here the spatial, temporal, taxonomic extent and resolution of the independent data identified in question 7. For example, if a data series is presented, what are the starting and ending time and the time-frequency of data acquisition; if biodiversity data is provided, what is the taxonomic resolution and the method used to determine taxonomic units.</i>
		9 <b>How representative are the independent data of the ecological processes?</b>	<i>This is a follow-up from question 8 to link data with key processes and patterns. For example, if a central process in the study is interannual variations in population numbers, and observational data of population numbers are available: do these data appropriately represent the annual abundance, or do they represent a snapshot in time or space?</i>



#	Question	Comments
		<i>Do not report on uncertainty estimates here, this is addressed in question 10.</i>
10	<b>Are there estimates of independent data accuracy, precision, bias, or uncertainty?</b>	<i>Uncertainty estimates for the independent data should be reported here (uncertainty estimates for the model outputs are reported in question 14).</i>
11	<b>How are the independent data processed to represent the selected pattern and are assumptions made to derive these patterns from the data?</b>	<i>Independent data – whether observational or modelled – may provide a representation of the patterns of interest (question 5) only after further processing. For example, survey data may be spatially interpolated to derive spatial distribution patterns. Another example: biomasses from several taxonomic units may be grouped to derive patterns of interannual changes in biomass for particular functional groups. Report these post-processing steps here.</i>
12	<b>Which model outputs are used for the evaluation?</b>	<i>This is a list of model outputs that have been selected based on the modelling objectives and related ecological patterns. The full set of raw outputs, which is often large, unprocessed, and not targeted towards the specific objectives of the modelling study, should not be reported here.</i>
13	<b>Have the outputs been post-processed, and how?</b>	<i>As for independent data, model outputs may provide a representation of the patterns of interest only after further processing (see question 11). Report here the post-processing steps that are used to go from raw model outputs to ecologically relevant patterns.</i>
14	<b>Are there estimates of model output accuracy, precision, bias, or uncertainty?</b>	<i>Uncertainty estimates for the model outputs should be reported here. Focus should be on model outputs that are used for the model evaluation.</i>

MODEL OUTPUTS

#	Question	Comments
15	<b>Are additional assumptions made when deriving patterns from model outputs?</b>	<i>Report here when some assumptions may be required to derive outputs at the appropriate scale or in the appropriate units. For example, a dry:wet weight ratio may be assumed across species/seasons/areas to derive weight wet estimates (the relevant pattern) from dry weight (the model output).</i>
EVALUATION EVALUATION METHODOLOGY	16 <b>Are sanity checks conducted? If so, what is the method used?</b>	<i>Sanity checks are informal steps that are taken throughout model development to ensure that the model is not behaving badly. They inform on key conditions that the model must satisfy to be considered useful. For example, checking that a population neither becomes extinct nor grows to unrealistic size.</i>
	a. <b>Which data and patterns are used for this?</b> b. <b>Does this apply to patterns that are not otherwise evaluated for this model application?</b>	
	17 <b>What is the methodology used to compare ecological patterns derived from independent data with patterns from the model?</b>	<i>This section describes how model outputs are evaluated against independent data. This is sometimes referred to as model "skill assessment". This section should describe the methodology used as well as the rationale for the choice of methods, i.e., how the methods relate to data, model outputs, objectives of the study, and relevant ecological patterns.</i>
	a. <b>What is the rationale for choosing this method?</b> b. <b>How are observational and/or model output uncertainties handled?</b> c. <b>Does the methodology rely on specific assumptions?</b>	
	18 <b>Is there a threshold level (match between observed and modelled patterns) that can separate acceptable from unacceptable models?</b>	
19 <b>How comparable are the patterns derived from the model and those derived from the independent data?</b>	<i>This section describes the result of the model skill assessment, plus any other qualitative features (patterns) that can be compared between model outputs and independent data.</i>	

#	Question	Comments
SENSITIVITIES	20 <b>Has a model sensitivity analysis been performed, and how?</b> a. <b>on the model structure?</b> b. <b>on the model parametrization?</b>	<i>This section describes the approach used to conduct model sensitivity analyses (SA), in a broad sense, from individual parameter SA to global SA. Various aspect of the methods used for SA can be reported here, including sensitivity to parameters, model structure, boundary/initial conditions, simulation design, and so on (see e.g. Pianosi et al. 2016).</i>
	21 <b>Which elements are the modelled patterns most sensitive to?</b> a. <b>input parameters</b> b. <b>priors and assumptions</b> c. <b>structural elements</b>	<i>If applicable, report here the results of the SA on parameters, model structure and assumptions.</i>
	22 <b>How sensitive are the modelled patterns to the choice of initial conditions, boundary conditions, spatial and temporal resolution?</b>	<i>If applicable, report here the results of the SA on the choice of initial conditions, spin-up time, boundary conditions, spatial and temporal resolution.</i>
	23 <b>How sensitive is the model evaluation to the independent data availability and uncertainty?</b>	<i>Could the model evaluation give significantly different results if other, new, or more precise data were used than those described in question 7?</i>
	24 <b>How much is the model evaluation constrained by computational or theoretical limits?</b>	<i>Models that are structurally simple and computationally fast can generally be explored through in-depth SA. It is more demanding to run appropriate SA on models that are structurally complex or that use substantial CPU resources to run. For some models, complexity &amp; run time make SA non-achievable in practice. These issues should be reported here.</i>
	25 <b>How does the perceived performance of the model depend on the chosen evaluation methodology?</b>	<i>Could the model evaluation give significantly different results if another evaluation approach had been used (other than reported in question 17)?</i>



## 4. Applications

We provide in the supplementary material (S2) examples of applications of the OPE protocol in the context of six modelling applications:

1. an Individual Based Model (IBM) used to quantify uncertainties in the estimates of mean biomass of the copepod *Calanus finmarchicus* as a function of sampling design,
2. a statistical food-web model used to quantify the association between capelin (*Mallotus villosus*) and its main two prey (krill and *Calanus* species),
3. simulations from the Non-Deterministic Network Dynamics (NDND) model to assess the persistence of trophic controls in the Barents Sea,
4. an Ecopath model to estimate trophic positions for ecological groups in the Barents Sea,
5. the Nordic and Barents Seas Atlantis Model (NoBa) simulations to assess cumulative impact of fisheries and climate in the Norwegian and Barents Seas, and
6. the reconstructions and predictions of selected physical and biogeochemical properties using the NorCPM1 model in the Barents Sea

These case studies cover a range of modelling practices, modelling tools and study objectives. Knowledge about context within which a model is developed and of the history of the model development is essential to understand the evaluation approach. We realise that the OPE case studies presented in this manuscript can be difficult to read without prior knowledge of each model context and history. In stand-alone modelling studies, model descriptions would normally be provided in full, but this is not the case here. To correct for this, we included introductory paragraphs that describe the models that were used in each case study and provide a brief history of the models, i.e., where they originate from and how they evolved to finally be used in the current case studies.

## 5. Discussion

The OPE protocol as we present it here is complementing other reporting protocols, in particular the ODD protocol and the extensions (e.g., ODDO, ODD+D), by focusing on the model evaluation. We argue that such a protocol can significantly contribute to improving model evaluation and can in general increase transparency and reproducibility of published models.

Model evaluation is essential and should accompany all model studies. We have therefore developed the OPE protocol for model evaluation, which is generic enough to apply to a wide range of ecological modelling studies, from coupled physical-chemical-biological systems (NORWECOM.E2E, NorCPM1, Atlantis), to simpler models focussed on food-webs interactions (NDND, Ecopath, Gompertz). In our experience, most modellers consider their model as somewhat special (i.e., not like other models) and therefore assume that it would be difficult to evaluate models using a standardised protocol like the OPE. Indeed, we found that it was often work-demanding for modellers to answer the 25 questions of the OPE protocol. Through the six case studies, we identified several challenges in documenting the OPE. Documenting model evaluation is not a standard step in most modelling studies. Lack of experience and training in doing so made it a time-consuming and demanding task that required several iterations, and substantial amount of thinking and discussion. At times, the OPE exercise was perceived as too time-consuming, little rewarding in the short term and easy to postpone. It was often difficult to find the balance between providing informative answers and remaining concise. In several cases, it was not always obvious what was the right amount of contextual information required to inform readers about the model. When sensitivity analysis had been performed in earlier studies, it could be unclear how much this should be reported. At first sight, some questions appeared unclear or redundant, though these issues were usually resolved after some iterations. Some questions were also of little relevance for some of the model applications explored here. Nevertheless, it was possible to successfully apply the OPE protocol to each specific case study, despite the diverse collection of model types. We therefore anticipate that the protocol will be applicable to many ecological modelling studies.

The protocol can be used from the start of a modelling study, to guide model evaluation throughout the study. Though the primary motivation for this protocol was to construct a tool to help modellers reporting how they evaluated their models given specific objectives, we found that answering the protocol questions for the individual case studies led to additional discussions and reflexions on model evaluation. In some instances, it was identified that additional evaluation steps could be taken or that some steps in the evaluation process could have been better specified. In the case of the Gompertz case study, documenting the OPE revealed that posterior predictive checks could have been considered to improve the evaluation. In the NDND case study, it was only after the OPE was documented that the issue of determining a threshold between acceptable and unacceptable models became clear. In the NoBa case study, it became apparent that many aspects of model evaluation for a complex end-

to-end model like Atlantis, were still under-developed, and that the OPE could guide future work towards improved model evaluation methodology. In all case studies the OPE helped to clarify existing evaluation procedures and identify possible improvements. Had the OPE been available at the start of these studies, the model evaluation would likely have been conducted more thoroughly. This highlights the potential utility of the OPE to stimulate higher standard of model evaluation, in addition to its original goal of merely reporting how evaluation was conducted.

It is important to note that the OPE protocol goes far beyond model skill assessment. Assessing the prediction skill of ecological models has been the focus of recent literature (see e.g., Stow *et al.*, 2009, Olsen *et al.*, 2016 or Steenbeck *et al.*, 2021 and references therein). Skill assessment is an integral part of model evaluation and is clearly identified in the first part of the *Evaluation* section of the OPE protocol (questions 17-19). The OPE protocol expands beyond skill assessment by addressing issues related to objective, patterns, data, and sensitivity analyses and puts balanced focus on these different elements.

Documenting model evaluation is not yet standard practice. The 25 questions outlined in the OPE protocol are a guide to present an extensive – but not exhaustive – description of a model evaluation. A full description of the evaluation is often too long to be included in the core part of a published manuscript. We advocate that the OPE documentation be presented as a technical supplement. By documenting the details of the model evaluation procedure, the OPE provides essential information for the peer-review of a modelling study and directly contributes to higher transparency. We encourage modellers to try the OPE protocol by using the word template (S1) and get help and inspiration from the answers provided in the six case studies (S2). We also encourage reviewers to use the OPE questions as a guide when evaluating modelling studies.

As noted by Grimm *et al.* (2014), building a 'culture' of model reporting is about *doing all these things as well as you can because you know that peers and model clients are expecting you to; there is no point any more in complaining about “additional effort” for these things*. We recognise that we are not there yet. Promoting the OPE and similar documentation during the peer review process would help in getting this culture in place.

The current version of the OPE protocol is a work-in-progress. Model evaluation is complex and the development of tools for reporting how evaluation is conducted is not a simple problem. During the discussions that formed the basis for the current protocol, a central point was that modellers have various cultures, experiences, and practices when it comes to model evaluation.

These points of view are not always easy to reconcile with each other. Further discussions based on the use of the protocol on a wider range of models are expected to lead to revisions of the OPE protocol in the future.

## 6. Conclusion

The OPE protocol is proposed as a tool to report the evaluation of ecological models. The reporting template is organised along 25 questions which make it easier and faster for modellers to report model evaluation. The OPE structure further promotes comprehensive reporting of the evaluation process, ranging from objectives, to data, skill assessment, and sensitivity analyses. Our experience is that structured reporting of model evaluation helps modellers to think more deeply about the evaluation of their models. From this last point, we suggest that it would be highly beneficial for modellers to consider the OPE early in the modelling process, in addition to using it as a reporting tool (as we have done here) and as a reviewing tool.

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## 9. References

- Allen, J.I., and Somerfield, P.J. 2009. A multivariate approach to model skill assessment. *Journal of Marine Systems* **76**(1): 83–94. doi:10.1016/j.jmarsys.2008.05.009.
- Augusiak, J., Van den Brink, P.J., and Grimm, V. 2014. Merging validation and evaluation of ecological models to “evaluation”: A review of terminology and a practical approach. *Ecological Modelling* **280**: 117–128. doi:10.1016/j.ecolmodel.2013.11.009.
- Babel, L., Vinck, D., and Karssenber, D. 2019. Decision-making in model construction: Unveiling habits. *Environmental Modelling & Software* **120**: 104490. doi:10.1016/j.envsoft.2019.07.015.
- Begley, C.G., and Ioannidis John, P.A. 2015. Reproducibility in Science. *Circulation Research* **116**(1): 116–126. doi:10.1161/CIRCRESAHA.114.303819.



