



A food-web assessment model for marine mammals, fish, and fisheries in the Norwegian and Barents Seas

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ABSTRACT

The Norwegian and Barents Seas host large commercial fish populations that interact with each other, as well as marine mammal populations that feed on plankton and fish. Quantifying the past dynamics of these interacting species, and of the associated fisheries in the Norwegian and Barents Sea is of high relevance to support ecosystem-based management. The purpose of this work is to develop a food-web model of intermediate complexity and perform a quantitative assessment of the Norwegian and Barents Sea ecosystems in the period 1988–2021 in a manner that is consistent with existing data and expert knowledge, and that is internally coherent. For this purpose, we use the modelling framework of chance and necessity (CaN). The model construction follows an iterative process that allows to confront, discuss, and resolve multiple issues as well as to recognise uncertainties in expert knowledge, data, and input parameters. We show that it is possible to reconstruct the past dynamics of the food-web only if recognising that some data and assumptions are more uncertain than originally thought. According to this assessment, consumption by commercial fish and catch by fisheries jointly increased until the early 2010s, after which consumption by fish declined and catches by fisheries stabilised. On an annual basis, fish have consumed an average of 135.5 million tonnes of resources (including 9.5 million tonnes of fish), marine mammals have consumed an average of 22 million tonnes of which 50 % (11 million tonnes) were fish. Fisheries and hunting have captured an average of 4.4 million tonnes of fish and 7 thousand tonnes of marine mammals.

1. Introduction

A fundamental principle in ecosystem-based management involves recognizing and assessing the trade-offs among various ecosystem goods and services. Understanding the implications of these trade-offs is crucial for achieving biological, economic, and social management objectives (Browman and Stergiou, 2004; Craig and Link, 2023; Dickey-Collas et al., 2022; Fogarty, 2014; Garcia et al., 2003; Pikitch et al., 2004). Examples of such trade-offs include simultaneously managing exploited species at maximum sustainable yield (Andersen et al., 2015; Fulton et al., 2022; May et al., 1979; Worm et al., 2009), joint

exploitation of predatory and forage resources in fluctuating environments (Goto et al., 2022), or exploitation of fish stocks that act as resource and forage on other valuable species (Anstead et al., 2021).

While single stock assessment models have been the backbone of fisheries management for decades (Beverton and Holt, 1957; Dichmont et al., 2016; Hilborn and Walters, 1992; Maunder and Punt, 2013), these are rarely suitable to address such ecological or management trade-offs that can involve complex ecological interactions (Skern-Mauritzen et al., 2016). In contrast, the effective application of ecosystem approaches to management typically necessitates the utilisation of ecosystem models (Grüss et al., 2017; Heymans et al., 2020, 2016; Plagányi, 2007;

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Plagányi et al., 2014).

Marine ecosystem models used to support ecosystem-based fisheries management (EBFM) have emerged from diverse origins (Espinoza-Tenorio et al., 2012) to meet diverse objectives (Plagányi, 2007). Some have emerged from the development of single-species assessment models into multi-species assessment (e.g. Begley and Howell, 2004; Garrison et al., 2010; Hollowed, 2000; Tjelmeland and Bogstad, 1998), from the expansion of biogeochemical models towards higher trophic levels (Heath, 2012; Petihakis et al., 2007), from mass balance principles of energy transfer within food-webs (Christensen and Pauly, 1992; Polovina, 1984), or from size-structured trophic dependencies (Shin and Cury, 2001; Travers-Trolet et al., 2014). These approaches have sometimes been combined to develop end-to-end models of various levels of complexity (Audzijonyte et al., 2019; Carozza et al., 2017; Fulton et al., 2011; Lehodey et al., 2008; Pelletier and Mahévas, 2005, and others).

An emerging consensus is that EBFM can be best supported by models of intermediate complexity, also called MICE, that can capture important features of relevant populations and ecosystem dynamics while remaining sufficiently simple to be tractable (Collie et al., 2014; Hannah et al., 2010; Plagányi et al., 2014). Nevertheless, even in the case of MICE, constructing ecosystem models remains a challenging undertaking. First, in contrast to single stock assessment models, ecosystem models are frequently constructed to serve various, sometimes broad, objectives and are progressively utilized to tackle a variety of questions (Fulton et al., 2011; Planque and Mullon, 2020). Evaluating the adequacy of an ecosystem model to support a well-defined purpose remains a challenge, mostly because the modelling purposes are often vaguely rather than precisely defined (Parker, 2020; Planque et al., 2022a; Reum et al., 2021). In addition, the high levels of uncertainty one must deal with when constructing MICE models remains a fundamental issue due to the complexity of ecosystem processes and to the limited knowledge about the dynamic of marine ecosystems, (Espinoza-Tenorio et al., 2012; Link et al., 2012).

Here, we focus on marine MICE models for the purpose of quantifying the past dynamics of multiple interacting species (i.e. simple food-webs), and the associated uncertainties. Though reconstructions of population dynamics and food consumption may exist for individual species (from, for example, stock assessments or diet surveys), one challenge is to reconstruct food-web dynamics that are consistent with available data across species and fisheries. Ideally the modelled food-web should be as simple as necessary, but not simpler. That is, it should include the dominant species groups, their major prey and predator, including relevant fisheries. Ecosystem components that are remotely connected or that contribute little to trophic flows should not be included as they risk increasing model complexity without providing information of significance to the assessment of food-web dynamics. The model should also include as few underlying assumptions as possible while being capable of incorporating as many observations as possible. For food-web models, this means that assumptions about trophic functional relationships that are often poorly rooted – but to which model outputs can be very sensitive (Fulton et al., 2003; Kearney et al., 2012; Williams and Martinez, 2004) – should be avoided while it would be preferable to directly include diet observations in the model building. Finally, uncertainties about model structure or parameterisation, and how these can propagate in the model outputs, should be made as explicit as possible.

The Norwegian and Barents Seas host large fish populations that interact with each other, as well as marine mammal populations that feed on plankton and fish (Loeng and Drinkwater, 2007). During recent decades, the management of living resources in Norwegian waters has been integrated into an ecosystem-based framework that recognises the necessity to jointly assess and regulate interacting species (Ministry of Fisheries and Coastal Affairs, 2009). Resolving the trade-off between conservation and exploitation of multiple fish and marine mammal populations is a central issue for resource management in the area, though most resources are still managed on a single species level. Marine

mammals consume large quantities of food, comprised of fish and lower trophic level species that support commercial fish stocks. The potential for resource competition between marine mammals and fisheries has been documented in a number of systems (Bogstad et al., 2015; Chasco et al., 2017; Skern-Mauritzen et al., 2022; Trites et al., 1997). This has led to diverging recommendations for and against culling of marine mammals to regulate competition between these animal groups, associated with often conflicting and polarized public opinions (Bowen and Lidgard, 2013; Corkeron, 2009; Kaschner and Pauly, 2005; Kellert et al., 1995). Scientific evidence is central to this debate, as it can provide the quantitative basis required to determine the relative consumption or extraction of resources by fish, fisheries, and marine mammals and to assess how variations in one of these components may have affected the dynamics of the others (Lindstrøm et al., 2009; Pedersen et al., 2021; Schweder et al., 2000).

