



Contribution to the Themed Section: 'Science in support of a nonlinear non-equilibrium world' Food for Thought

Modelling chance and necessity in natural systems

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Nearly 30 years ago, emerged the concept of deterministic chaos. With it came sensitivity to initial conditions, nonlinearities, and strange attractors. This constituted a paradigm shift that profoundly altered how numerical modellers approached dynamic systems. It also provided an opportunity to resolve a situation of mutual misunderstanding between scientists and non-scientists about uncertainties and predictability in natural systems. Our proposition is that this issue can be addressed in an original way which involves modelling based on the principles of chance and necessity (CaN). We outline the conceptual and mathematical principles of CaN models and present an application of the model to the Barents Sea food-web. Because CaN models rely on concepts easily grasped by all actors, because they are explicit about knowns and unknowns and because the interpretation of their results is simple without being prescriptive, they can be used in a context of participatory management. We propose that, three decades after the emergence of chaos theories, CaN can be a practical step to reconcile scientists and non-scientists around the modelling of structurally and dynamically complex natural systems, and significantly contribute to ecosystem-based fisheries management.

Keywords: chaos theory, constraints, nonlinear systems, participatory modelling, uncertainty, viability theory

Introduction

Nearly 30 years ago, emerged the notions of deterministic chaos, sensitivity to initial conditions, nonlinearities, and strange attractors (Gleick, 2011). This initiated a series of works investigating the implications of chaos theory in ecology in general (Hastings *et al.*, 1993), in marine ecology (Huisman and Weissing, 1999), in fisheries modelling (Beddington and May, 1977; May *et al.*, 1978), and in fisheries management (Wilson *et al.*, 1994, 1996; Fogarty, 1995; Fogarty *et al.*, 1997; Acheson *et al.*, 1998).

Smith (1990) considered the developments in the science of deterministic chaos as an opportunity to change the nature of the interactions between scientists and other actors involved in fisheries management. She was focused on the different positions taken by the actors involved in management, particularly with regard to uncertainty and predictability. She saw a group of actors, fishermen, processors, traders, used to constantly adapt to an uncertain, and changing universe. In contrast, the other actors, scientists, and managers, were attached to the search for rules, balances, and

determinisms. Smith wondered if the new chaos theories could help to resolve the situation of mutual misunderstanding she had observed in these two groups of actors. More specifically she asked if chaos theory could lead scientists and managers to think about uncertainties and predictability in a way more compatible with the perceptions of the other actors. The issue is particularly relevant in the context of ecosystem-based fisheries management (EBFM), which was formalized after the publication of Smith's opinion and is becoming a focal point of fisheries management and research see e.g. Browman *et al.* (2004), Smith *et al.* (2007), Rice (2011), Fulton *et al.* (2014), DePiper *et al.* (2017), Marshall *et al.* (2019), Link *et al.* (2019), and Trochta *et al.* (2018).

We use Smith position at the starting point of this “food for thought” and ask what has changed from the situation described in 1990? We certainly note progress (i) in the identification of chaos within ecological series and its use for short-term prediction purposes [from Turchin and Taylor (1992), to Sugihara *et al.* (2012)], (ii) in the parameterization of nonlinear models using

Bayesian methods, for example state-space models (Dowd and Meyer, 2003).