- Beisner, B.E., Haydon, D.T., and Cuddington, K. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* **1**(7): 376–382. doi:10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2.
- Bennett, N.D., Croke, B.F.W., Guariso, G., Guillaume, J.H.A., Hamilton, S.H., Jakeman, A.J., Marsili-Libelli, S., Newham, L.T.H., Norton, J.P., Perrin, C., Pierce, S.A., Robson, B., Seppelt, R., Voinov, A.A., Fath, B.D., and Andreassian, V. 2013. Characterising performance of environmental models. *Environmental Modelling & Software* **40**: 1–20. doi:10.1016/j.envsoft.2012.09.011.
- Boulesteix, A., Hoffmann, S., Charlton, A., and Seibold, H. 2020. A replication crisis in methodological research? *Significance* **17**(5): 18–21. doi:10.1111/1740-9713.01444.
- Box, G.E.P., and Draper, N.R. 1987. *Empirical Model Building and Response Surfaces*. John Wiley & Sons, New York, NY.
- Camerer, C.F., Dreber, A., Forsell, E., Ho, T.-H., Huber, J., Johannesson, M., Kirchler, M., Almenberg, J., Altmejd, A., Chan, T., Heikensten, E., Holzmeister, F., Imai, T., Isaksson, S., Nave, G., Pfeiffer, T., Razen, M., and Wu, H. 2016. Evaluating replicability of laboratory experiments in economics. *Science* **351**(6280): 1433. doi:10.1126/science.aaf0918.
- Cartwright, S.J., Bowgen, K.M., Collop, C., Hyder, K., Nabe-Nielsen, J., Stafford, R., Stillman, R.A., Thorpe, R.B., and Sibly, R.M. 2016. Communicating complex ecological models to non-scientist end users. *Ecological Modelling* **338**: 51–59. doi:10.1016/j.ecolmodel.2016.07.012.
- Christensen, V., and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities, and limitations. *Ecological Modelling* **172**: 109–139. doi:10.1016/j.ecolmodel.2003.09.003.
- Conn, P.B., Johnson, D.S., Williams, P.J., Melin, S.R., and Hooten, M.B. 2018. A guide to Bayesian model checking for ecologists. *Ecol Monogr* **88**(4): 526–542. doi:10.1002/ecm.1314.
- Eker, S., Rovenskaya, E., Langan, S., and Obersteiner, M. 2019. Model validation: A bibliometric analysis of the literature. *Environmental Modelling & Software* **117**: 43–54. doi:10.1016/j.envsoft.2019.03.009.
- Eker, S., Rovenskaya, E., Obersteiner, M., and Langan, S. 2018. Practice and perspectives in the validation of resource management models. *Nature Communications* **9**. doi:10.1038/s41467-018-07811-9.
- EPA. 2009. *Guidance on the development, evaluation, and application of environmental models*. Technical Report, Environmental Protection Agency. Available from [https://www.epa.gov/sites/production/files/2015-04/documents/cred\\_guidance\\_0309.pdf](https://www.epa.gov/sites/production/files/2015-04/documents/cred_guidance_0309.pdf).
- Frey, H.C. 2002. Introduction to Special Section on Sensitivity Analysis and Summary of NCSU/USDA Workshop on Sensitivity Analysis. *Risk Analysis* **22**(3): 539–545. doi:10.1111/0272-4332.00037.
- Grabner, C. 2018. How to Relate Models to Reality? An Epistemological Framework for the Validation and Verification of Computational Models. *Jasss* **21**(3): 26. doi:10.18564/jasss.3772.
- Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., and Railsback, S.F. 2014. Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. *Ecological Modelling* **280**: 129–139. doi:10.1016/j.ecolmodel.2014.01.018.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., and Huse, G. 2006. A standard protocol for describing

- individual-based and agent-based models. *Ecological Modelling* **198**(1–2): 115–126. doi:10.1016/j.ecolmodel.2006.04.023.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., and Railsback, S.F. 2010. The ODD protocol: A review and first update. *Ecological Modelling* **221**(23): 2760–2768. doi:10.1016/j.ecolmodel.2010.08.019.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmański, J., and Wissel, C. 1996. Pattern-oriented modelling in population ecology. *Science of The Total Environment* **183**(1): 151–166. doi:10.1016/0048-9697(95)04966-5.
- Grimm, V., and Railsback, S.F. 2012. Pattern-oriented modelling: a “multi-scope” for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**(1586): 298–310. doi:10.1098/rstb.2011.0180.
- Grimm, V., Railsback, S.F., Vincenot, C.E., Berger, U., Gallagher, C., DeAngelis, D.L., Edmonds, B., Ge, J.Q., Giske, J., Groeneveld, J., Johnston, A.S.A., Milles, A., Nabe-Nielsen, J., Polhill, J.G., Radchuk, V., Rohwader, M.S., Stillman, R.A., Thiele, J.C., and Ayllon, D. 2020. The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. *Jasss* **23**(2). doi:10.18564/jasss.4259.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., and DeAngelis, D.L. 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. *Science* **310**(5750): 987–991. doi:10.1126/science.1116681.
- Hipsey, M.R., Gal, G., Arhonditsis, G.B., Carey, C.C., Elliott, J.A., Frassl, M.A., Janse, J.H., de Mora, L., and Robson, B.J. 2020. A system of metrics for the assessment and improvement of aquatic ecosystem models. *Environmental Modelling & Software* **128**: 104697. doi:10.1016/j.envsoft.2020.104697.
- Hora, J., and Campos, P. 2015. A review of performance criteria to validate simulation models. *Expert Systems* **32**(5): 578–595. doi:10.1111/exsy.12111.
- Ives, A.R. 2018. Informative irreproducibility and the use of experiments in ecology. *BioScience* **68**(10): 746–747. doi:10.1093/biosci/biy090.
- Jakeman, A.J., Letcher, R.A., and Norton, J.P. 2006. Ten iterative steps in development and evaluation of environmental models. *Environmental Modelling & Software* **21**(5): 602–614. doi:10.1016/j.envsoft.2006.01.004.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., and Grimm, V. 2007. Patterns for parameters in simulation models. *Ecological Modelling* **204**(3–4): 553–556. doi:10.1016/j.ecolmodel.2007.01.018.
- Laatabi, A., Marilleau, N., Nguyen-Huu, T., Hbid, H., and Babram, M.A. 2018. ODD+2D: An ODD Based Protocol for Mapping Data to Empirical ABMs. *Jasss* **21**(2). doi:10.18564/jasss.3646.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**: 1943–1967. doi:10.2307/1941447.
- Link, J.S., Fulton, E.A., and Gamble, R.J. 2010. The northeast US application of ATLANTIS: A full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography* **87**(1–4): 214–234. doi:10.1016/j.pocean.2010.09.020.
- Mahévas, S.; P. 2019. Practical Guide for Conducting Calibration and Decision-Making Optimisation with Complex Ecological Models. Preprints **2019120249**. doi:10.20944/preprints201912.0249.v1.
- Makridakis, S., Spiliotis, E., and Assimakopoulos, V. 2020. The M4 Competition: 100,000 time series and 61 forecasting methods. *International Journal of Forecasting* **36**(1): 54–74. doi:10.1016/j.ijforecast.2019.04.014.

- Müller, B., Bohn, F., Dreßler, G., Groeneveld, J., Klassert, C., Martin, R., Schlüter, M., Schulze, J., Weise, H., and Schwarz, N. 2013. Describing human decisions in agent-based models – ODD + D, an extension of the ODD protocol. *Environmental Modelling & Software* **48**: 37–48. doi:10.1016/j.envsoft.2013.06.003.
- Nichols, J.D., Kendall, W.L., and Boomer, G.S. 2019. Accumulating evidence in ecology: once is not enough. *Ecology and Evolution* **9**(24): 13991–14004. doi:10.1002/ece3.5836.
- Nichols, J.D., Oli, M.K., Kendall, W.L., and Boomer, G.S. 2021. Opinion: A better approach for dealing with reproducibility and replicability in science. *Proceedings of the National Academy of Sciences* **118**(7): e2100769118. doi:10.1073/pnas.2100769118.
- Oreskes, N. 1998. Evaluation (not validation) of quantitative models. *Environmental Health Perspectives* **106**(Suppl 6): 1453–1460. doi:10.1289/ehp.98106s61453.
- Parker, W.S. 2020. Model evaluation: an adequacy for purpose view. *Philosophy of Science* **87**(3): 457–477. doi:10.1086/708691.
- Pashler, H., and Wagenmakers, E.-J. 2012. Editors’ Introduction to the Special Section on Replicability in Psychological Science: A Crisis of Confidence? *Perspectives on Psychological Science* **7**(6): 528–530. doi:10.1177/1745691612465253.
- Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P.E., Nascimento, M.C., Blanchet, M.-A., Ellingsen, I.H., Jørgensen, L.L., and Blanchet, H. 2021. Overexploitation, Recovery, and Warming of the Barents Sea Ecosystem During 1950–2013. *Front. Mar. Sci.* **8**: 732637. doi:10.3389/fmars.2021.732637.
- Pianosi, F., Beven, K., Freer, J., Hall, J.W., Rougier, J., Stephenson, D.B., and Wagener, T. 2016. Sensitivity analysis of environmental models: A systematic review with practical workflow. *Environmental Modelling & Software* **79**: 214–232. doi:10.1016/j.envsoft.2016.02.008.
- Polovina, J.J. 1984. An overview of the Ecopath model. *Fishbyte* **2**: 5–7.
- Powers, S.M., and Hampton, S.E. 2019. Open science, reproducibility, and transparency in ecology. *Ecological Applications* **29**(1): e01822. doi:10.1002/eap.1822.
- Radach, G., and Moll, A. 2006. Review of three-dimensional ecological modelling related to the North Sea shelf system. Part II: model validation and data needs. *In Oceanography and marine biology. An annual review.*, 1st edition. pp. 1–60. Available from <https://www.taylorfrancis.com/chapters/mono/10.1201/9781420006391-4/review-three-dimensional-ecological-modelling-related-north-sea-shelf-system-part-ii-model-validation-data-needs-gibson-atkinson-gordon?context=ubx&refId=41590f7c-dd00-46e8-84b1-4d56031bd254>.
- Saltelli, A., Bammer, G., Bruno, I., Charters, E., Di Fiore, M., Didier, E., Nelson Espeland, W., Kay, J., Lo Piano, S., Mayo, D., Pielke Jr, R., Portaluri, T., Porter, T.M., Puy, A., Rafols, I., Ravetz, J.R., Reinert, E., Sarewitz, D., Stark, P.B., Stirling, A., van der Sluijs, J., and Vineis, P. 2020. Five ways to ensure that models serve society: a manifesto. *Nature* **582**(7813): 482–484. doi:10.1038/d41586-020-01812-9.
- Saltelli, A., Jakeman, A., Razavi, S., and Wu, Q. 2021. Sensitivity analysis: A discipline coming of age. *Environmental Modelling & Software* **146**: 105226. doi:10.1016/j.envsoft.2021.105226.
- Saltelli, A., Tarantola, S., Campolongo, F., and Ratto, M. 2004. *Sensitivity Analysis in practice. A Guide to Assessing Scientific Models.* John Wiley and Sons, Chichester, New York.
- Sherratt, J.A., and Smith, M.J. 2008. Periodic travelling waves in cyclic populations: field studies and reaction–diffusion models. *Journal of the Royal Society Interface* **5**(22): 483–505. doi:10.1098/rsif.2007.1327.
- Stow, C.A., Jolliff, J., McGillicuddy Jr, D.J., Doney, S.C., Allen, J.I., Friedrichs, M.A.M., Rose, K.A., and Wallhead, P. 2009. Skill assessment for coupled biological/physical models

- of marine systems. *Journal of Marine Systems* **76**(1–2): 4–15. doi:10.1016/j.jmarsys.2008.03.011.
- Travers-Trolet, M., Shin, Y.-J., and Field, J. 2014. An end-to-end coupled model ROMS-N<sub>2</sub>P<sub>2</sub>Z<sub>2</sub>D<sub>2</sub>-OSMOSE of the southern Benguela foodweb: parameterisation, calibration and pattern-oriented validation. *African Journal of Marine Science* **36**(1): 11–29. doi:10.2989/1814232X.2014.883326.
- Wenger, S.J., and Olden, J.D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* **3**(2): 260–267. doi:10.1111/j.2041-210X.2011.00170.x.
- Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H., Bamford, A.J., Ban, S., Barbosa, A.M., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N., Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S., Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C., Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Opper, S., Ortuño Crespo, G., Peterson, A.T., Rapacciuolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D., Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger, S., Whittingham, M.J., Zharikov, Y., Zurell, D., and Sequeira, A.M.M. 2018. Outstanding Challenges in the Transferability of Ecological Models. *Trends in Ecology & Evolution* **33**(10): 790–802. doi:10.1016/j.tree.2018.08.001.

# Paper IV

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## QUANTIFICATION OF TROPHIC INTERACTIONS IN THE NORWEGIAN SEA PELAGIC FOOD-WEB OVER MULTIPLE DECADES

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1 Quantification of trophic interactions in the Norwegian Sea pelagic food-web  
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13 ***Abstract:***

14 While ecosystem-based fisheries management calls for explicit accounting for interactions  
15 between exploited populations and their environment, moving from single species to  
16 ecosystem-level assessment is a significant challenge. For many ecologically significant  
17 groups, data may be lacking, collected at inappropriate scales or be highly uncertain. In this  
18 study, we aim to reconstruct trophic interactions in the Norwegian Sea pelagic food-web during  
19 the last three decades. For this purpose, we develop a food-web assessment model compatible  
20 with existing observations and knowledge. The model is based on inverse modelling and is  
21 designed to handle input observations and knowledge that are uncertain. We analyse if the  
22 reconstructed food-web dynamics are supportive of top-down or bottom-up controls on  
23 zooplankton and small pelagic fish and of competition for resources between the three small  
24 pelagic species. Despite high uncertainties in the reconstructed dynamics, the model results  
25 highlight that interannual variations in the biomass of herring, mackerel and blue whiting can  
26 primarily be explained by changes in consumption rather than by predation or fishing.  
27 Variations in the biomass of copepods and krill were also linked to variations in consumption,

28 while the past dynamics of amphipods can be explained by both consumption and predation.  
29 The model results provide little support for the hypothesised competition for resources between  
30 the three small pelagic species, despite their overlapping diets. We conclude that it is unlikely  
31 that the assessment and management of these commercial stocks during the last 30 years would  
32 have benefited from explicit incorporation of trophic interactions.

### 33 ***Keywords:***

34 Linear inverse modelling, herring, mackerel, blue whiting, copepods, krill, amphipods,  
35 Norwegian Sea, competition

## 36 ***1. Introduction***

37 The gradual implementation of ecosystem-based fisheries management (EBFM) and associated  
38 integrated ecosystem assessments (IEAs, Levin *et al.*, 2009) has called for models that can  
39 account for interactions between exploited populations and their physical and biological  
40 environment (Fulton, 2010; Link *et al.*, 2010; Collie *et al.*, 2014; Guo *et al.*, 2020). Of relevance  
41 to IEAs are models that explicitly account for trophic interactions between species or groups  
42 of species. Plagányi (2007) reviewed several such models, which include – among others -  
43 multi-species assessment models, mass balanced food-web models, size-based trophic models,  
44 and end-to-end models. The latter resolve a collection of complex processes that can include  
45 ocean circulation, biogeochemistry, trophic interactions across multiple trophic levels,  
46 population dynamics, and human pressures (including fishing).