The purpose of this study is to perform a quantitative assessment of past interactions between marine mammals, fish, and fisheries in the Norwegian and Barents Seas. We do so by providing a set of coherent reconstructions of the past dynamics of the main commercial fish and marine mammal populations, their trophic interactions, and their exploitation. These reconstructions, that we also term trajectories or histories, are derived from a food-web model of intermediate complexity constrained by diverse sets of observations and expert knowledge. The model is constructed using the CaN modelling framework (Chance and Necessity, Drouineau et al., 2023; Planque and Mullon, 2020). The model structure is tailor-made to address marine mammals-fish-fisheries interactions. It is data driven and does not include assumptions about trophic functional relationships and is constrained by observations of diet and consumption. Uncertainties in the input data and knowledge are explicitly stated and propagate into model outputs. In this contribution we present the model structure and inputs, and a set of selected outputs. We discuss the consistency and uncertainties in the input information used to construct the model and how these affect the consistency and the certainty of the model outputs across different ecosystem components. We also discuss how the iterative model building process is used to reveal – and sometimes resolve – conflicting knowledge and expertise regarding the Barents Sea functioning and observations. The model outputs provide a first assessment of the dynamics of marine mammals, fish and fisheries for the period 1988–2021. A detailed analysis and interpretation of the model outputs to understand the drivers of interactions between fish-fisheries-mammals is not performed here and will be the topic of further research.

2. Material and method

2.1. The Norwegian and Barents Sea fish-mammals-fisheries system

The Barents Sea is a shelf sea delimited by land masses as well as by the continental slope towards the Norwegian Sea in the west and the Arctic Ocean in the north (Jakobsen and Ozhigin, 2011, Fig. 1). In contrast, the Norwegian Sea is a deep ocean between Norway and the Iceland and Greenland seas, with a southern boundary at 62°N (Skjoldal, 2004). The Norwegian Sea and Barents Sea host some of the largest fisheries in the world, demersal fisheries (mainly cod, *Gadus morhua*) dominating in the Barents Sea while pelagic fisheries (herring, *Clupea harengus*, mackerel, *Scomber scombrus*, and blue whiting, *Micromesistius poutassou*) dominate in the Norwegian Sea. Capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) are also abundant pelagic species in the Barents Sea, and large fluctuations in their abundance can have significant ecological impacts on their prey and predators (Loeng and Drinkwater, 2007).

The Norwegian and Barents Sea ecosystems are connected through many processes which include zooplankton advection, as well as fish and marine mammal migrations. Mesozooplankton is advected from the Norwegian Sea to the Barents Sea, which is of particular significance for the population dynamics of the copepod *Calanus finmarchicus*

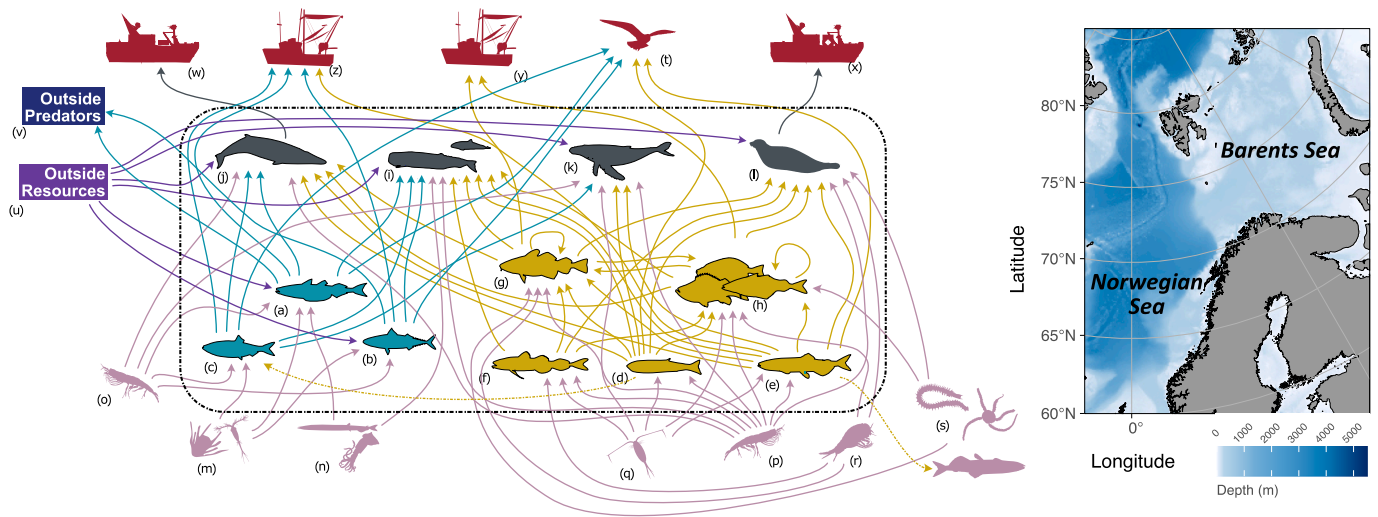


Fig. 1. Left: A graphical illustration of the food-web. Species located within the dashed box are inside the model domain, while other species are outside the model domain (only the fluxes to-and-from these species are considered, not their biomass). Plain arrows indicate trophic fluxes and fisheries catch. Dotted arrows refer to non-trophic fluxes i.e. recruitment of juvenile herring in the Barents Sea to the adult population in the Norwegian Sea, and post-spawning mortality of capelin in the Barents Sea. Arrows are coloured according to the originating prey. a) blue whiting, b) mackerel, c) Herring (3 +) in the Norwegian Sea, d) juvenile herring, e) capelin, f) polar cod, g) cod, h) other demersals, i) toothed whales, j) minke whales, k) other baleen whales, l) seals, m) zooplankton Norwegian Sea, n) mesopelagic fauna, o) krill in the Norwegian Sea, p) krill in the Barents Sea, q) copepods in the Barents Sea, r) amphipods in the Barents Sea, s) benthos and other plankton in the Barents Sea, t) seabirds, u) outside resources, v) outside predators, w) minke whale hunting, x) seal hunting, y) demersal fishery, z) pelagic fishery. Right: the geographical extent of the model that includes the Norwegian and Barents Seas.

(Edvardsen et al., 2003) and euphausiids (*Thysanoessa longicaudata*, *Meganctiphanes norvegica*, Eriksen et al., 2016). Several fish populations (cod, herring, capelin) have a wide geographical distribution but spawn along the coast of Norway. Herring juveniles spend the first 3–4 years in the Barents Sea and then join the adult stock in the Norwegian Sea (Holst and Slotte, 1998). Other fish species such as haddock (*Melanogrammus aeglefinus*), Greenland halibut (*Reinhardtius hippoglossoides*), and beaked redfish (*Sebastes mentella*) spawn along the continental slope. Greenland halibut and beaked redfish also migrate between the Barents and the Norwegian Seas. Polar cod spawns in the Barents Sea and migrate between spawning and feeding areas. Blue whiting and mackerel populations undertake large seasonal migrations associated with feeding and spawning (dos Santos Schmidt et al., 2024; Ekerhovd, 2010; Nøttestad et al., 2016; Ono et al., 2022; Payne et al., 2012; Uriarte and Lucio, 2001; Belikov, 1988). The spatial distribution of these populations extends beyond the Norwegian Sea, towards the west and south. Large populations of marine mammals also inhabit the Norwegian and Barents Seas, and can seasonally migrate in and out of the region (Nøttestad et al., 2015). These include common minke whale (*Balaenoptera acutorostrata*), fin whale (*Balaenoptera physalus*), blue whale (*Balaenoptera musculus*), bowhead whale (*Balaena mysticetus*), sei whale (*Balaenoptera borealis*), humpback whale (*Megaptera novaeangliae*), several dolphin species (Delphinidae), sperm whale (*Physeter macrocephalus*), killer whale (*Orcinus orca*), harbour porpoise (*Phocoena phocoena*), pilot whales (*Globicephala* spp.), beluga (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), beaked whales (*Ziphiidae*), hooded seal (*Cystophora cristata*), harp seal (*Pagophilus groenlandicus*), ringed seal (*Pusa hispida*), grey seal (*Halichoerus grypus*), harbour seal (*Phoca vitulina*), bearded seal (*Erignathus barbatus*), and walrus (*Odobenus rosmarus*). Seabirds, often migratory, also inhabits Norwegian and Barents Sea waters. These include amongst others, guillemots (*Uria* spp.), Atlantic puffins (*Fratercula arctica*), and northern fulmars (*Fulmarus glacialis*) which feed on fish and invertebrates (Barrett et al., 2002).

2.2. Principles of “Chance and Necessity” modelling

To reconstruct the joint dynamics of fish, marine mammals, and fisheries, we use the dynamic food-web modelling framework CaN

(Planque and Mullon, 2020). CaN modelling is based on the general idea that complex ecological systems such as marine systems are inherently uncertain while their dynamics are bounded by physical, biological, and ecological constraints. Food-web models constructed in the CaN framework comprise a network of species (or trophospecies, i.e. a set of species with similar prey and predators) interacting with each other by exchanging biomass through trophic links, mostly predation. These species, that are located within the model domain, can also interact with prey, predators, fisheries, or other components that are outside the model domain. The model domain is defined as the set of species whose dynamics are fully defined by the considered trophic flows (not to be confused with the geographical domain of the model which is defined by geographical coordinates).

CaN models are mass-balanced, i.e., the variations in the biomass of species primarily result from inputs (feeding, migration, recruitment) and outputs (metabolic losses, predation, catches). In that sense, they are similar to other food-web models such as Ecopath-with-Ecosim (Christensen and Walters, 2004; Polovina, 1984). The process by which biomass of individual species changes from one time step to the next is expressed in the CaN master equation:

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

where $B_{i,t}$ is the biomass of component i at time t , $F_{ij,t}$ and $F_{ji,t}$ are the fluxes between components i and j between t and $t + 1$, and μ_i , γ and κ are input parameters related to metabolic losses, digestibility and assimilation efficiency respectively (see Planque and Mullon, 2020 and supplementary material S1 for details). The unknowns in a CaN model are the individual fluxes of biomass at every time steps (F 's in the master equation) and the biomasses at the initial time-step. The fluxes can specify trophic as well as non-trophic interactions (migrations, fisheries catch, recruitment). To bound possible values of F 's, the above process-model is complemented by an ensemble of constraints that reflect available knowledge and observations on the biology, physiology, life-history, and historical dynamics of the species in the modelled system (Planque and Mullon, 2020).

CaN modelling is based on a system of linear (in)equalities that

reflect the master equation combined with multiple constraints that bounds the set of possible solutions. Mathematically, this results in a convex multidimensional polygon or polytope. The polytope is sampled multiple times and each sample corresponds to one possible trajectory of the food-web, i.e. the biomass of all species at the initial time-step and every flux at every time-step (Drouineau et al., 2023).

2.3. Model structure and parametrisation

A complete description of the model structure and parametrisation is provided in [Supplementary material S1](#) following the ODD protocol (Overview, Design concepts, and Details, Grimm et al., 2020; Grimm et al., 2006; Grimm et al., 2010). A shorter description is provided below to highlight the salient features of the model.

To address marine mammals-fish-fisheries interactions, the model domain includes ecologically significant species of marine mammals and commercial fish in the Norwegian and Barents Seas. These are minke whales, other baleen whales, toothed whales, seals, adult herring in the Norwegian Sea, blue whiting, mackerel, Atlantic cod, other demersals, polar cod, capelin, and juvenile herring in the Barents Sea. The fisheries and hunts of minke whales and seals are also added as fluxes pointing outside the model domain (these fluxes represent the catches). Finally, the model includes incoming and outgoing fluxes from 10 groups of prey and predators that are directly interacting with marine mammals and fish. These groups include zooplankton in the Norwegian Sea, mesopelagic fauna, and other resources in the Norwegian Sea, krill in the Norwegian and Barents Seas, copepods, amphipods, other plankton and benthos in the Barents Sea, and seabirds. Some modelled species may expand their geographical distribution beyond the geographical limits of the model, either because their geographical distribution is wider or because they seasonally migrate in and out of the Norwegian and Barents Seas. When they do so, they can interact with prey and predators outside the model domain. Two additional components are added to reflect these prey and predators located outside the geographical domain of the model. The food-web includes 79 trophic fluxes between prey and predators, 8 non-trophic fluxes towards fisheries, a non-trophic flux from juvenile to adult herring and a non-trophic flux – from capelin to benthos – that represents capelin post-spawning mortality. The 26 model components and the 89 fluxes connecting them are presented in [Fig. 1](#).

The master equation that expresses changes in biomass over time only applies to the 12 species groups within the model domain. For the remaining 14 components outside the model domain, it is only the interactions (i.e. biomass fluxes) that are considered, and the biomasses of these components are not modelled. The complete set of input parameter values and their units is provided in the model description (ODD, [Supplementary material S1](#)). Five input parameters are provided for each of the 12 species within the model domain: metabolic and other losses (μ in equation (1)); the ratio of maximum consumption per unit biomass (satiation, σ); the proportion of ingested prey that can be digested (digestibility, κ in equation (1)); the proportion of digested prey that can be assimilated by a predator (assimilation efficiency, γ in equation (1)); and the maximum rate of species increase and decrease (inertia, ρ). Digestibility is prey specific and is also required for all prey outside the model domain. Assimilation efficiency is predator specific. These two parameters are adjusted for the carbon-to-wet weight ratio (CWW) of the prey and predators and, when combined, provide the absorption efficiency. CaN parameters are primarily derived from the metabolic theory of ecology (Gillooly et al., 2001; Savage et al., 2004), life-history theory (Makarieva et al., 2008; Yodzis and Innes, 1992) and earlier model developments that have compiled parameter estimates (Lindstrøm et al., 2017; Pedersen et al., 2021; Planque et al., 2022b; Sivel et al., 2023). Despite extensive literature on the derivation of metabolic and life-history parameters these remain highly uncertain. In the present case, the different estimation approaches above-mentioned could lead to significant variations in parameter estimates. When this was the case, we

choose parameter values that were plausible (i.e. within the range of existing estimates) and that led to plausible dynamics. In the model, input parameter values are time-invariant.

2.4. Past observations used to constrain ecosystem dynamics

The purpose of CaN modelling is to sample food-web trajectories that are consistent with a variety of observations and constraints. The food-web structure, combined with the input parameters, provides a complete description of the processes controlling the dynamics of the food-web but without further information, the possible set of trajectories would be very broad and possibly disconnected from past observations (see e.g., Sivel et al., 2021). The current model relies on multiple observational time-series of species biomass (derived from surveys or stock assessments), consumption, and diet, fisheries catches and marine mammal hunts. These observations are used to constrain the set of possible dynamics by applying a series of (in)equalities termed “constraints”. In CaN, a constraint is a linear (in)equality that express the relation between biomass and/or fluxes and/or observations. For example, if one wants to ensure that the reconstructed food-web dynamics is compatible with the cod stock biomass reported in the stock assessment, this can be expressed by writing a constraint in the form: $cod.in.the.model \leq max. cod.in.the.assessment$ and $cod.in.the.model \geq min.cod.in.the.assessment$. In this way, only the food-web trajectories that are compatible with the cod stock assessment are sampled. This way of incorporating observations explicitly accounts for uncertainties in the observations, reflected here in the minimum and maximum values for biomass of cod reported in the assessment.

The main sources of information used to constraint the model include estimates of biomass and catch from fish stock assessments (Howell et al., 2022; ICES, 2022, 2019 and calculations by U. Lindstrøm), estimates of consumption (Bachiller et al., 2018; Howell et al., 2022) and estimates of diet (Mousing et al., 2023; Skern-Mauritzen et al., 2022; Townhill et al., 2021; Howell et al., 2022, and calculations by B. Bogstad). Observations can be provided as time-series, for individual years or averaged over specified time-periods. The complete list of observational time-series and the corresponding data source are provided in [Supplementary material S1](#).