47 Moving from single species to ecosystem-level modelling is a significant leap for several  
48 reasons. For many ecologically significant groups, data may be lacking, collected at  
49 inappropriate scales or highly uncertain. The rationale for including or excluding particular  
50 ecosystem components (e.g., jellyfishes, top predators, mesopelagic fauna, etc.) is not always  
51 easy to clarify. It is common that some model input parameters may not be readily available,  
52 may be uncertain or may vary in time and space in ways that are not well described or  
53 understood (Levins, 1974). For example, fish diet composition is known to vary with graphical  
54 locations, seasons, years, age, and size but there is rarely enough data to describe these  
55 variations accurately. Given the high uncertainties associated with food-web models inputs –  
56 whether this concerns observations, parameters, model structure or assumptions – it is likely  
57 that different models based on the same inputs may reconstruct different food-web dynamics.



58 Modelling food-webs from low to high trophic levels requires contributions from a range of  
59 experts who may have different conceptual representations of the food-web as well as different  
60 practices in collecting data and in modelling. The inclusion of participants with diverse  
61 expertise during the modelling process, from the conception of the model to the interpretation  
62 of the results, is therefore important to build trust and to allow for the appropriation of the  
63 model results.

64 Our point of view is that food-web models that support IEAs should 1) be inclusive of various  
65 types of expertise in all phases of the modelling process, 2) acknowledge that input data may  
66 be lacking or may be highly uncertain, 3) recognize that, rather than a single trajectory, an  
67 ensemble of past food-web trajectories may be equally supported by available data and  
68 knowledge. One modelling framework that matches these requirements is the “Chance and  
69 necessity” modelling approach (CaN, Planque and Mullon, 2020). CaN modelling is an inverse  
70 modelling approach that explicitly accounts for uncertainties in input data/information and  
71 provides multiple possible reconstruction of food-web trajectories as outputs. CaN models are  
72 possibilistic, i.e., they provide possible reconstructions of food-web dynamics, without  
73 assigning probability or likelihood (‘probabilistic’ models would provide these). In CaN  
74 models, food-web dynamics are controlled by the flow of biomass between ecosystem  
75 components, and these dynamics are considered possible when they are compatible with the  
76 biological and observational constraints that reflect the knowledge and uncertainties shared by  
77 multiple experts.

78 In this study, we use CaN modelling to quantify trophic interactions in the pelagic food-web  
79 over multiple decades, in order to support the integrated ecosystem assessment of the  
80 Norwegian Sea (ICES, 2021a). The motivation is to provide a better understanding of the  
81 energy flows within the food-web of the pelagic ecosystem and to understand the connections  
82 between these flows and the interannual changes in the biomass of commercial pelagic fish and  
83 their planktonic prey. The pelagic system in the Norwegian Sea is well studied and monitored,  
84 with regular surveys for commercial species and plankton and accurate reporting of fisheries  
85 catches (ICES, 2021a). In addition, single stock assessments for the main epipelagic fish stocks  
86 (herring, mackerel and blue whiting) provide reliable and consistent biomass estimates (ICES,  
87 2020). There remain, however, large gaps in knowledge and observations. Most observations  
88 take place during the spring and summer months when productivity is high and when several  
89 fish species seasonally migrate into the Norwegian Sea (Skjoldal, 2004). Zooplankton  
90 patchiness and vertical migrations combined with a diversity of escaping behaviour of

91 planktonic groups makes it difficult to obtain absolute biomass estimates for the different  
92 planktonic prey from vertical net sampling. The biomass of the mesopelagic fauna and its  
93 contribution to trophic flows is highly uncertain (Siegelman-Charbit and Planque, 2016). There  
94 is also a large uncertainty about the proportion of the annual net primary production (NPP) that  
95 is transferred to higher trophic levels, as this proportion depends on plankton community  
96 composition (Sigman and Hain, 2012) and trophic transfer efficiency that can be highly  
97 variable (Eddy *et al.*, 2021). These make it challenging for experts to assess whether model  
98 results are plausible and can lead to disagreements about the role of particular species or species  
99 groups, their abundance or contribution to the food-web, and ultimately how these should be  
100 represented within a food-web model.

101 The major pelagic fish stocks in the Sea comprise Norwegian spring spawning herring (*Clupea*  
102 *harengus*), Northeast Atlantic mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius*  
103 *poutassou*) which together form the Northeast Atlantic pelagic fish complex. All three stocks  
104 perform large scale seasonal feeding migrations and overlap spatially and temporally during  
105 the feeding season (Utne *et al.*, 2012). Several studies have investigated potential important  
106 ecological interactions within the complex including interspecific competition (Prokopchuk  
107 and Sentyabov, 2006; Langøy *et al.*, 2012; Utne *et al.*, 2012; Bachiller *et al.*, 2016; Mousing  
108 *et al.*, in prep.), regulatory processes such as predation on larvae by older individuals (Skaret  
109 *et al.*, 2015) and redistribution of energy within different ecosystem compartments and adjacent  
110 ocean regions (e.g., Varpe *et al.*, 2005). In addition, the pelagic fish complex is reported to  
111 interact with other species such as amphipods, krill, and mesozooplankton, through both  
112 bottom-up and top-down controls (Melle *et al.*, 2004; Olsen *et al.*, 2007). Bottom-up control  
113 occurs when the abundance or biomass of predators is dependent on available resources from  
114 lower trophic levels, while in top-down control it is the mortality imposed by higher trophic  
115 levels that drives variations in prey biomass (Cury *et al.*, 2003).

116 Huse *et al.* (2012) concluded that “the planktivorous fish populations feeding in the Norwegian  
117 Sea have interactions that negatively affect individual growth, mediated through depletion of  
118 their common zooplankton resource”. *Ibid* argued for the importance of accounting for these  
119 interactions in future ecosystem-based management.

120 The objectives of this study are threefold. First, we aim to reconstruct an ensemble of possible  
121 trajectories of the Norwegian Sea food web during the last three decades, compatible with  
122 existing observations and knowledge. The second aim is to analyse if the model results support  
123 top-down or bottom-up controls on zooplankton and small pelagic fish. Third, we aim to

124 identify if there was possible competition for resources between the three small pelagic species.  
125 We stress the importance of uncertainties associated with the inputs and outputs of this  
126 modelling study and discuss the implication of the results in the context of integrated ecosystem  
127 assessment and fisheries management advice.

## 128 **2. Material and Method**

### 129 **2.1. The Norwegian Sea pelagic food-web**

130 The Norwegian Sea is located northwest of Norway between 62°N and 75°N (Figure 1),  
131 covering an area of about 1.1 million km<sup>2</sup>. Its average depth is 1800 m (Skjoldal, 2004) and is  
132 composed of two basins deeper than 3000 m: the Lofoten Basin in the North and the Norwegian  
133 Basin in the South. The Norwegian Sea is a highly productive, seasonally mixed ecosystem  
134 with an annual primary production of ca. 80 gC m<sup>-2</sup> y<sup>-2</sup> (Rey, 2004; Skogen *et al.*, 2007). The  
135 Norwegian Sea exhibits strong seasonal changes in temperature, light and nutrients conditions  
136 (Rey, 2004; Nilsen and Falck, 2006), leading to a typical spring-bloom dominated system with  
137 initial dominance by diatoms, followed by smaller flagellates as silicate becomes depleted. The  
138 spring bloom begins in May in the south-eastern part and propagates northwards and westwards  
139 (Rey, 2004). Copepods is the dominant zooplankton group in terms of abundance in the  
140 Norwegian Sea and the species *Calanus finmarchicus* (Gunnerus, 1770) constitutes the main  
141 part of the total zooplankton biomass (Melle *et al.*, 2004). The larger zooplankton krill and  
142 amphipods are also abundant in this area. The Norwegian Sea is a feeding area for some of the  
143 largest exploited fish stocks in the world, such as the Norwegian spring spawning herring  
144 (*Clupea harengus*, Linnaeus, 1758), blue whiting (*Micromesistius poutassou*, Risso, 1827) and  
145 Northeast Atlantic mackerel (*Scomber scombrus*, Linnaeus, 1758) which feed on the  
146 aforementioned zooplankton groups (Langøy *et al.*, 2012; Bachiller *et al.*, 2016). The deep  
147 basins and the slopes are characterised by the presence of a deep scattering layer populated by  
148 mesopelagic fauna. Commonly found species in this layer includes the armhook squid  
149 (*Gonatus steenstrupi*, Kristensen 1981), ribbon barracudina (*Arctozenus risso*, Bonaparte  
150 1840), beaked redfish (*Sebastes mentella*, Travin 1951), helmet jellyfish (*Periphylla*  
151 *periphylla* Péron & Lesueur, 1810), and glacier lanternfish (*Benthosema glaciale*, Reinhardt  
152 1837). The degree of trophic interaction between mesopelagic species and the epipelagic food-  
153 web is highly uncertain, though the deep scattering layer may hold a total biomass similar or  
154 greater to that in the epipelagic layer (Siegelman-Charbit and Planque, 2016). The Norwegian  
155 Sea is an important feeding area for several marine mammals (Skern-Mauritzen, M. *et al.*,

156 submitted) such as fin-, minke-, sperm- and humpback whales. *Ibid* study suggest that marine  
157 mammals in the Norwegian Sea consume an average of 4.6 million tonnes annually, which is  
158 significantly more than the average fisheries catch (1.45 million tonnes in the period 2006-  
159 2015).

## 160 *2.2. The Norwegian Sea CaN model*

161 The food-web model for the Norwegian Sea was constructed in a participatory manner. Two  
162 workshops were organised in December 2020 and February 2021, followed by several short  
163 meetings between February and May 2021. These were attended by members of the ICES  
164 working group on the integrated assessment of the Norwegian Sea (WGINOR, ICES, 2021a)  
165 and selected specialists for the Norwegian and Barents Sea ecosystem working at the Institute  
166 of Marine Research, Norway. These meetings were used to refine the objectives of the CaN  
167 model, to elaborate the food-web structure, to identify relevant data and to discuss the model  
168 outputs. In parallel, model input parameters were derived from literature reviews. The  
169 description of the CaN model for the Norwegian Sea food-web is provided below, following  
170 the standard ODD model description protocol (Grimm *et al.*, 2006, 2010, 2020).

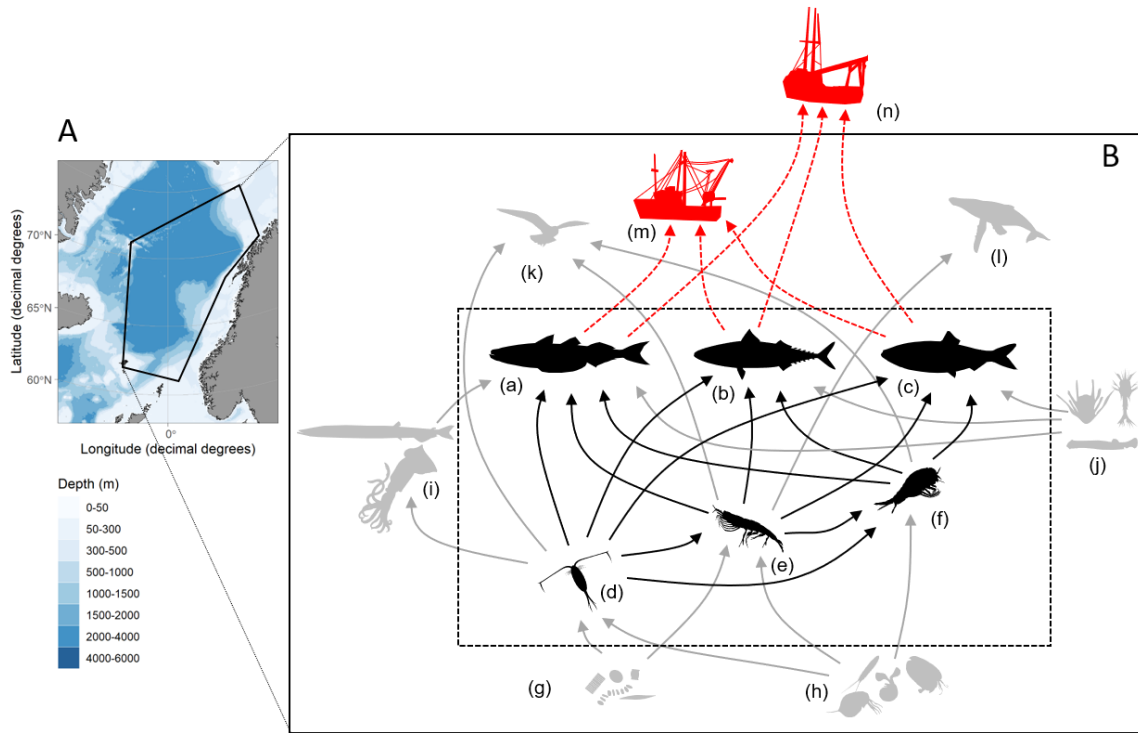
### 171 *2.2.1. Purpose and patterns*

172 CaN is a framework for modelling the dynamics of food-webs. The purpose of using CaN  
173 models is to reconstruct the possible trajectories of a food-web given existing knowledge and  
174 observations about its past dynamics. The primary ecological patterns are the interannual  
175 fluctuations in the biomass of the different species groups and the fluctuations in the fluxes of  
176 biomass between them. Other patterns can be derived, such as emerging trophic functional  
177 relationships, diet composition, or correlations between species biomass and trophic fluxes.  
178 The latter are used to address the objectives of the present study regarding trophic controls and  
179 competition for resources.

### 180 *2.2.2. Entities, state variables and scales*

181 In CaN, food-webs are defined by a set of components (species or tropho-species) and a set of  
182 fluxes between them (feeding interactions). The state variables are the biomass of the different  
183 species at each time step. In the Norwegian Sea CaN model, there are six trophospecies within  
184 the model domain: copepods, krill, amphipods, herring, mackerel, and blue whiting. We  
185 consider six additional components outside the model domain which contribute to the transfer  
186 of biomass in and out of the model domain: primary producers, small mesozooplankton  
187 (< 2mm), large mesozooplankton (> 2mm), mesopelagic species, marine birds, and mammals.

188 Also, fisheries catch for the three main fish species, are included in the model. The time step  
 189 of the model is annual, covering the period 1988-2020. The geographical extent is the open  
 190 basin of the Norwegian Sea (Figure 1). The model is not spatialised and considers the  
 191 Norwegian Sea as one single entity.



192  
 193 Figure 1. Schematic representation of the Norwegian Sea CaN model. A: geographical extent of the model. B:  
 194 Food-web structure. a: blue whiting, b: mackerel, c: herring, d: copepods, e: krill, f: amphipods, g: primary  
 195 producers, h: small zooplankton, i: mesopelagic fauna, j: large zooplankton, k: birds, l: marine mammals, m:  
 196 fisheries operating in the Norwegian Sea, n: fisheries operating outside the Norwegian Sea. Arrow symbolise  
 197 trophic (plain) and non-trophic (dashed) fluxes. Species coloured in black are included in the model domain. For  
 198 species coloured in grey, only the fluxes in/out from these species are considered in the model.