2.5. Model implementation

The model construction and sampling were done using the Graphical User Interface RCanConstructor and the R library RCanmodel (Drouineau et al., 2023). The complete set of inputs necessary to document and build the model is provided in [Supplementary material S2](#) (the CaN-file in xlsx format). The building and sampling of the model, as well as the production of figures and tables were performed in R. The R code for building and sampling the model is provided in [Supplementary material S4](#).

2.6. Model outputs

The output of CaN sampling is a set of food-web trajectories for the Norwegian and Barents Sea fish and marine mammal populations and of the fisheries/hunt operating upon them during the period 1988–2021. Each reconstructed trajectory is mass-balanced (i.e., variations in biomass are explained by trophic interactions and exploitation) and is consistent with past observations. The dataset that contains the sampling outputs is archived at the Norwegian Marine Data Centre (NMDC). A total of 100,200 food-web trajectories were sampled and only one for every 100 samples were retained (a procedure known as thinning, designed to reduce autocorrelation between MCMC samples). The resulting 1002 trajectories are presented in the results. In the following text, we use the terms “sample”, “reconstruction”, “trajectory”, and “history” interchangeably.

2.7. Uncertainties in model inputs/outputs

Observational inputs to the model are known with variable degrees of certainty and these uncertainties are explicitly accounted for. While biomass and catch data from stock assessments are often robust and are provided with associated uncertainty estimates, diet fractions or consumption estimates are more uncertain, and these uncertainties may not always be estimated or reported. In a CaN model, those uncertainties are explicitly accounted for through the formulation of constraints that express the range of acceptable values for each individual observation. The model output consists of a collection of possible food-web trajectories and the diversity of these trajectories reflects the uncertainties in the model output.

2.8. Iterative process for model building and sanity checks

CaN food-web model building is achieved through an iterative process which cycles repeatedly through the following steps: 1) identify the question/objective of the modelling exercise; 2) identify the main species, their prey and predators, including fisheries and additional components outside the model domain; 3) specify the geographical domain and time period; 4) compile data on biology, physiology, and life-history from existing literature and derive model input parameters; 5) compile data about past changes in the food-web (catches, biomasses, diets, etc.); 6) define “constraints” that relate the model to input data, 7) build the model (i.e., build the polytope) and check that it constitutes a bounded set of solutions; 8) sample the model, and 9) visualise the results and interpret them. In early iterations, steps 7 and 9 may lead to revisions of the model structure, parametrisation, constraint formulation, or choice of input data. In the present case, we performed multiple iterations during a 2-year period. The model was repeatedly reviewed by experts who confronted model outputs against their expert knowledge. These verifications, termed sanity checks, included examinations of mean, distribution, and dynamics of biomass and catches, and examinations of diet and consumption matrix (proportions of prey and total consumption of prey for each predator). Through this process the model gradually converged towards a reconstructed dynamics that conforms to multiple ecological patterns, following the principles of Pattern Oriented Modelling (Grimm and Railsback, 2012). In addition, the MCMC sampling chains were checked for possible autocorrelation. When sanity

checks were not passed, possible solutions to the problem were discussed and the model was revised accordingly.

3. Results

3.1. An individual food-web trajectory

Food-web assessment using CaN modelling produces multiple food-web trajectories. Each trajectory is a possible realisation of the food-web dynamics given the set of information provided to build the model (i.e., food-web structure, input parameters, constraints, and input data). One possible food-web trajectory is illustrated in Fig. 2, with a focus on Atlantic cod. The time-series of inter-annual fluctuations in the biomass of cod is fully determined by a combination of consumption, predation, and catches that are compliant with the entire set of model constraints and observational data. Interannual estimates of cod consumption are compatible with food requirements necessary to achieve given levels of growth and mortality (set by the input parameters: saturation, assimilation efficiency, and other losses). Thus, total consumption fluctuates between ca. 5 and 12 million tonnes, with capelin and benthos (including shrimps) being the major prey groups, consistent with cod diet estimates that are annually provided by the Arctic Fisheries Working Group of ICES (<https://www.ices.dk/community/groups/Pages/AFWG.aspx>). Likewise, predation and catches are also compatible with biomass and food requirements of cod predators as well as with reported fishing catch. In this particular case, predation and catches fluctuate between ca. 1 and 3 million tonnes, with catches constituting about 25 % of the total flux of biomass. In this single reconstruction, fluctuations in the biomass of the 11 other species within the model domain are also compatible with reported biomass and are explained by consumption, predation and catch that are themselves consistent with available data (graphs for all species are provided in Supplementary Figure S5).

3.2. Multiple trajectories

Assuming that each individual food-web trajectory is equally probable, it is possible to assess the distribution and derive summary statistics (e.g. mean or median) of biomass, diets, consumption, or other relevant food-web properties across all CaN samples. Results of the sampling shows that reconstructed biomass trajectories generally span

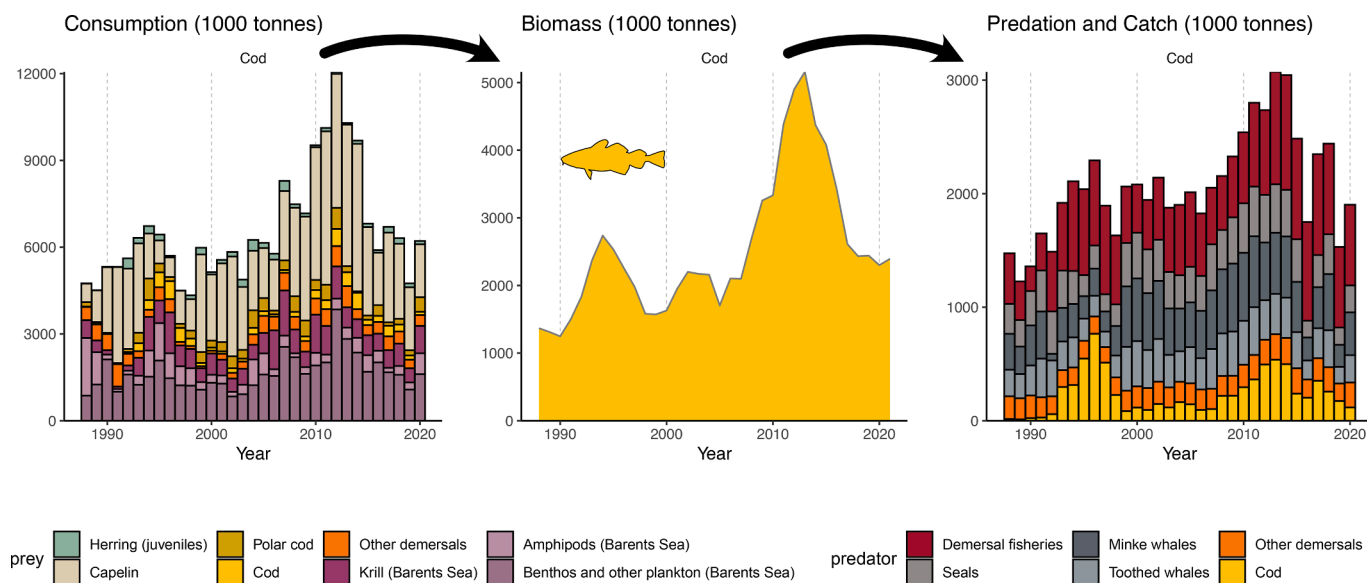


Fig. 2. An example of reconstruction of the food-web dynamics highlighting cod. Changes in the biomass of cod (centre) result from variation in the annual consumption of prey (left) and from variations in predation and fisheries (right). This single reconstruction is one possibility among a set of plausible food-web trajectories given the model structure, parametrisation, constraints, and observational data.

the range of input biomass limits and are, for most species, evenly distributed (Fig. 3). There are however noticeable exceptions. For capelin and polar cod, sampled biomasses fall outside the range of input data when these stocks are at very low levels. In other words, it was not possible to find a single food-web reconstruction compatible with these reported extreme lows, and in these instances, upper biomass constraints had to be relaxed. Biomass trajectories for other demersal fish tend to be on the high side of the inputs derived from single species assessment and survey estimates. The set of seal biomass trajectories occupy a range of values that is much narrower than the range of possible biomass provided as an input. In addition, seals biomass reconstructions follow interdecadal variations that appear to be associated with prey biomass, namely capelin and polar cod.

For each species, the mean biomass, consumption (= sum of inflows), production (= sum of outflows), and ratios of consumption-over-biomass (C/B) and production-over-biomass (P/B) are summarised in Table 1. Small pelagic fish have dominated the overall biomass with capelin, blue whiting, herring, and polar cod totalling an average of 18.5 million tonnes annually. The annual biomass of cod and other demersal fish sums to an average of 5.5 million tonnes, while marine mammals contributed to an average of 3.2 million tonnes. The combined biomass for these animal groups averaged 27.3 million tonnes with an annual consumption of 157 million tonnes. The C/B ratios range from 2.6 for cod to 19 for seals and P/B ratios range from 0.5 for adult herring to 2.7 for capelin. Several species have P/B ratios close to or greater than one reflecting fast biomass turnover, i.e., high consumption and population growth rates that allows for high predation and catch rates.

The average diet of predator species, and the catch of fisheries and hunting are summarised in Fig. 4. Species that migrate in-and-out of the Norwegian and Barents Seas and species that have a broad geographical distribution (blue whiting, mackerel, and marine mammals) feed

Table 1

Summary of biomass (B), consumption (C), production (P), consumption-over-biomass (C/B), production-over-biomass (P/B), and Production over Consumption (P/C) ratios. Consumption is defined as the sum of incoming flows (consumption and recruits, y^{-1}) and production is defined here as the sum of outgoing flows (predation and catches, y^{-1}). Each value is the mean over the period 1988–2021. Biomass, consumption, and production are given in 1000 tonnes.

Species	B: Biomass	C: Inflows	P: Outflows	C/B	P/B	P/C
Blue whiting	4,006	12,504	2,233	3.1	0.6	0.18
Mackerel	3,217	25,601	2,008	8.0	0.6	0.08
Herring (adults)	4,408	32,064	2,395	7.3	0.5	0.07
Herring (juveniles)	3,111	21,191	6,597	6.8	2.1	0.31
Capelin	2,426	16,570	6,657	6.8	2.7	0.40
Polar cod	1,330	7,349	1,486	5.5	1.1	0.20
Cod	2,524	6,572	2,065	2.6	0.8	0.31
Other demersals	2,945	13,153	3,726	4.5	1.3	0.28
Toothed whales	421	3,579	–	8.5	–	–
Minke whales	816	5,650	3	6.9	0	0
Other baleen whales	1,691	6,555	–	3.9	–	–
Seals	324	6,152	4	19	0	0

partially on outside resources. The diet of small pelagic fishes in the Norwegian Sea is dominated by zooplankton and to a lesser extent by krill. In the Barents Sea, juvenile herring and capelin have a diet dominated by copepods and krill while polar cod also feeds on amphipods and benthic prey. The mean diet of cod and other demersal fish is more diverse and includes small pelagic fish, planktonic and benthic prey groups. Capelin is a major component of cod diet. Marine mammals have the most diverse diet and feed on a collection of planktonic,

Biomass (1000 tonnes)

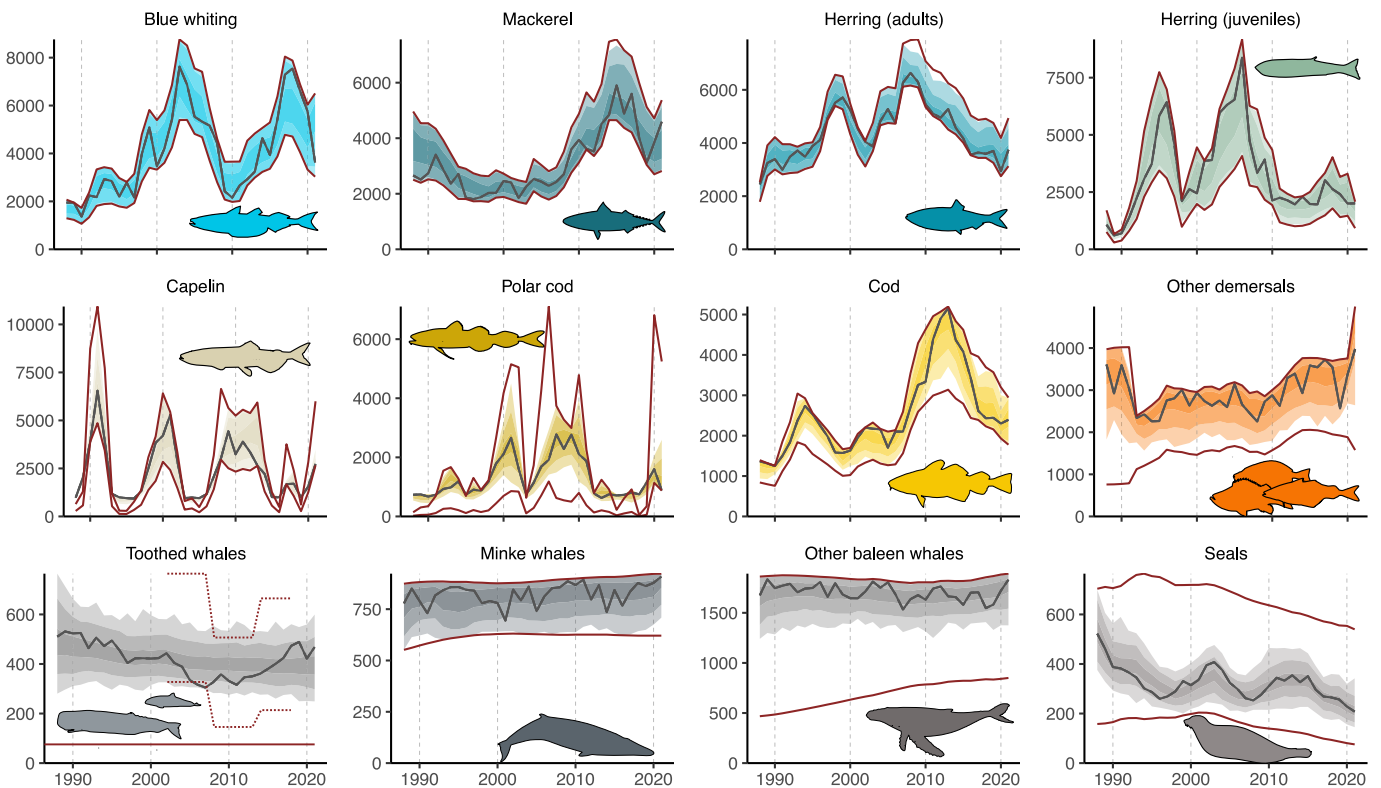


Fig. 3. Biomass trajectories of the 12 species within the model domain. The shaded areas display the envelopes containing 100% (light), 95% (medium) and 50% (dark) of the sampled trajectories. One individual trajectory is provided for illustration (plain gray lines). Red plain lines show the input upper and lower limits of biomass that were used as constraints. For toothed whales, the biomass constraints were provided as multi-annual means (shown as dotted lines), so biomass in individual years may cross the limit, but the average over 5y periods cannot.