199 *2.2.3. Process overview and scheduling*

200 A CaN model reconstruct the dynamics of the biomass of species from the balance between  
 201 ingoing fluxes (consumption or import) and outgoing fluxes (predation, export, or fisheries).  
 202 The model is discrete in time and the biomasses at time  $t+1$  are fully determined by the  
 203 biomasses at time  $t$  and the fluxes operating between  $t$  and  $t+1$ . This is the deterministic part  
 204 of the model. The fluxes between compartments are not deterministic. Instead, they are drawn  
 205 randomly within a set of possible values that fulfils pre-defined constraints. This is the  
 206 stochastic part of the model. The Norwegian Sea model includes 32 trophic links, which  
 207 express the prey-predator interactions in the food-web, and 6 non-trophic links which represent  
 208 fishing of the small pelagic fish species by fisheries operating inside and outside the Norwegian  
 209 Sea.

210           2.2.4. *Design concepts*

211                   2.2.4.1. *Basic principles*

212 CaN models are biomass-based dynamic food-web models. The principles are similar to those  
213 outlined in other food-web models such as Ecopath (Polovina, 1984) or Ecopath with Ecosim  
214 (Christensen and Walters, 2004) with the notable differences that 1) the food-web is not  
215 assumed to be at equilibrium and 2) the trophic flows are modelled as a stochastic process,  
216 within some specified constraints (section 2.2.7) and 3) the master equation of Ecopath and  
217 CaN are slightly different (appendix 1 in Planque *et al.*, 2014).

218                   2.2.4.2. *Emergence*

219 The raw outputs of CaN models are time-series of all biomass fluxes and the initial biomass of  
220 the modelled species. From these, it is possible to derive emergent properties of the food-web  
221 such as diet fractions for individual predator species, total consumption, ratios of consumption  
222 over biomass, production, throughflow, or other indices relevant to ecological network analysis  
223 (ENA, Ulanowicz, 2004; Fath *et al.*, 2007; Guesnet *et al.*, 2015). In this application of the CaN  
224 model, the focus is on three emergent properties: the relationship between consumption and  
225 population growth which can be indicative of bottom-up control, the relationship between  
226 predation and population growth which can be indicative of top-down control and the  
227 relationship between consumption rates of predatory species with overlapping diets, which can  
228 be indicative of resource competition.

229                   2.2.4.3. *Adaptation, objectives, learning, prediction, sensing and interaction*

230 These ODD descriptors, that are mostly relevant to individual based models, are not applicable  
231 for the description of the CaN model presented here.

232                   2.2.4.4. *Stochasticity*

233 CaN models are stochastic. The principle in CaN is to draw many random food-web trajectories  
234 within the set of possible ones. The food-web trajectories are referred to as "CaN samples".  
235 There is no probability associated with an individual CaN sample, which represents one  
236 possible trajectory of the food-web dynamics. The CaN model is said to be possibilistic.

237                   2.2.4.5. *Collectives*

238 This section is not relevant for CaN models.

239                   2.2.4.6. *Observation*

240 We derive 3 types of observations from CaN simulations:

- 241       1. Time-series of species biomass and fluxes between species/fishery

- 242 2. Diet composition  
 243 3. Correlations between biomasses and fluxes

244 These three types of observations can be derived from individual CaN samples. We use many  
 245 CaN samples to explore the range and the distribution of these observations.

246 *2.2.5. Initialization*

247 The elements necessary to build the CaN model for the Norwegian Sea are:

- 248 - The list of species and the biomass fluxes (Figure 1)
- 249 - The species-specific input parameters used for the CaN master equation and the implicit  
 250 constraints (Table 1)
- 251 - The list of available observations, often in the form of data-series (Table 2)
- 252 - The list of explicit constraints (Supplementary material S3)

253 The biomass of species at the start of the modelling time-period (year 1988) constitutes the  
 254 initial conditions. These do not need to be specified in the initialisation phase as they are  
 255 sampled during CaN modelling.

256 Table 1: input parameter values for RCaN

	<i>Tropho-species</i>	<i>Satiation</i> ( $\sigma$ )	<i>Inertia</i> ( $\alpha$ )	<i>Other losses</i> ( $\mu$ )	<i>Assimilation efficiency</i> ( $\gamma$ )	<i>Digestability</i> ( $\kappa$ )	<i>Refuge biomass</i> ( $\beta$ )
<b>Outside the model domain</b>	Phytoplankton	/	/	/	/	0.65	/
	Small zooplankton	/	/	/	/	0.90	/
	Large zooplankton	/	/	/	/	0.90	/
	Mesopelagics	/	/	/	/	0.90	/
<b>Inside the model domain</b>	Copepods	141.6	8.22	9.22	1.0	0.84	500
	Krill	60.0	4.05	5.19	1.0	0.84	165
	Amphipods	34.0	3.67	7.04	1.0	0.84	10
	Herring	12.0	0.55	3.40	0.9	0.90	175
	Blue whiting	9.3	0.72	3.00	0.9	0.90	105
	Mackerel	12.0	0.52	4.20	0.9	0.90	175

257

258 *2.2.6. Input data*

259 Many data time-series for the Norwegian Sea ecosystem are compiled and reported annually  
 260 by WGINOR (ICES, 2019). In addition to these series which mostly originate from dedicated  
 261 monitoring programs, there are punctual observations, i.e. for one or few years only. Some  
 262 input data are directly derived from field measurements, like survey indices of zooplankton  
 263 biomass (ICES, 2021b). Others can result from complex modelling operations, such as fish  
 264 stock biomass derived from fish stock assessment models (ICES, 2020) or net primary  
 265 production derived from satellite-based primary production models (Arrigo and van Dijken,

266 2011). Diet data for herring, mackerel and blue whiting have been collected through stomach  
 267 sampling programs (Langøy *et al.*, 2012) starting in 2004 and total consumption estimates for  
 268 small pelagic fish species are taken from bioenergetic model results (Bachiller *et al.*, 2018).  
 269 The complete list of input data series and punctual observations used in this study is provided  
 270 in Table 2.

271 Table 2: list of data series/input information, used to inform and constrain the model

Observational series	Years	Sources
Primary production	2003 – 2019	Unpublished results
Zooplankton biomass	1995 - 2019	WGINOR 2019, figure 2.4
Herring biomass	1988 - 2020	WGWIDE 2020, table 4.5.1.4
Blue whiting biomass	1988 - 2020	WGWIDE 2020, table 2.4.2.5
Mackerel biomass	1988 - 2020	WGWIDE 2020, table 8.7.3.1
Consumption/Biomass herring	2005 - 2010	Bachiller <i>et al.</i> , 2018, figure 9
Consumption/Biomass blue whiting	2005 – 2010	Bachiller <i>et al.</i> , 2018, figure 9
Consumption/Biomass mackerel	2005 - 2010	Bachiller <i>et al.</i> , 2018, figure 9
Herring diet	2004 - 2016	Unpublished results from IMR diet database
Blue whiting diet	2004 - 2016	Unpublished results from IMR diet database
Mackerel diet	2004 - 2016	Unpublished results from IMR diet database
Herring catches	1988 - 2019	WGWIDE 2020, table 4.4.1.1
Blue whiting catches	1988 - 2019	WGWIDE 2020, table 2.3.1.1
Mackerel catches	1988 - 2019	WGWIDE 2020, table 8.4.1.1

272

273 *2.2.7. Model constraints*

274 Constraints are specific to CaN models (and therefore not listed in the items of the ODD  
 275 protocols).

276 In CaN models, constraints express our knowledge about the system, and how we distinguish  
 277 possible from impossible dynamics. CaN model outputs are stochastic solutions within a set of  
 278 predefined constraints. All CaN models contain implicit/compulsory constraints which reflect  
 279 that: biomasses are always positive, fluxes are always positive, the growth and mortality rates  
 280 of a tropho-species is bounded (inertia constraint) and feeding by unit time/biomass is also  
 281 bounded (satiation constraint). Additional explicit constraints can be specified to reflect  
 282 additional knowledge about the food-web, such as information on the production, biomass, or  
 283 consumption of different trophospecies. Explicit constraints are written in the form of symbolic  
 284 expressions (equalities or inequalities) that relate model components, fluxes, and observations.  
 285 CaN model deals with uncertainties through the constraints. For example, if the biomass of an



286 animal group is not monitored but has been inferred to be between a minimum and a maximum  
287 bound, these bounds can be used to constrain the possible dynamics of the food-web. Similarly,  
288 if diet data is available for some groups for some years, these can be used to constrain the  
289 possible food-web trajectories within these dietary limits. The construction of different types  
290 of constraints is further developed in Drouineau et al. (2021).

291 The CaN model for the Norwegian Sea includes several types of constraints that can directly  
292 and/or indirectly restrict fluxes by constraining the range of possible biomass. Constraints on  
293 fish catches directly affect fluxes from pelagic fish to fisheries. Constraints on satiation directly  
294 limit incoming fluxes for the six species within the model domain. Constraints on NPP directly  
295 affect fluxes from primary producers to copepods and krill and indirectly affect fluxes from  
296 small zooplankton to copepods and krill. Constraints associated with diet or total consumption  
297 estimates affect the fluxes from zooplankton and mesopelagic fauna towards small pelagic fish.  
298 The range of possible biomass for the six main species is additionally constrained by inertia,  
299 refuge biomass and compliance with biomass observations. While some constraints apply for  
300 the entire model period (1988-2020) others only apply for selected years when appropriate data  
301 were available. In total 107 constraints were used in this study. The list of constraints used in  
302 this model, their period of application as well as their sources can be found in Supplementary  
303 Material S3.

#### 304 2.2.8. *Submodels*

305 CaN models have only one main model structure which is summarised by its master equation  
306 and the set of constraints. The CaN master equation accounts for how temporal changes in  
307 biomass in the various model components are related to the biomass fluxes between  
308 components:

$$309 \quad B_{i,t+1} = e^{(-\mu_i)} B_{i,t} + \frac{(1-e^{(-\mu_i)})}{\mu_i} [\gamma_i \sum_j \kappa_j F_{ji} - \sum_j F_{ij}] \quad (1)$$

310 where  $B_{i,t}$  is the biomass of component  $i$  at time  $t$ ,  $F_{ij}$  and  $F_{ji}$  are the biomass fluxes between  
311 components  $i$  and  $j$ , and  $\mu$ ,  $\gamma$  and  $\kappa$  are input parameters. Model input parameters were derived  
312 from life history theory (Hoenig, 1983), metabolic theory of ecology (Savage et al, 2004),  
313 allometric relationships (Yodzis and Innes, 1992; Gillooly et al., 2001; Makarieva et al., 2008)  
314 or direct measurements (Johnstone et al., 1993). For each species within the model domain, six  
315 biological parameters are provided: satiety ( $\sigma$ ), inertia ( $\alpha$ ), metabolic losses ( $\mu$ ), assimilation  
316 efficiency ( $\gamma$ ), digestibility ( $\kappa$ ) and refuge biomass ( $\beta$ ) (Table 1). For trophospecies outside the  
317 model, no input parameter is required except for prey species for which the digestibility ( $\kappa$ )

318 must be provided. The details of the derivation and calculation of the input parameters are  
319 presented in Lindstrøm *et al.* (2017) and in Supplementary Material S2.

320 Sampling of CaN trajectories is achieved using a Gibbs polytope sampling algorithm which is  
321 efficient for problems of high dimensionality (Aditi Laddha and Santosh Vempala, 2020;  
322 Drouineau *et al.*, 2021). A total of 100,000 food-web trajectories were sampled and only one  
323 for every 1000 samples were retained (a procedure known as thinning, designed to avoid non-  
324 independence between MCMC samples). The resulting 1000 trajectories were analysed to  
325 explore past food-web trajectories and trophic-controls.

### 326 2.2.9. *Summary*

327 The Norwegian Sea CaN model is a food-web model defined by 1) six main trophospecies and  
328 six additional components, 2) 32 biomass fluxes, 3) a master equation that relate biomass to  
329 fluxes, 4) 6 input parameters for each species, 5) 4 species-specific implicit constraints, 6) 107  
330 explicit constraints and 7) observational data.

331 The steps for the implementation of CaN models include 1) model design (defining the  
332 components and the fluxes), 2) entry of input parameters, 3) provision of observational data,  
333 4) definition of explicit constraints, 5) construction of the system of in/equalities that defines  
334 possible trajectories, 6) sampling possible trajectories and 7) graphical representation and  
335 analysis of the model results. The model was built using the R library RCaN and the Java  
336 graphical user interface RCaNconstructor (Drouineau *et al.*, 2021) which integrate all these  
337 steps into an interactive platform that can be used in a participatory context.

### 338 2.3. *Analysis of CaN model outputs*

339 The primary outputs of CaN models consist of time-trajectories of the biomass and fluxes.  
340 These provide a first level assessment of the past dynamics of the food-web. This assessment  
341 explicitly includes uncertainties about biomass and fluxes, which reflect the degree of precision  
342 in the input knowledge and data. From these trajectories, it is possible to derive additional  
343 patterns that are relevant for the investigation of the food web dynamics. These patterns include  
344 for example the representation of diet fractions, i.e. the proportion of different prey in the diet  
345 of individual predator species.

346 The present study has a primary focus on trophic controls, either by predation pressure (top-  
347 down) or by resource availability (bottom-up). We investigated the relationship between  
348 individual species growth and the relative predation pressure (the fluxes going out) and food  
349 consumption (the fluxes coming in). Species growth is defined as the ratio of species biomass

350 between two time-steps  $B_{i,t+1}/B_{i,t}$ . Relative predation pressure is defined by the sum of  
351 outgoing fluxes relative to the species biomass  $\sum_j F_{i,j}/B_{i,t}$ , while relative consumption is  
352 defined by the sum of ingoing fluxes relative to the species biomass  $\sum_j F_{j,i}/B_{i,t}$ . A positive  
353 Pearson correlation coefficient between species growth and consumption provides an  
354 indication for the presence of bottom-up control. A negative Pearson correlation coefficient  
355 between species growth and predation provides an indication for the presence of top-down  
356 control.