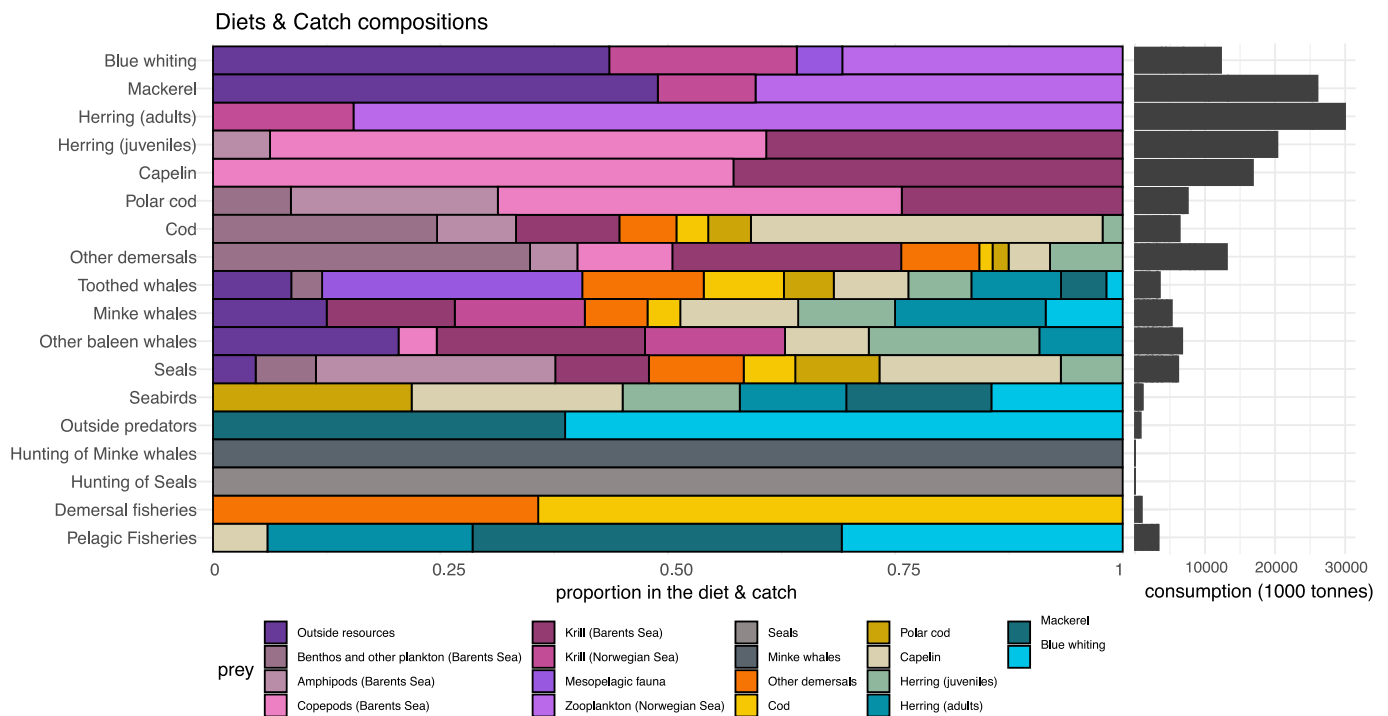


Fig. 4. Left: Diet fraction of individual prey species (colour) for each predator or fishery (row). Predators are named on the vertical axis and the proportions of prey in the diet are indicated by colour bars. Each colour refers to a specific prey and the sum of proportions always add up to unity. Right: annual consumption by each predator or fishery, average over the period 1988–2021.

mesopelagic, and benthic prey at different trophic levels. Seabirds feed on a diversity of small pelagic fish. The proportion of different species groups in the catch of the marine mammal hunts and of the demersal and pelagic fisheries reflects the catch statistics available for the period 1988–2021.

3.3. Emerging patterns

The total secondary production required to sustain fish and marine mammal populations considered in this assessment is on average 137 million tonnes, with 11 million tonnes for marine mammals and 126 million tonnes for fish (Fig. 5). This consumption has varied greatly between years. There has been an increasing trend in fish consumption until the early 2010s. No similar trend is visible for marine mammals though high interannual variations are present. Around 9.5 million tonnes of fish have been consumed annually by other fish and this has dramatically increased from the late 1980s to the early 2010s. This increase is for a large part explained by planktonic food being channelled through capelin in the Barents Sea which then served as feed to piscivorous fish species. On average, 50 % of marine mammals’ consumption has been provided by fish prey, which represent an average of 11 million tonnes per year. At the end of the assessment period total fish catches were around their maximum, while the total marine mammals’ catches were at their minimum. During the assessment period, fisheries catch accounted on average for 18 % of the total fish removal while 44 % were removed by marine mammals and 38 % by fish themselves (therefore being partly recycled as new fish biomass).

4. Discussion

The purpose of this study was to perform a quantitative assessment of the joint dynamics of marine mammals, fish, and fisheries in the Norwegian and Barents Seas that can ultimately support EBFM. In a way comparable to traditional single-species fish stock assessments that aims to reconstruct the past-trajectory of a stock and of its interactions with a

fishery, this approach aims to reconstruction in a consistent manner, the dynamics of many species affected by fisheries and trophic interactions. Motivated by this original objective, the model construction involved expertise in modelling, ecology, and fisheries, and followed an iterative process. These iterations have been essential to refine the model purpose, structure, parametrisation, input knowledge and data. At the end of this iterative process, we have reconstructed a set of possible dynamics for the main commercial fish species in the region, the main marine mammal groups, the trophic interactions between them, and the associated fisheries and hunts. One reassuring feature emerging from the assessment is the possibility to jointly explain the dynamics of all groups in a way that is internally consistent and compatible with (most) observational data, as well as multiple expert assumptions and knowledge. Because precise observational data is only available for some trophospecies and for very few diets, there is a large degree of variations between individual reconstructions of the food-web dynamics. It is nevertheless possible to identify some key features of the marine mammals-fish-fishery system and how these have varied over time. Our results demonstrate that it is possible to estimate the general flow of biomasses between ecological groups, and to provide descriptions of their interannual variations and of the associated uncertainties (Fig. 5).

The current CaN model is not a simulation or a predictive model. Instead, it provides reconstructions of past interactions within a food-web that can explain what we have observed. In other words, CaN reconstructs the past trajectories of the ecosystem by assembling diverse and heterogeneous sets of knowledge and observations. By doing this it can inform us about what we don’t know about a food-web (mostly trophic interactions) on the basis of what we know (usually first principles for marine trophic systems and observations of biomass and of some fluxes). The idea is that an in-depth knowledge of what occurred in the past of an ecosystem, combined with a limited set of assumptions can help to understand and reconstruct its internal dynamics.