357 We investigated the potential for competition between small pelagic fish species by running  
358 pairwise comparisons of relative consumption. A negative correlation between consumptions  
359 is indicative of resource competition i.e., when one species consumes more the other consumes  
360 less and vice-versa. The competition was investigated by comparing consumption of all  
361 planktonic prey (total consumption) and by comparing consumption of individual prey groups  
362 (prey-specific consumption). For total consumption we performed pairwise comparisons  
363 between pelagic fish species. In this case, a negative correlation supports the hypothesis that  
364 the total consumption by one species is negatively affected by (or affecting) the total  
365 consumption by the other. For prey-specific consumption, we performed comparisons between  
366 one pelagic fish and the two other combined. In this case, a negative correlation supports the  
367 hypothesis that the consumption of a given prey by the first pelagic fish is affected by (or  
368 affecting) the consumption of the same prey by the two others pelagic fish.

369 For the trophic control and competition analyses, we computed the Pearson correlation  
370 coefficients for each RCaN trajectory. We then plotted the density distribution of the  
371 correlation coefficients based on the full set of trajectories.

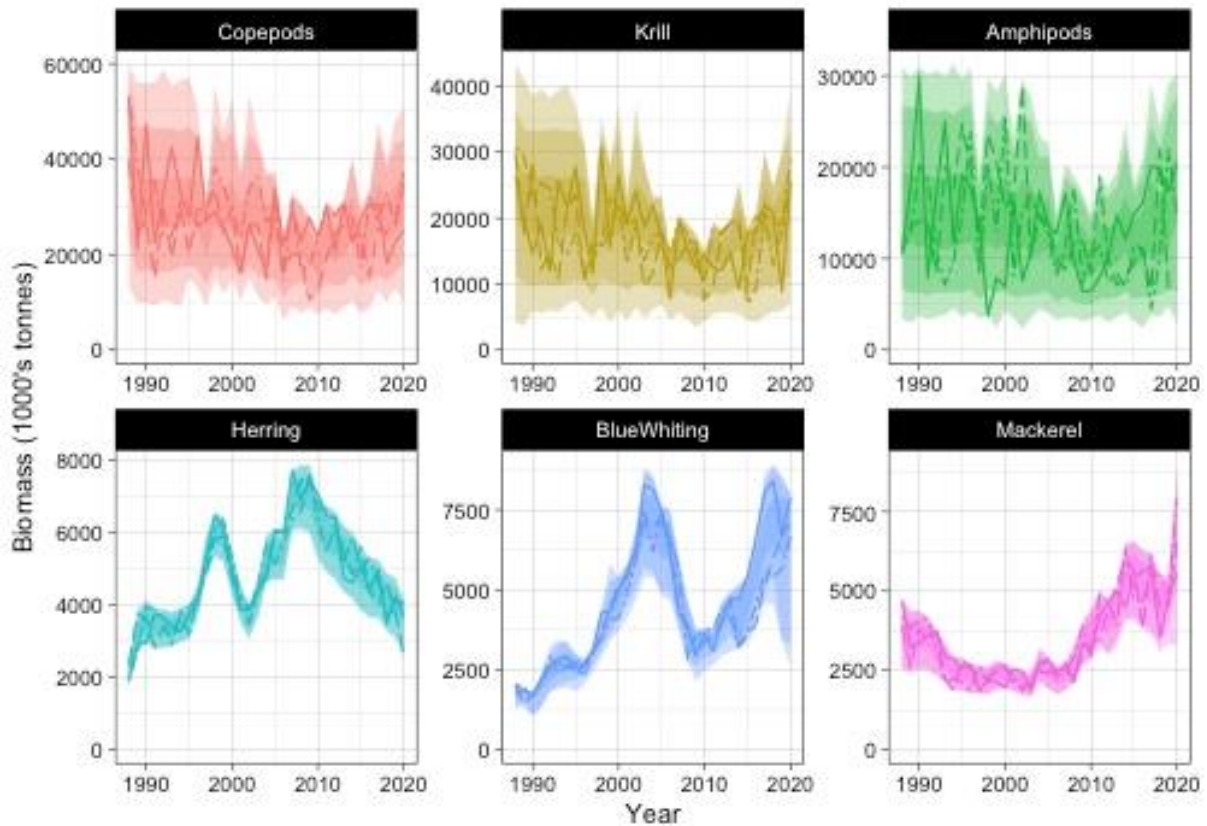
### 372 **3. Results**

373 The primary output of the CaN model is a set of possible food-web trajectories. Each trajectory  
374 is composed of six biomass time-series and 38 flux time-series that are compatible with each  
375 other and with every model constraint.

#### 376 **3.1. Biomass trajectories**

377 The envelopes of the biomass trajectories of the six species reflect the uncertainty around the  
378 input observational data. The biomass time series of the pelagic fish have a relatively high  
379 certainty, unlike the biomass time series of zooplankton groups (Figure 2). Individual  
380 trajectories display high year-to-year variations within these envelopes, and individual time-

381 series tend to reach extreme high or low biomass (i.e., close to the limit of the envelope) in at  
382 least one year of the sampling period 1988-2020.



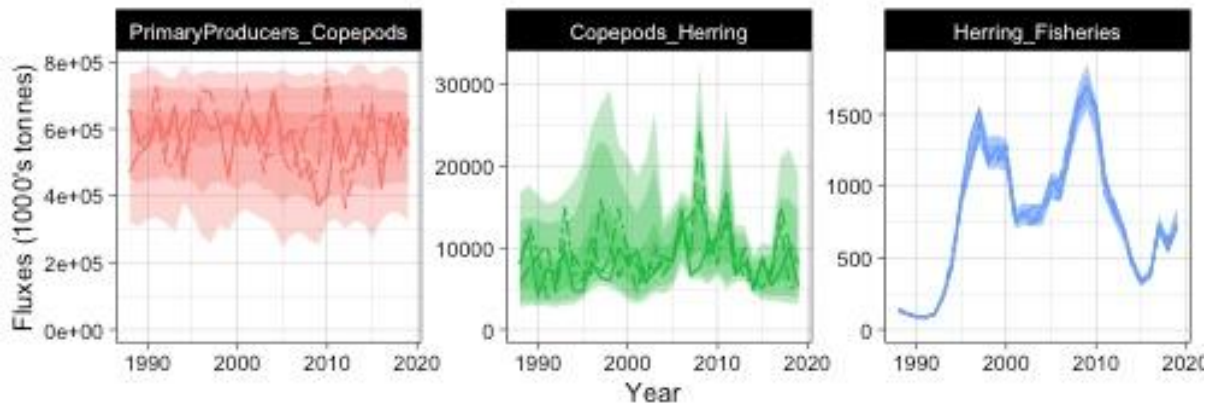
383

384 Figure 2. Reconstructed time-series of biomass for the six species within the model domain: copepods, krill,  
385 amphipods, herring, blue whiting, and mackerel. Each panel shows the envelopes containing 100% (light), 95%  
386 (medium) and 50% (dark) of the 1000 sampled trajectories. Three individual trajectories are provided for  
387 illustration in plain, dashed and dash-dotted lines.

### 388 **3.2. Fluxes trajectories**

389 The envelopes of the flux time-series highlight how certain or uncertain the reconstructions of  
390 historical fluxes may be, given currently available data and knowledge (Figure 3). For the  
391 consumption of primary producers by copepods, the CaN reconstructions range between 300  
392 and 800 Mt.year<sup>-1</sup>. No clear temporal trend can be detected while there is high variability  
393 between years and between CaN trajectories. The consumption of copepods by herring is  
394 provided with slightly greater certainty, in particular for the period 2004-2016 when estimates  
395 of consumption are available based on stomach contents analysis of fish collated at specific  
396 surveys. Note the higher uncertainties in years 2008 and 2011, when these estimates were not  
397 available. The reconstructions of fluxes from the herring population to the fishery are heavily  
398 constrained by the catch data, which are known with high precision. As was the case for  
399 biomass time-series, flux time-series display high year-to-year variations and reach extreme

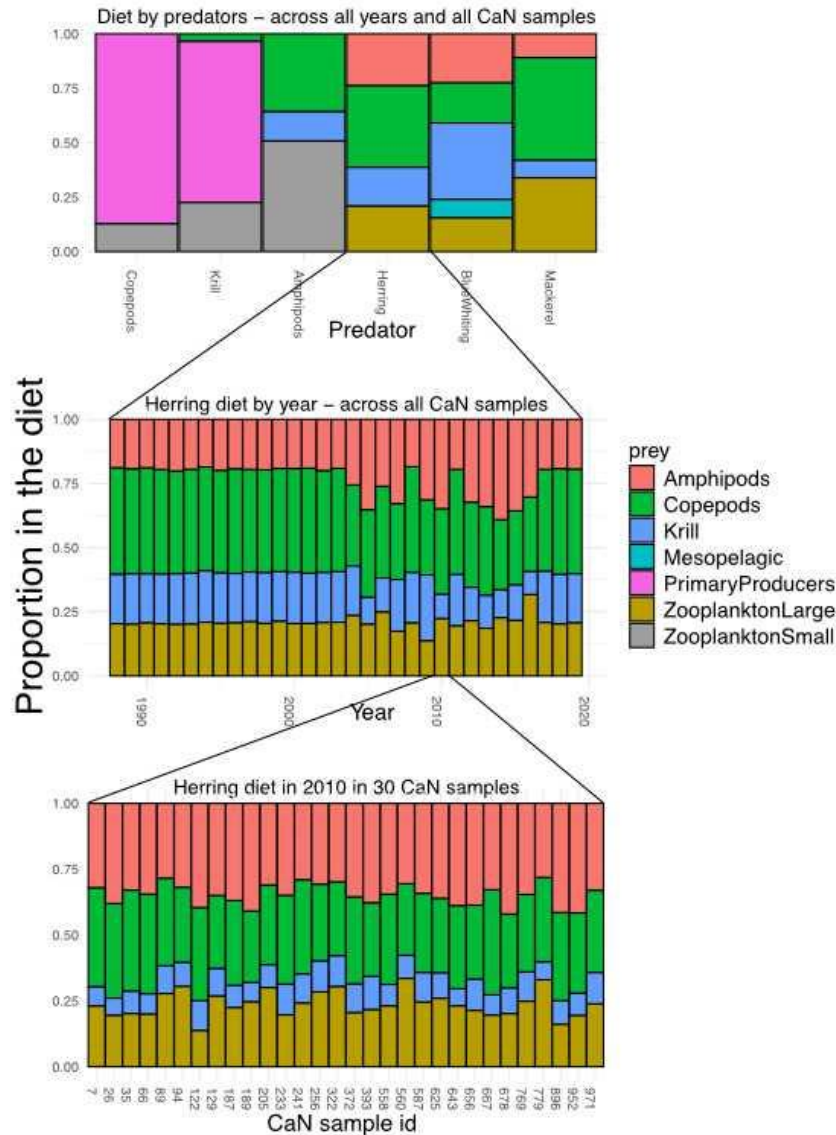
400 high or low fluxes (i.e., close to the limit of the envelope) in at least one year of the period  
401 1988-2020. The complete set of reconstructed fluxes is provided in Supplementary Material  
402 S4.



403  
404 Figure 3. Reconstructed time-series of biomass for three selected fluxes: primary producers to copepods (left),  
405 copepods to herring (middle) and herring to fisheries (right). Each panel shows the envelopes containing 100%  
406 (light), 95% (medium) and 50% (dark) of the 1000 sampled trajectories. Three individual trajectories are provided  
407 for illustration in plain, dashed and dash-dotted lines.

### 408 3.3. Diets

409 It is possible to derive the proportion of prey in the diet of copepods, krill, amphipods, herring,  
410 blue whiting, and mackerel (Figure 4) from the CaN reconstructions. These diets reflect the  
411 information provided in constraints (e.g., constraint 11 which specifies that the proportion of  
412 small zooplankton in the diet of copepods cannot exceed 20%, or constraints 57 and 58 which  
413 relate the consumption of copepods by herring in the model to the consumption reported in  
414 field observations). These diets also reflect the dynamic balance between resource  
415 requirements and prey availability which is expressed in the CaN master equation. From these  
416 results, the diets of herring, blue whiting and mackerel appear to be diversified and overlap  
417 with each other (Figure 4-top). When averaged over many trajectories, the diets display little  
418 interannual variability as exemplified for herring (Figure 4-middle). However, estimates from  
419 individual trajectories highlight the within-year uncertainty in the proportion of individual prey  
420 (Figure 4-bottom).



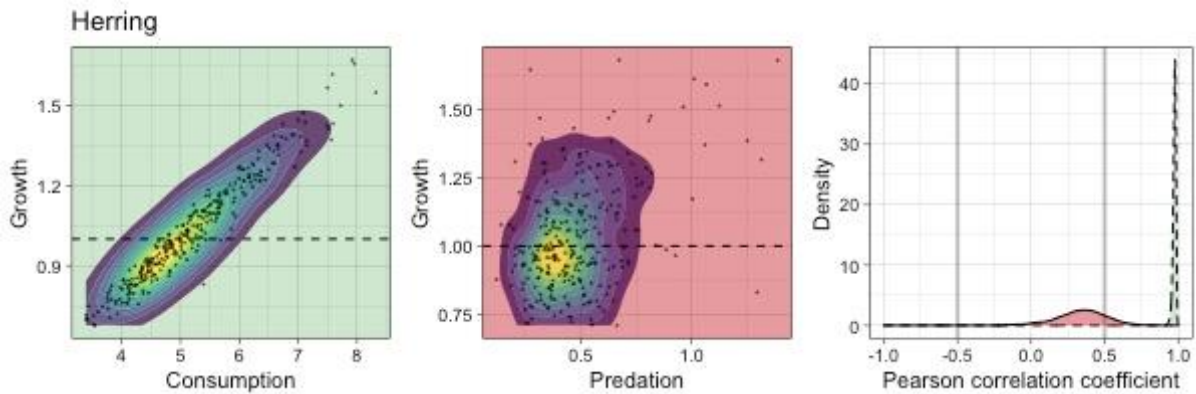
421

422 Figure 4. Reconstruction of diets. Average diet for each of the six modelled species (top), annual diet for herring  
 423 in individual years averaged over all CaN samples (middle) and in one year (2010) for 30 selected CaN sample.  
 424 Coloured bars indicate the proportion of each prey consumed by each predator (top) or for herring in each  
 425 individual year (middle) or individual CaN samples (bottom).