The CaN modelling approach is explicit about uncertainties. At every step, data integration, modelling, and analysis of the model results, emphasis was put on what we don’t know. By taking this stance, the

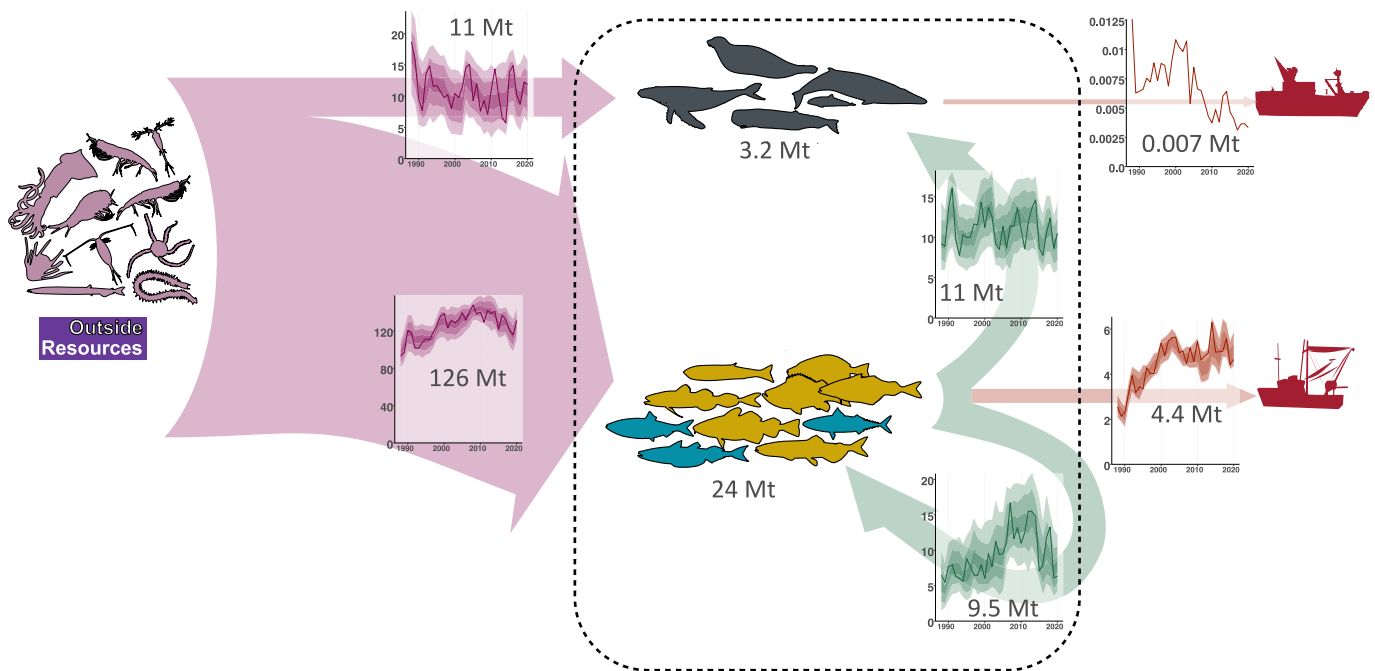


Fig. 5. Consumptions by fish and marine mammals and catches, during the period 1988–2021. Numerical figures on the arrows are averages for the whole time-period, in million tonne-year⁻¹. Individual panels show time-series of consumption or catches from 1002 CaN samples. For each panel, the shaded areas display the envelopes containing 100% (light), 95% (medium) and 50% (dark) of the sampled trajectories, and one individual trajectory is provided for illustration (plain line). Arrow and time-series panels are coloured to illustrate incoming fluxes (pink), fluxes within the model domain (green) and outgoing fluxes to fisheries and hunts (red). The mean biomass of all fish and all mammals combined are also indicated.

model was constructed in a participatory manner that focused on common understanding and robust knowledge while recognising that some level of ignorance must often be acknowledged and can sometimes be irreducible.

In practice, building a CaN model requires very little coding and the main requirement is to provide input information (food-web structure, input parameters, constraints, observations, and *meta*-data) in the RCaN file, either via the RCaNconstructor or directly using an xlsx file editor. This forces the focus to be mostly on understanding how data and knowledge relate to the dynamics of the system. Documenting, i.e. providing *meta*-data is time consuming, and our experience is that modellers are easily tempted to skip this step while building and revising the model. Nevertheless, we have found that explicitly documenting every aspect of the model as well as the steps of the model development is best achieved when done in real time and is essential for the communication and later revision of the model. The combination of all input information, including *meta*-data and model development timeline, inside a single file (the RCaN xlsx file, [Supplementary material 2](#)) simplified the archiving and access to the multitude of components that are necessary to run and understand the food-web model.

From a practical standpoint, the model acted as the boundary object used to collectively confront expertise and knowledge ([Gray et al., 2018](#)). One recurrent situation during the model development was the identification of incompatibilities between model structure, parametrisation, constraints, and data. In the worst case, this resulted in the inverse linear problem having no solution, meaning that no food-web reconstruction could comply simultaneously with all model inputs. This implied that experts had to explore the possible reasons for such incompatibilities and deliberate on how to resolve the issue. An example of such incompatibilities was the observations of low biomasses of capelin and polar cod in some years and their subsequent increase (see [Fig. 3](#)). The low biomass and recovery rates were incompatible with the population growth rates specified in the input parameters, and with the predation rates derived from diet consumption estimates of cod. There are multiple ways to interpret and resolve this incompatibility. The

multi-expert deliberation led to opt for the relaxation of the stock assessment data as it was considered most likely that the very low abundance estimates of capelin and polar cod were in fact underestimates. This is because parts of the populations are not well detected during the surveys, either because they reside under the ice and migrates between the Barents and Kara seas (polar cod, [ICES, 2021](#)) or because there is a demersal component that is not observed from the pelagic surveys (capelin). In other cases, we found that some emerging properties of the model did not align with existing literature. This was the case, for example, of the consumption rates of herring and mackerel in the Norwegian Sea. While earlier models report consumption rates (C/B ratios) between 9 and 12 ([Bachiller et al., 2018](#)), we found average rates that were substantially lower, 8 and 7.4 for mackerel and herring respectively. Here again, there was multiple ways to interpret and resolve this discrepancy, by e.g., adjusting metabolic rates, assimilation and digestibility parameters, or carbon-to-wet weight ratios of prey and predators. The multi-expert deliberation led to the decision to retain the lower consumption rates. It was considered plausible that the previously published rates had been over-estimated, and that the values of the current consumption fell within a credible range.

A third category of deliberation concerned situations when there is little empirical evidence to decide on a particular model aspect. This was generally the case for selecting the values of the metabolic parameter (other losses) for most species. Field metabolic rates are notoriously difficult to determine, especially when integrated at the population level and over annual time scales, as is the case here. We used multiple sources to calculate metabolic losses ([Gillooly et al., 2001](#); [Karamushko and Christiansen, 2002](#); [Makarieva et al., 2008](#); [Noren and Rosen, 2023](#); [Savage et al., 2004](#); [Williams et al., 2006](#); [Yodzis and Innes, 1992](#)) or derived these values from other food-web models (e.g. ecotrophic efficiency in Ecopath can be converted to other losses in RCaN, see [Planque et al., 2014](#)). From these sources, the range of possible parameter values was often so large that it was difficult to decide which one to use as input to the CaN model. In most cases, we adopted an iterative approach, starting with the mean of the values derived from multiple sources and

revising it if the model was behaving badly (see sanity checks in [Supplementary material 3](#)), while remaining within the range of plausible estimates. In line with [Reum et al. \(2021\)](#), the iterative development of the food-web assessment model can be understood as a journey to advance system understanding, reveal knowledge uncertainties, and improve the model credibility. These advances should ultimately help implementing multispecies models in applied fisheries contexts.

One specific feature, and a challenge for end-users, is that RCaN does not produce a single 'best' history of the food-web dynamics, but instead a set of histories that are equally possible. Presenting an average of these histories is informative to describe the general trends in biomass, consumption, predation, or catches, but at the same time such an average lacks the year-to-year variability of individual trajectories, which is an important ecological feature of the food-web dynamics. We have learned that representing individual trajectories rather than average dynamics is useful when one wants to provide end-users with a more accurate representation of the system year-to-year variability. Working with individual trajectories is also critical if one wants to explore how the variability in one part of the food-web is related to variability in another part, for example when studying trophic controls. This is because the variability in individual trajectories aligns with the model assumptions while the variability in the average trajectory is much lower, by construction.