426 **3.4. Top-down and bottom-up controls**

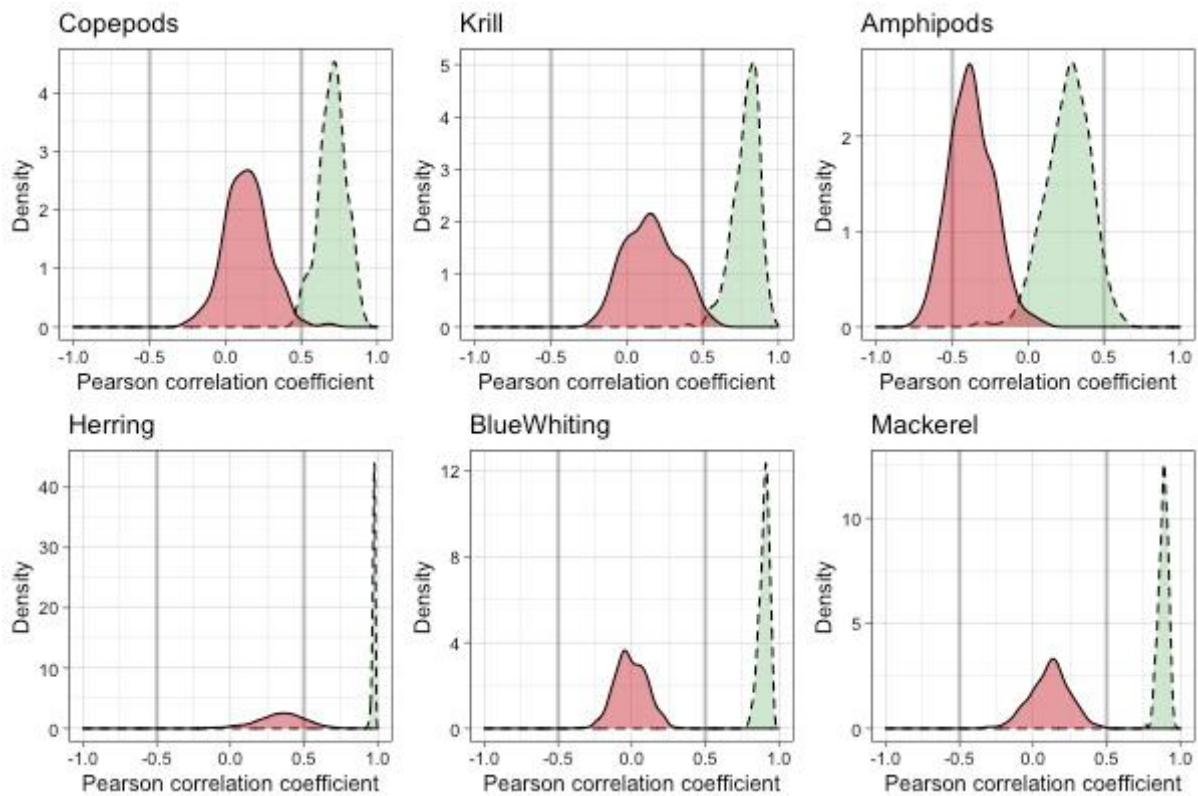
427 For herring, there is a clear positive link between consumption and population growth across  
 428 all trajectories (Figure 5-left), despite uncertainties in the consumption of individual prey  
 429 (Figure 4 and S4). This is in line with a possible bottom-up control. On the other hand, there is  
 430 no clear relationship between herring population growth and predation/fishing (Figure 5-  
 431 middle), which suggests that top-down control is not operative. The density distribution of the  
 432 correlations - between population growth and consumption/predation - calculated at the  
 433 individual trajectory level confirms the support for apparent bottom-up control and lack of

434 support for top-down control (Figure 5-right). A similar pattern of trophic control is observed  
435 for mackerel and blue whiting and to a lesser extent for copepods and krill (Figure 6). The case  
436 of amphipods is more complex. There appears to be a possible combination of top-down and  
437 bottom-up controls. There are few trajectories for which the correlation between consumption  
438 and growth are positive-high (bottom-up) and few trajectories for which the correlation  
439 between predation and growth are negative-high (top-down). The hypotheses that amphipods'  
440 population growth could be limited by either predation or food availability are both plausible.



441

442 Figure 5. The relationship between population growth of herring and relative consumption (left) or relative  
443 predation, including fishing (middle). Each dot represents the estimated growth and feeding/predation for a given  
444 year in a given RCaN sample. The coloured density contours help to visualise the shape of the scatterplot. The  
445 distribution of the correlation coefficients between feeding (green-dotted) or predation (red-plain) and  
446 population growth are shown on the right panel.



447

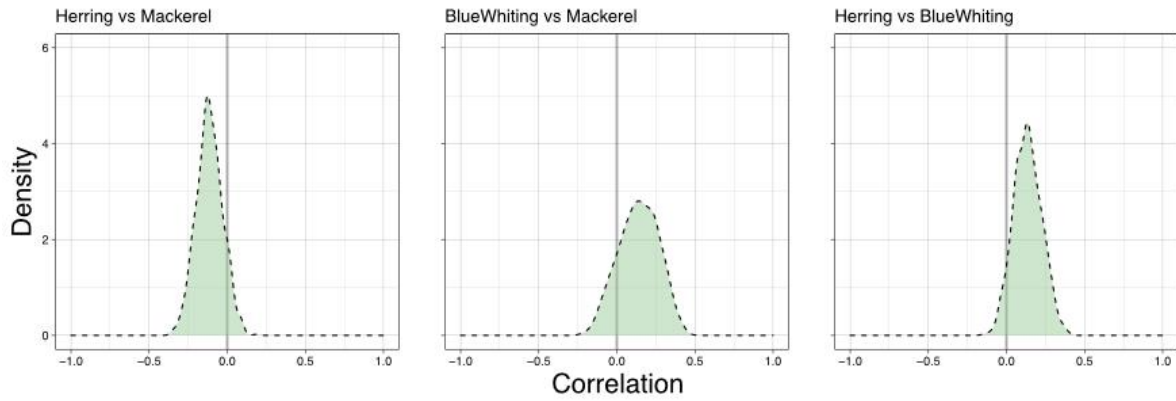
448 Figure 6. Distribution of the correlation coefficients between consumption (green-dotted) or predation (red-plain)  
 449 and population growth. A positive correlation between growth and consumption is indicative of bottom-up  
 450 control. A negative correlation between growth and predation is indicative of top-down control. The bottom-left  
 451 panel (herring) is the same as in Figure 5.

### 452 **3.5. Competition between small pelagic fish**

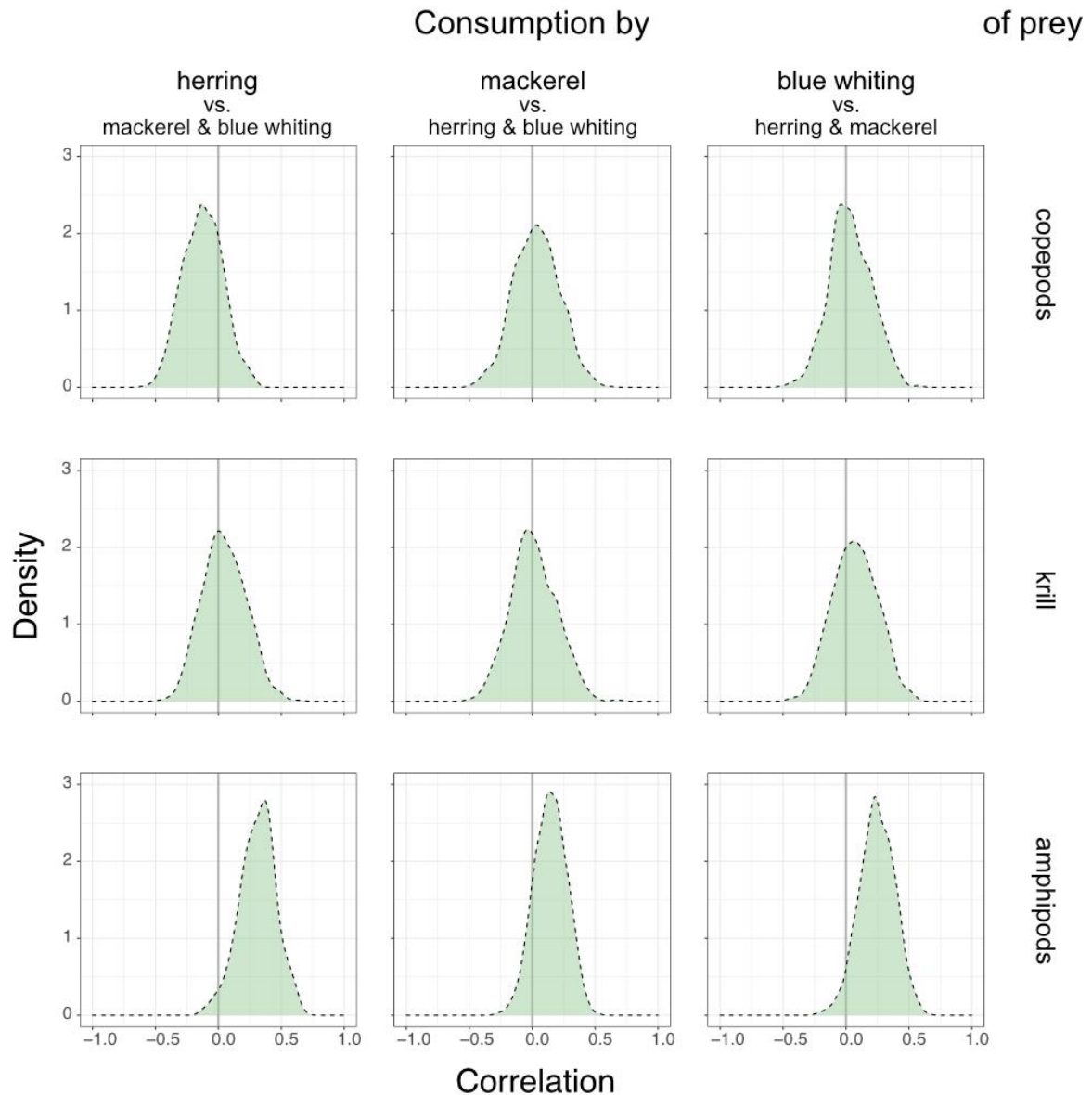
453 The pairwise correlations between total prey consumption by herring, mackerel and blue  
 454 whiting are generally close to zero, which is indicative of absent or weak competition for  
 455 resources between the three species (Figure 7). The slight negative correlation between herring  
 456 and mackerel suggests a possible but limited competition between the two species while the  
 457 positive correlations for blue-whiting vs mackerel and blue whiting vs herring suggest that  
 458 these may jointly have increased consumption when more resources became available. To  
 459 further investigate how competition for specific prey resources may operate, we represented  
 460 the correlation between the consumption of specific resources (copepods, krill and amphipods)  
 461 by herring, mackerel and blue whiting (Figure 8). Most correlations are centred around zero,  
 462 which suggests absence or weak competition between the three pelagic species. The slightly  
 463 negative correlation between copepod consumption by herring and by mackerel + blue whiting  
 464 (Figure 8) is consistent with the negative correlation between herring and mackerel total  
 465 consumption (Figure 7). This supports a possible resource limitation for herring feeding on  
 466 copepods when mackerel feed heavily on copepods. The slight positive correlations for the



467 consumption of amphipods suggested that amphipods production has possibly been driving  
468 variations in consumption by the three pelagic fish. These positive correlations do not support  
469 the hypothesis of competition for amphipod resources by the three pelagic fish populations.



470  
471 Figure 7: Distribution of the correlation coefficients between herring, mackerel, and blue whiting consumptions  
472 in the Norwegian Sea. Each panel shows the density distribution of the correlation coefficient between species  
473 consumption. Positive correlations are indicative of similar variations in consumption between predators.  
474 Negative correlations are indicative of competition.



476

477 Figure 8: Distribution of the correlation coefficients between the consumption of copepods (top), krill (middle)  
 478 and amphipods (bottom) by herring (left), mackerel (centre), and blue whiting (right) and the consumption of  
 479 the same prey by the 2 other pelagic fish. Positive correlations are indicative of joint variations in consumption  
 480 between predators. Negative correlations are indicative of resource limitations due to competition for specific  
 481 prey.

482

## 483 **4. Discussion**

### 484 **4.1. Trophic interactions between small pelagic fish and their prey**

485 Using CaN modelling we have reconstructed a collection of food-web trajectories for the  
 486 Norwegian Sea, compatible with existing data and knowledge, and explicitly accounting for

487 uncertainties. From these trajectories we have reconstructed the diets of herring, mackerel, and  
488 blue whiting and of their planktonic prey: copepods, krill and amphipods. We have estimated  
489 correlations between population growth, prey consumption and predation pressure. Our results  
490 show that for all species except amphipods, there is a clear positive correlation between  
491 population growth and consumption of prey, supportive of a possible bottom-up control. On  
492 the other hand, we have found no evidence for top-down controls by any of the predators on  
493 their planktonic prey. Our results also suggest no or very limited support for interspecific  
494 competition between the small pelagic species at the population scale, as no significant  
495 covariations in biomass and consumption of the three species was observed on an interannual  
496 time scale.

497 These results are in contrast with previous studies that have argued for strong top-down  
498 controls by planktivorous fish on zooplankton (Skjoldal, 2004; Huse *et al.*, 2012). Large stocks  
499 of herring and concomitant increased entry of blue whiting have been correlated with low  
500 copepod biomasses the following year (Olsen *et al.*, 2007). Similarly, long term trends seem to  
501 indicate a decreased zooplankton biomass coordinated with an increase in planktivorous fish  
502 biomass (Huse *et al.* 2012). It has also been suggested that small pelagic fish may compete for  
503 limiting resources at local scales and that this can affect somatic growth (Huse *et al.*, 2012;  
504 Olafsdottir *et al.*, 2016).

505 A recent modelling study, assessing the impact of sampling design on zooplankton biomass  
506 estimates, suggests that the above zooplankton trends are highly uncertain, mainly as a result  
507 of zooplankton patchy distribution (Hjøllo *et al.*, 2021). While previous works have focused  
508 on the copepod species *Calanus finmarchicus*, the dominant mesozooplankton species in the  
509 Norwegian Sea (Melle *et al.*, 2004), the CaN model presented here includes multiple prey  
510 groups. This provides more flexibility to account for possible changes in diet or in trophic  
511 controls that are known to vary spatially and seasonally (Olsen *et al.*, 2007; Varpe and Fiksen,  
512 2010). The apparent lack of interspecific competition could be explained by differences in  
513 phenology with different timing of the main/peak feeding season (Langøy *et al.*, 2012) and/or  
514 behavioural differences in their daily movement patterns (Debes *et al.*, 2012). Furthermore,  
515 changes in migration behaviour may also have been a major factor affecting food availability  
516 and the potential for competition between pelagic fish. The standing biomass, production, and  
517 spatiotemporal dynamics of zooplankton during the feeding season may affect the pelagic fish  
518 complex. Separate areas and water masses in the Nordic seas differ in the relative abundance  
519 of zooplankton during the feeding season due to differences in, among others, growth rate,

520 species composition and seasonal vertical migration (Dalpadado *et al.*, 1998; Broms *et al.*,  
521 2009, in prep.; Bagøien *et al.*, 2012). Generally, the seasonal zooplankton development in the  
522 Norwegian Sea and adjacent areas is progressively delayed from southeast to northwest and  
523 from coastal- to Atlantic and further to Arctic waters (Broms and Melle, 2007; Bagøien *et al.*,  
524 2012). The feeding migration pattern of herring have been suggested to follow spatial gradients  
525 in prey availability (Broms *et al.*, 2012) and the geographical expansion of mackerel since the  
526 mid-2000s have partly been explained by food limitation (Olafsdottir *et al.*, 2019).

527 Interspecific competition depends on the degree of spatiotemporal overlap between predator  
528 species. Even when species do co-occur, intra- and interspecific competition implies resource  
529 limitation. Bachiller *et al.* (2016) reported dietary overlap between herring and mackerel to be  
530 larger when the fish co-occurred indicating that the species were preying on the same  
531 zooplankton patches. In addition, they argued that the lack of prey switching indicated limited  
532 interspecific competition. In our study, we found possible but limited competition between  
533 mackerel and herring which is in accordance with Utne *et al.* (2012) who, based on a modelling  
534 study, reported only a minor increase in annual consumption when species were simulated  
535 individually (i.e., with no interspecific competition). We found no indication of competition  
536 between blue whiting and the two other pelagic species.

#### 537 **4.2. Model uncertainties and sensitivity**

538 Uncertainties in the outputs of the CaN model presented here are generally high, at least in  
539 comparison with other commonly used food-web models for the same region (Skaret and  
540 Pitcher, 2016; Bentley *et al.*, 2017; Pedersen *et al.*, 2021). This may appear, at first sight, as a  
541 limitation of the CaN modelling approach. Rather, we contend that these high uncertainties are  
542 a true representation of uncertainties in input data and knowledge. Constructing a CaN model  
543 compatible with the entire set of available input information is an iterative process during  
544 which 'precisely wrong' models are gradually eliminated by relaxing model constraints or  
545 decreasing certainty in some of the input observations. This process, which was conducted in  
546 a participatory manner, is a way to identify where information might be lacking, biased, not  
547 easily scalable to the entire Norwegian Sea or simply uncertain. One key feature of the CaN  
548 models emerging from this process is that the outputs – i.e. all individual food-web trajectory  
549 sampled with CaN - are always compatible with input data and knowledge. This is often not  
550 the case for EwE models for which at least part of the past observations lie outside the  
551 confidence bounds of the model outputs (see for example Figure 5 in Bentley *et al.*, 2017; and  
552 Figure 2 in Pedersen *et al.*, 2021).

553 It is possible to draw robust conclusions on trophic controls and competition for the three  
554 pelagic fish stocks and their prey in the Norwegian Sea, despite the large uncertainties in  
555 individual biomass and trophic flux estimates. This is because all food-web components are  
556 linked to each other and to the input observations, thereby constraining the range of possible  
557 trophic interactions.

558 As with any model, the results obtained with the CaN model and the conclusions drawn from  
559 them depend on the modelling choices and, in particular, on the values of the input parameters.  
560 Presently, it's not yet possible to handle uncertainty in model input parameters in RCaN, but  
561 the sensitivity of the model to uncertain parameter values can be assessed through standard  
562 sensitivity analyses (EPA, 2009). We explored the sensitivity of our main conclusions to a  
563 range of parameter values and assumptions, including primary production, fishing intensity,  
564 metabolic losses, inertia, and satiation (Supplementary material S5). When primary production  
565 is reduced to extreme low levels (10% of the baseline level) there is no solution i.e., the primary  
566 production is not sufficient to sustain the observed food-web dynamics. When fisheries catches  
567 are raised to significantly higher levels (200% of the baseline level), the CaN sampling is  
568 suboptimal. Extreme decrease or increase in metabolic losses of mackerel are also incompatible  
569 with the remainder of the model parameters (i.e. no model solution). Increasing the satiation of  
570 blue whiting or increasing the satiation of mackerel led to few trajectories in which blue whiting  
571 and mackerel consumptions were negatively correlated, suggesting apparent competition.  
572 Aside from these few extreme cases, our conclusions are robust to uncertainties in model  
573 parameters and inputs.

574 The evaluation of the model was performed based on the match between observed and  
575 simulated ecological patterns. These patterns primarily include time-series of biomass and  
576 fluxes, and diet patterns. The sampling performance of the model was also diagnosed by  
577 inspecting that the MCM sampling chains were mixing properly and were not autocorrelated.  
578 A detailed report on the model evaluation is provided in supplementary material S6.

### 579 ***4.3. Contribution to integrated assessment and management***

580 Ecological models are important tools to perform marine integrated ecosystem assessments.  
581 The present modelling study was stimulated from discussions within the IEA group for the  
582 Norwegian sea (WGINOR, ICES, 2021a). Ecological observations on their own could not  
583 clarify matters concerning competition between the small pelagic fish species and the role of  
584 their main zooplankton prey. Food-web modelling represented a suitable approach to integrate

585 existing information, but this was further complicated by uncertainties and variability in many  
586 ecological parameters, and the lack of precise population estimates of biomasses and trophic  
587 fluxes. Building and tuning ecosystem models often requires extensive time and effort  
588 (Plagányi, 2007), and the resulting models may be perceived as ‘black boxes’ for non-  
589 modelers. In comparison, the CaN model presented here is transparent and relatively simple,  
590 which provides an opportunity for participatory modelling. This, in turn, promotes better  
591 communication and a sense of ownership of the model and its results, by a wider community.  
592 Adding new observations and modifying model constraints is straightforward in CaN models.  
593 This flexibility supports joint explorations of the model results under varying assumptions and  
594 input data, which favours trust building between modelers, experimental and observational  
595 scientists, and end-users. Because the precision of the model outputs is directly related to the  
596 precision of the input information, CaN model also helps modellers and users in defining where  
597 information is critical and where it might be lacking or be of insufficient quality.

598 A key task of the IEA group in the Norwegian sea is to consider if single-species assessments  
599 could be improved by adding multispecies interactions, either through competition or bottom-  
600 up/top-down controls. In a way similar to single-species assessment, which are used to  
601 reconstruct populations’ dynamics, CaN model can reconstruct past dynamics of the food web,  
602 and give insights into past and present multispecies interactions that can inform management.  
603 The present CaN model results do not support resource competition as a main driver for the  
604 dynamics of individual small pelagic fish populations, which points to the likely limited impact  
605 of including competition for the management of herring, mackerel and blue whiting. On the  
606 other hand, the population growth of the three species is tightly coupled to their prey  
607 consumption which could point towards a possible use of zooplankton monitoring data to  
608 directly inform management. This can however be challenging. In a recent modelling study,  
609 Kaplan *et al.* (2020) added the level of mesozooplankton as a control mechanism in the harvest  
610 control rule for mackerel but this resulted in higher variability, both in the catches and in the  
611 biomass of the mackerel. The potential large uncertainties associated with zooplankton biomass  
612 estimates (Hjøllo *et al.*, 2021) add a further challenge to the prospect of incorporating  
613 zooplankton into management. In addition, the CaN results do not show any evidence for a  
614 relation between zooplankton consumption by small pelagic fish and available zooplankton  
615 biomass. So, while fluctuations in pelagic fish population growth have been tightly coupled to  
616 consumption during the last three decades, this doesn't imply that food resources have been  
617 limiting.

618 Though ecosystem models have been available for several decades (e.g. Ecopath with Ecosim,  
619 Polovina, 1984; Walters *et al.*, 1997; Christensen and Walters, 2004; Heymans *et al.*, 2016),  
620 they remain underused in management (Hyder *et al.*, 2015; Schuwirth *et al.*, 2019). Some major  
621 challenges are the large uncertainties, the lack of transparency that emerge from their  
622 complexity, and the difficulty to communicate complex models to stakeholders (Plagányi and  
623 Butterworth, 2004; Lehuta *et al.*, 2016; Grüss *et al.*, 2017; Schuwirth *et al.*, 2019). The CaN  
624 framework presents the advantage of explicitly including data uncertainties, of avoiding  
625 explicit representation of complex processes that are difficult to observe and parameterise, a of  
626 presenting assumptions, parameters, data, and outputs in a transparent manner (Planque and  
627 Mullon 2020). It is also easily communicable to peer scientists and stakeholders, as it  
628 transparently uses the existing expertise and data collected on the system.

## 629 **5. Conclusion**

630 Reconstructing the past dynamics of marine food-webs is a challenge because many species  
631 and trophic fluxes are poorly sampled and because model inputs are often highly uncertain.  
632 Using CaN modelling we have reconstructed an ensemble of possible past dynamics for the  
633 Norwegian Sea pelagic food-web, with focus on the three main small pelagic fish species and  
634 their planktonic prey. Our reconstructions are fully compatible with existing observations and  
635 knowledge. We show that despite large uncertainties in reconstructed food-web dynamics, it is  
636 possible to draw conclusion on the trophic interactions in this system. Population growth of  
637 herring, mackerel and blue whiting are tightly coupled to consumption. Copepods and krill  
638 dynamics are also explained by consumption while population growth of amphipods can be  
639 controlled by consumption and by predation. There is little evidence for resource competition  
640 between the three small pelagic species. This suggests that the assessment and management of  
641 these commercial stocks during the last 3 decades would have likely benefited little from  
642 explicit incorporation of trophic interactions.

## 643 **6. Acknowledgments**

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645 Assessment of the Norwegian Sea (WGINOR) who actively contributed to early discussions  
646 which motivated the present study. This work was supported by the Norwegian Research  
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648 provided by the member countries contributing to the PGNAPES database.

## 649 **7. Supplementary material**

650 S1: xlsx formatted RCaN file. This contains all the necessary input data and meta-information  
651 to fully describe the food-web model for the Norwegian Sea.

652 S2: The methods used to derive the values of the species-specific input parameters, based on  
653 life-history and metabolic theory.

654 S3: Description of all the constraints used in the food-web model for the Norwegian Sea, with  
655 associated rationale and references.

656 S4: plots of the time-series for the 32 fluxes in the food-web model for the Norwegian Sea

657 S5: description of the outputs of the analyses conducted to evaluate the sensitivity of the model  
658 to input parameter values and associated standardised plots.

659 SM6: model evaluation report based on the OPE (Objectives, Patterns, Evaluation) protocol.

## 660 **8. References**

661 Aditi Laddha, and Santosh Vempala. 2020. Convergence of Gibbs Sampling: Coordinate Hit-  
662 and-Run Mixes Fast. arXiv, 2009.11338.

663 Arrigo, K. R., and van Dijken, G. L. 2011. Secular trends in Arctic Ocean net primary  
664 production. *Journal of Geophysical Research*, 116: C09011.

665 Bachiller, E., Skaret, G., Nøttestad, L., and Slotte, A. 2016. Feeding Ecology of Northeast  
666 Atlantic Mackerel, Norwegian Spring-Spawning Herring and Blue Whiting in the  
667 Norwegian Sea. *PLoS ONE*, 11: e0149238.

668 Bachiller, E., Utne, K. R., Jansen, T., and Huse, G. 2018. Bioenergetics modeling of the annual  
669 consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLoS*  
670 *ONE*, 13: e0190345.

671 Bagøien, E., Melle, W., and Kaartvedt, S. 2012. Seasonal development of mixed layer depths,  
672 nutrients, chlorophyll and *Calanus finmarchicus* in the Norwegian Sea – A basin-scale  
673 habitat comparison. *Progress in Oceanography*, 103: 58–79.

674 Bentley, J. W., Serpetti, N., and Heymans, J. J. 2017. Investigating the potential impacts of  
675 ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic  
676 food-web model. *Ecological Modelling*, 360: 94–107.

677 Broms, C., and Melle, W. 2007. Seasonal development of *Calanus finmarchicus* in relation to  
678 phytoplankton bloom dynamics in the Norwegian Sea. *Deep Sea Research Part II:*  
679 *Topical Studies in Oceanography*, 54: 2760–2775.

680 Broms, C., Melle, W., and Kaartvedt, S. 2009. Oceanic distribution and life cycle of *Calanus*  
681 species in the Norwegian Sea and adjacent waters. *Deep Sea Research Part II: Topical*  
682 *Studies in Oceanography*, 56: 1910–1921.

683 Broms, C., Melle, W., and Horne, J. K. 2012. Navigation mechanisms of herring during feeding  
684 migration: the role of ecological gradients on an oceanic scale. *Marine Biology*  
685 *Research*, 8: 461–474.

686 Broms, C., Børsheim, K. Y., Skagseth, Ø., Utne, K., Surma, S., Skogen, M. D., Lam, M. E., *et*  
687 *al.* in prep. Effects of bottom-up and top-down processes on lower trophic levels in the  
688 Norwegian and adjacent seas during the last decade.

689 Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities, and  
690 limitations. *Ecological Modelling*, 172: 109–139.



691 Collie, J. S., Botsford, L. W., Hastings, A., Kaplan, I. C., Largier, J. L., Livingston, P. A.,  
692 Plagányi, É., *et al.* 2014. Ecosystem models for fisheries management: finding the  
693 sweet spot. *Fish and Fisheries*, 17: 101–125.

694 Cury, P., Shannon, L. J., and Shin, Y.-J. 2003. The functioning of marine ecosystems: A  
695 fisheries perspective. *In Responsible fisheries in the marine ecosystem.*, pp. 103–123.  
696 Ed. by M. Sinclair and G. Valdimarson. FAO.

697 Dalpadado, P., Ellertsen, B., Melle, W., and Skjoldal, H. R. 1998. Summer distribution patterns  
698 and biomass estimates of macrozooplankton and micronekton in the Nordic Seas.  
699 *Sarsia*, 83: 103–116.