One important feature of the CaN model presented here is its simplicity relative to other ecosystem models that exist for the region, such as Ecopath with Ecosim ([Bentley et al., 2017](#); [Blanchard et al., 2002](#); [Dommasnes et al., 2001](#); [Pedersen et al., 2021](#); [Skaret and Pitcher, 2016](#)), Atlantis ([Hansen et al., 2016](#); [Nilsen et al., 2022](#)), or NORWECOM ([Holmin et al., 2020](#); [Skogen et al., 2018](#); [Skogen and Sjøiland, 1998](#)). The present model focuses on few (12) selected species groups that are central to the assessment objective. Other species groups were purposely left outside the model domain, which means that they didn't require to be parameterised (except for the digestibility for prey groups). In addition, CaN relaxes assumptions about trophic functional relationships which are common to other modelling approaches. Most trophic models are highly sensitive to the formulation of trophic functional relationships ([Fulton et al., 2003](#); [Williams and Martinez, 2004](#); [Yodzis, 1994, 1988](#)), although these are difficult to parametrise from field data. Our approach results in a simpler model with fewer species and fewer parameters per species, that can more easily be grasped by multiple experts.

CaN is designed as an assessment model. It is data driven and its primary goal is to reconstruct historical dynamics. The model is based on a minimal set of assumptions and on a single dynamic process represented by the CaN master equation (1). Most food-web models that are informed by observational data are usually fitted to (rather than constrained by) data. This doesn't guarantee that the model outputs don't depart greatly from existing observations, at least for some species biomass, diets, or consumption estimates. In this respect, it is noticeable that while fish stock assessment models report residual plots as a standard evaluation of the model fit to data, this is seldom practised in the case of food-web models. CaN models are not fitted, but are constrained by observations, which entails that model outputs always align with input data within the limits that are determined by data uncertainty.

The relative simplicity and the focus of the model on assessment purpose makes it well-suited for food-web assessment but possibly less versatile than other approaches. In its current configuration this model cannot address issues related to e.g. drivers of seasonal or spatial dynamics (e.g. [dos Santos Schmidt et al., 2024](#); [Fernö et al., 1998](#); [Huse, 2016](#); [Nascimento et al., 2023](#)), biodiversity ([Certain and Planque, 2015](#); [Johannesen et al., 2012](#)), management strategy evaluation ([Howell and Bogstad, 2010](#); [Kaplan et al., 2021](#); [Punt et al., 2016](#); [Rochet and Rice, 2009](#)), or ecological forecasts ([Clark et al., 2001](#); [Dietze et al., 2018](#); [Fransner et al., 2023](#)) than can possibly be addressed by more complex regional ecosystem models.

There remain several hurdles when building a CaN model, many of

which are common to other ecosystem or food-web models. Defining the food-web structure is not a trivial issue. This is because food-webs are conceptual constructions that require simplification of complex trophic interactions that occur in the wild ([Jordán, 2003](#)). They therefore rely on multiple choices and assumptions that may be subject for disagreement between experts. This issue is particularly serious because different choices of structure to represent the same food-web can lead to rather different results when analysing food-web properties or dynamics ([Olivier and Planque, 2017](#)). The delineation of the model geographical domain is also a complex matter, given that some species may reside in the entire domain, while other may only occupy a small fraction of it, may have distributions that extend beyond it, or may operate seasonal migrations in and out of the model geographical domain. Here, we used two additional components termed *outside resources* and *outside predators*, that can account for these geographical mismatches. We acknowledge that it has been difficult to document actual spatial distribution for several species groups and how these align with the geographical domain of the model. The meaning and representativeness of input data can also be challenging. For example, stock assessment estimates are associated with entire fish stocks but not with a specific geographical domain; diet data may reflect feeding during the sampling season (often spring and summer) while the model is dealing with diets integrated over the entire year; information on spatial distribution may exist for few years but not for the entire period of the assessment. In each case, additional assumptions are required to connect the observational data with the model. Often this has been done by adjusting the uncertainty associated with the input data. CaN relies on few (5) input parameters for each species but these may be difficult to directly measure or derive from life-history and metabolic theory, may be variable in time, space, and among individuals in a trophospecies. For this reason, the input parameter values are often uncertain. A global sensitivity analysis would be required to assess the robustness of the model results to uncertain inputs ([Morris et al., 2014](#); [Morris, 1991](#); [Saltelli et al., 2004](#)). Like for many other ecosystem models this is difficult to achieve because of the dimensionality of the system (5 parameters times 12 species is already 60 parameters), of the computing time involved (about 6 h for the current sampling, on a personal computer), and of the intrinsic stochasticity of the model which is difficult to handle in sensitivity analyses. The iterative approach used here is a long process. It involved many participants, over the course of several years. At each step, discussions were needed to resolve issues, clarify objectives, definitions, and interpretation of the results, or discuss the implications of the results for model revision. Working with a diversity of participants in a long timeframe also makes documentation essential and this was an essential but time-consuming task.

The results from this food-web assessment are internally consistent, compliant with data and expert knowledge, and reflect uncertainties in the underlying data and knowledge base. The ecological patterns (in the sense of Pattern oriented modelling, [Grimm and Railsback, 2012](#); [Wiegand et al., 2003](#)) emerging from these results are potentially useful for assessing critical issues for the management and conservation of fish and marine mammals in the Norwegian and Barents Seas. For example, in-depth analysis of the year-to-year changes in consumption by fish and marine mammals can be used to resolve the long-standing debate about competition between marine mammals, fish, and fisheries. Contradictory analyses can also be envisaged to quantify biological production required to jointly support marine mammal populations, commercial fish stocks, and associated fisheries. The identified discrepancies between stock assessment inputs and other CaN assumptions and parameters could be used to guide future monitoring surveys, to ensure that all components of fish stocks are adequately observed. CaN outputs can also be used to derive estimates of otherwise hard-to-measure rates like natural mortality or metabolic losses.

5. Conclusion

We have constructed a food-web model of intermediate complexity, based on linear inverse modelling, to reconstruct the dynamics of marine mammals, commercial fish, and fisheries in the Norwegian and Barents Seas for the period 1988–2021. This was achieved through an iterative process that involved diverse experts and which permitted to confront, discuss, and resolve many issues as well as to recognise uncertainties in expert knowledge, data, and input parameters. These uncertainties are reflected in the model outputs. We found that a coherent reconstruction of the food-web past dynamics is possible, if one recognises that some data and assumptions that are used as input to the model were more uncertain than originally thought. According to this assessment, consumption by commercial fish and catch by fisheries jointly increased until the early 2010s, after which consumption by fish declined and catches by fisheries stabilised. Fish have consumed an average of 135.5 million tonnes of resources annually (including 9.5 million tonnes of fish). Marine mammals have consumed an average of 22 million tonnes annually of which 50 % (11 million tonnes) were fish. Fisheries and hunting have extracted 4.4 million tonnes of fish and 7 thousand tonnes of marine mammals annually.

CRedit authorship contribution statement

Benjamin Planque: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lucas Bas:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Martin Biuw:** Writing – review & editing, Validation. **Marie Anne Blanchet:** Writing – review & editing, Validation. **Bjarte Bogstad:** Writing – review & editing, Writing – original draft, Validation. **Elena Eriksen:** Validation. **Hilaire Drouineau:** Writing – review & editing, Validation, Software, Methodology. **Cecilie Hansen:** Validation. **Bérengère Husson:** Writing – review & editing, Writing – original draft, Visualization, Validation. **Erik Askov Mousing:** Writing – review & editing, Writing – original draft, Validation. **Christian Mullon:** Writing – review & editing, Writing – original draft. **Torstein Pedersen:** Writing – review & editing, Validation. **Morten D. Skogen:** Writing – review & editing, Validation. **Arl Slotte:** Writing – review & editing, Validation. **Arved Staby:** Writing – review & editing, Validation. **Ulf Lindström:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The input data are available in [Supplementary Material S2](#). The output data are available from the Norwegian Marine Data Center (<https://doi.org/10.21335/NMDC-442913850>)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2024.103361>.

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