700 Debes, H., Homrum, E. Í., Jacobsen, J. A., Hátun, H., and Danielsen, J. 2012. The feeding  
701 ecology of pelagic fish in the southwestern Norwegian Sea – Inter species food  
702 competition between herring (*Clupea harengus*) and mackerel (*Scomber scombrus*).  
703 *ICES CM 2012/*, M:07: 19pp.

704 Drouineau, H., Planque, B., and Mullon, C. 2021. RCaN : a software for Chance and Necessity  
705 modelling. *bioRxiv*: 2021.06.09.447734.

706 Eddy, T. D., Bernhardt, J. R., Blanchard, J. L., Cheung, W. W. L., Colléter, M., du Pontavice,  
707 H., Fulton, E. A., *et al.* 2021. Energy Flow Through Marine Ecosystems: Confronting  
708 Transfer Efficiency. *Trends in Ecology & Evolution*, 36: 76–86.

709 EPA. 2009. Guidance on the development, evaluation, and application of environmental  
710 models. Technical Report, EPA/100/K-09/003. Environmental Protection Agency.  
711 [https://www.epa.gov/sites/production/files/2015-](https://www.epa.gov/sites/production/files/2015-04/documents/cred_guidance_0309.pdf)  
712 [04/documents/cred\\_guidance\\_0309.pdf](https://www.epa.gov/sites/production/files/2015-04/documents/cred_guidance_0309.pdf).

713 Fath, B. D., Scharler, U. M., Ulanowicz, R. E., and Hannon, B. 2007. Ecological network  
714 analysis: network construction. *Ecological Modelling*, 208: 49–55.

715 Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. *Journal of Marine Systems*,  
716 81: 171–183.

717 Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. 2001. Effects of  
718 Size and Temperature on Metabolic Rate. *Science*, 293: 2248.

719 Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., *et*  
720 *al.* 2006. A standard protocol for describing individual-based and agent-based models.  
721 *Ecological Modelling*, 198: 115–126.

722 Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., and Railsback, S. F. 2010.  
723 The ODD protocol: A review and first update. *Ecological Modelling*, 221: 2760–2768.

724 Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L.,  
725 Edmonds, B., *et al.* 2020. The ODD Protocol for Describing Agent-Based and Other  
726 Simulation Models: A Second Update to Improve Clarity, Replication, and Structural  
727 Realism. *Jasss-the Journal of Artificial Societies and Social Simulation*, 23.

728 Grüss, A., Rose, K. A., Simons, J., Ainsworth, C. H., Babcock, E. A., Chagaris, D. D., De  
729 Mutsert, K., *et al.* 2017. Recommendations on the Use of Ecosystem Modeling for  
730 Informing Ecosystem-Based Fisheries Management and Restoration Outcomes in the  
731 Gulf of Mexico. *Marine and Coastal Fisheries*, 9: 281–295.

732 Guesnet, V., Lassalle, G., Chaalali, A., Kearney, K., Saint-Béat, B., Karimi, B., Grami, B., *et*  
733 *al.* 2015. Incorporating food-web parameter uncertainty into Ecopath-derived  
734 ecological network indicators. *Ecological Modelling*, 313: 29–40.

735 Guo, C., Fu, C., Olsen, N., Xu, Y., Grüss, A., Liu, H., Verley, P., *et al.* 2020. Incorporating  
736 environmental forcing in developing ecosystem-based fisheries management strategies.  
737 *ICES Journal of Marine Science*, 77: 500–514.

738 Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., and Christensen,  
739 V. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based  
740 management. *Ecological Modelling*, 331: 173–184.

- 741 Hjøllø, S., Hansen, C., and Skogen, M. 2021. Assessing the importance of zooplankton  
742 sampling patterns with an ecosystem model. *Marine Ecology Progress Series*,  
743 DYNMOD. [https://www.int-res.com/abstracts/MEPS/dynmod/p\\_av3/](https://www.int-res.com/abstracts/MEPS/dynmod/p_av3/) (Accessed 6  
744 October 2021).
- 745 Huse, G., Holst, J. C., Utne, K., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., *et al.* 2012.  
746 Effects of interactions between fish populations on ecosystem dynamics in the  
747 Norwegian Sea – results of the INFERNO project. *Marine Biology Research*, 8: 415–  
748 419.
- 749 Hyder, K., Rossberg, A. G., Allen, J. I., Austen, M. C., Barciela, R. M., Bannister, H. J.,  
750 Blackwell, P. G., *et al.* 2015. Making modelling count - increasing the contribution of  
751 shelf-seas community and ecosystem models to policy development and management.  
752 *Marine Policy*, 61: 291–302.
- 753 ICES. 2020. Working group on widely distributed stocks (WGWIDE). ICES Scientific  
754 Reports, 2: 1074pp.
- 755 ICES. 2021a. Working Group on the Integrated Assessments of the Norwegian Sea (2020).  
756 ICES Scientific Reports, 3: 114pp.
- 757 ICES. 2021b. Working Group of International Pelagic Surveys (WGIPS). ICES.  
758 [https://www.ices.dk/sites/pub/Publication  
759 Reports/Forms/DispForm.aspx?ID=37581](https://www.ices.dk/sites/pub/Publication%20Reports/Forms/DispForm.aspx?ID=37581)  
760 (Accessed 15 November 2021).
- 760 Johnstone, A. D. F., Wardle, C. S., and Almatar, S. M. 1993. Routine respiration rates of  
761 Atlantic mackerel, *Scomber scombrus* L., and herring, *Clupea harengus* L., at low  
762 activity levels. *Journal of Fish Biology*, 42: 149–151.
- 763 Kaplan, I. C., Hansen, C., Morzaria-Luna, H. N., Girardin, R., and Marshall, K. N. 2020.  
764 Ecosystem-Based Harvest Control Rules for Norwegian and US Ecosystems. *Frontiers  
765 in Marine Science*, 7: 652.
- 766 Langøy, H., Nøttestad, L., Skaret, G., Broms, C., and Fernö, A. 2012. Overlap in distribution  
767 and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning  
768 herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the  
769 Norwegian Sea during late summer. *Marine Biology Research*, 8: 442–460.
- 770 Lehuta, S., Girardin, R., Mahévas, S., Travers-Trolet, M., and Vermard, Y. 2016. Reconciling  
771 complex system models and fisheries advice: Practical examples and leads. *Aquat.  
772 Living Resour.*, 29: 208.
- 773 Levin, P. S., Fogarty, M. J., Murawski, S. A., and Fluharty, D. 2009. Integrated Ecosystem  
774 Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the  
775 Ocean. *PLoS Biology*, 7: e14.
- 776 Levins, R. 1974. Discussion paper: the qualitative analysis of partially specified systems.  
777 *Annals of the New York Academy of Sciences*, 231: 123–138.
- 778 Lindstrøm, U., Planque, B., and Subbey, S. 2017. Multiple patterns of food web dynamics  
779 revealed by a minimal non deterministic model. *Ecosystems*, 20: 163–182.
- 780 Link, J. S., Fulton, E. A., and Gamble, R. J. 2010. The northeast US application of ATLANTIS:  
781 A full system model exploring marine ecosystem dynamics in a living marine resource  
782 management context. *Progress in Oceanography*, 87: 214–234.
- 783 Makarieva, A. M., Gorshkov, V. G., Li, B.-L., Chown, S. L., Reich, P. B., and Gavrilov, V. M.  
784 2008. Mean mass-specific metabolic rates are strikingly similar across life's major  
785 domains: Evidence for life's metabolic optimum. *Proceedings of the National Academy  
786 of Sciences*, 105: 16994–16999.
- 787 Melle, W., Ellertsen, B., and Skjoldal, H. R. 2004. Zooplankton: The link to higher trophic  
788 levels. *In The Norwegian Sea ecosystem*, pp. 137–202. Ed. by H. R. Skjoldal, R. Sætre,  
789 A. Færnø, O. A. Misund, and I. Røttingen. Tapir Academic Press, Trondheim, Norway.

790 Mousing, E. A., Planque, B., Arneberg, P., Bjørndal, V. R., Keulder-Stenevik, F., Liebig, P.  
791 L., Langøy, H., *et al.* in prep. Weight vs occurrence for assessing major prey group diet  
792 composition for pelagic fish in the Norwegian Sea.

793 Nilsen, J. E. Ø., and Falck, E. 2006. Variations of mixed layer properties in the Norwegian Sea  
794 for the period 1948–1999. *Progress in Oceanography*, 70: 58–90.

795 Olafsdottir, A. H., Slotte, A., Jacobsen, J. A., Oskarsson, G. J., Utne, K. R., and Nøttestad, L.  
796 2016. Changes in weight-at-length and size-at-age of mature Northeast Atlantic  
797 mackerel (*Scomber scombrus*) from 1984 to 2013: effects of mackerel stock size and  
798 herring (*Clupea harengus*) stock size. *ICES Journal of Marine Science*, 73: 1255–1265.

799 Olafsdottir, A. H., Utne, K. R., Jacobsen, J. A., Jansen, T., Óskarsson, G. J., Nøttestad, L.,  
800 Elvarsson, B. Þ., *et al.* 2019. Geographical expansion of Northeast Atlantic mackerel  
801 (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by  
802 stock size and constrained by low temperatures. *Deep Sea Research Part II: Topical  
803 Studies in Oceanography*, 159: 152–168.

804 Olsen, E. M., Melle, W., Kaartvedt, S., Holst, J. C., and Mork, K. A. 2007. Spatially structured  
805 interactions between a migratory pelagic predator, the Norwegian spring-spawning  
806 herring *Clupea harengus* L., and its zooplankton prey. *Journal of Fish Biology*, 70: 799–  
807 815.

808 Pedersen, T., Mikkelsen, N., Lindstrøm, U., Renaud, P. E., Nascimento, M. C., Blanchet, M.-  
809 A., Ellingsen, I. H., *et al.* 2021. Overexploitation, Recovery, and Warming of the  
810 Barents Sea Ecosystem During 1950–2013. *Frontiers in Marine Science*, 8: 732637.

811 Plagányi, É. E., and Butterworth, D. S. 2004. A critical look at the potential of Ecopath with  
812 ecosim to assist in practical fisheries management. *African Journal of Marine Science*,  
813 26: 261–287.

814 Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical  
815 Paper. Food and Agriculture Organisation of the United Nations, Rome.

816 Planque, B., Lindstrøm, U., and Subbey, S. 2014. Non-Deterministic Modelling of Food-Web  
817 Dynamics. *PLoS ONE*, 9: e108243.

818 Planque, B., and Mullon, C. 2020. Modelling chance and necessity in natural systems. *ICES  
819 Journal of Marine Science*, 77: 1573–1588.

820 Polovina, J. J. 1984. An overview of the Ecopath model. *Fishbyte*, 2: 5–7.

821 Prokopchuk, I., and Sentyabov, E. 2006. Diets of herring, mackerel, and blue whiting in the  
822 Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature  
823 conditions. *ICES Journal of Marine Science*, 63: 117–127.

824 Rey, F. 2004. Phytoplankton: The grass of the sea. *In* *The Norwegian Sea Ecosystem*, pp. 97–  
825 137. Tapir Academic Press, Trondheim, Norway.

826 Schuwirth, N., Borgwardt, F., Domisch, S., Friedrichs, M., Kattwinkel, M., Kneis, D.,  
827 Kuemmerlen, M., *et al.* 2019. How to make ecological models useful for environmental  
828 management. *Ecological Modelling*, 411: 108784.

829 Siegelman-Charbit, L., and Planque, B. 2016. Abundant mesopelagic fauna at oceanic high  
830 latitudes. *Marine Ecology Progress Series*, 546: 277–282.

831 Sigman, D. M., and Hain, M. P. 2012. The biological productivity of the ocean. *Nature  
832 Education Knowledge*, 3: 16.

833 Skaret, G., Bachiller, E., Langoy, H., and Stenevik, E. K. 2015. Mackerel predation on herring  
834 larvae during summer feeding in the Norwegian Sea. *ICES J. Mar. Sci.*, 72: 2313–2321.

835 Skaret, G., and Pitcher, T. J. 2016. An Ecopath with Ecosim model of the Norwegian Sea and  
836 Barents Sea validated against time series of abundance. *Fisken og Havet*. Institute of  
837 Marine Research, Bergen, Norway.

- 838 Skern-Mauritzen, M., M., Lindstrøm, U., Biuw, M., Elvarsson, B. T., Gunnlaugsson, T., Haug,  
839 T., Kovacs, K. M., *et al.* submitted. Marine mammal consumption and fisheries  
840 removals in the Nordic and Barents Seas. ICES Journal of Marine Science.  
841 Skjoldal, H. R. 2004. The Norwegian Sea ecosystem. Tapir academic press, Trondheim. 559  
842 pp.  
843 Skogen, M. D., Budgell, W. P., and Rey, F. 2007. Interannual variability in Nordic seas primary  
844 production. ICES Journal of Marine Science, 64: 889–898.  
845 Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. Computational  
846 Biology and Chemistry, 28: 321–339.  
847 Utne, K. R., Huse, G., Ottersen, G., Holst, J. C., Zabavnikov, V., Jacobsen, J. A., Oskarsson,  
848 G. J., *et al.* 2012. Horizontal distribution and overlap of planktivorous fish stocks in the  
849 Norwegian Sea during summers 1995-2006. Marine Biology Research, 8: 420–441.  
850 Varpe, Ø., Fiksen, Ø., and Slotte, A. 2005. Meta-ecosystems and biological energy transport  
851 from ocean to coast: the ecological importance of herring migration. Oecologia, 146:  
852 443–451.  
853 Varpe, Ø., and Fiksen, Ø. 2010. Seasonal plankton–fish interactions: light regime, prey  
854 phenology, and herring foraging. Ecology, 91: 311–318.  
855 Walters, C. J., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited  
856 ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and  
857 Fisheries, 7: 139–172.  
858 Yodzis, P., and Innes, S. 1992. Body size and consumer-resource dynamics. Am. Nat., 139:  
859 1151–1175.  
860

## 861 **9. Authors contributions**

862 BP and BH developed the concept and idea for the workshops which led to the modelling study.  
863 BP, AF, BH, EM, CH, CB, UL and ES contributed to design and methods, including model  
864 development, reporting, parametrization, and evaluation. AF implemented and tested the  
865 model. BP, AF, BH, EM, CH, CB, UL and ES contributed to input data collection and  
866 interpretation of the model results. BP, AF, BH, EM, CH, CB, UL and ES contributed to  
867 manuscript preparation, editing, or reviewing.