However, it seems that, despite some advances, the perceptible gap between the two types of actors has not yet been bridged and the problem of involving all actors in fisheries management is still open (Röckmann *et al.*, 2012). Although it is recognized as a necessity for fisheries policies (Symes, 1997; Gray and Hatchard, 2008), involving actors in participatory marine resource management operations remains a difficult task (Gray and Hatchard, 2008; Pita *et al.*, 2010, 2016; Gopnik *et al.*, 2012; Kraan *et al.*, 2014). Actors' lack of belief in the need for planning, divergent objectives, difficult dialogue (Bailey and Jentoft, 1990; Bailey *et al.*, 2017), mutual misunderstanding (Johannes *et al.*, 2000), or mistrust between professionals and researchers (De Vos and Van Tatenhove, 2011; Glenn *et al.*, 2012; Eggert *et al.*, 2016) are still common problems. Miscommunication results, at least partly, from different actors thinking from different perspectives built on different representations of the natural world. There is often a divorce between the understanding of the fisheries system by the actors and the numerical modelling principles and terminology used by scientists. To improve this situation, Röckmann *et al.* (2015) propose that EBFM requires transparent interaction among scientists, decision makers, and other actors, in which salience, legitimacy, and credibility are promoted. Numerical modelling can positively contribute to this interaction triangle if conducted in a transparent and participatory manner. A challenge is to reconcile the numerical modelling approaches used by scientists and approved by managers, together with the understanding by other actors of the functioning of fisheries systems and marine ecosystem dynamics. Group model building is a way to achieve this reconciliation, by raising trust and empowerment of all parties involved, but it may not be easy to achieve and has been described as a messy problem (Vennix, 1999).

Our proposition is that this issue can be addressed in an original way which involves the development of new types of models. We posit that all actors, even if they do not express it explicitly, possess their own personal positions about many of the ideas that the chaos theory illustrates: determinism/indeterminism, continuities/ruptures, predictability/unpredictability. Even if they can experience this in very different ways, they all look for a combination of the notions of necessity (expressed by constraints) and chance (related to a lack of knowledge, the uncertainty, and unpredictability of the system.) We expect that putting forward this common point of view can help establishing a revised and more effective management mode in which different actors can better share their understanding of the fisheries system and its uncertainties. For this purpose, we advocate models in which principles, equations, and results are expressed as clearly as possible in terms of chance and necessity.

Below, we review briefly the motivations behind the development of mathematical models for fisheries management. We then discuss the importance of communication about models as part of participatory management. We introduce the basic principles of chance and necessity modelling (CaN) using the logistic equation as a toy model. We then present an application of CaN modelling to perform a simplified food-web assessment. Finally, we discuss how the model results can serve as a basis for elaborated discussions between parties and how CaN modelling can promote a participatory framework in modelling, assessment, and management.

Mathematical modelling and fisheries management

Mathematical models of exploited marine ecosystems

When constructing and evaluating a numerical model, a common rule is that the model should be designed to answer a specific question (or set of questions) (Jakeman *et al.*, 2006). Fish stock assessment models fall in this category. They are designed to (i) reconstruct the historical trajectory of individual populations (e.g. biomass or numbers) and of their exploitation (e.g. fishing mortality) and (ii) provide some predictions of the expected consequence of exploitation on the state of the modelled population. In contrast, models of marine ecosystems are rarely designed to address a specific question and rather serve several, and more diffuse, purposes such as: increase understanding of system dynamics; identification of major processes, drivers, and responses; highlight of major gaps in knowledge; and provision of mechanisms to “road test” management strategies before implementing them in reality (Fulton *et al.*, 2011). In other words, ecosystem models are used to quantitatively represent and integrate what we know, to identify or clarify what we do not know and to make predictions about the consequences of our actions or of particular external events. Simulation models are useful tools to display the expected response of the system to specific management actions in a way that scientists hope to easily communicate to managers and stakeholders.

Constructing ecosystem models with such wide and diffuse objectives is challenging. It is difficult to define which ecosystem components to incorporate, which processes to include, and which temporal, spatial, and ecological scales to consider. The temptation can be great to inflate model complexity (Hellweger, 2017), but there is no assurance that this can result in better model performance. Given that knowledge regarding ecosystems structure and processes is always incomplete, more complex models can reflect additional assumptions and noise as much as they can reflect better understanding of ecosystem dynamics. Model evaluations and sensitivity analyses also get harder to conduct as models become more complex. Without proper evaluation, numerical model simulations may be unreliable (Planque, 2016) and therefore of little use for management. In this context, Collie *et al.* (2016) and Plagányi *et al.* (2014) have argued that the challenge for modellers is to find the *sweet spot*, i.e. a compromise among model complexity, parameter uncertainties, and model fit.

A central tenet to most marine ecosystem models—whether they are bioenergetic models, predator–prey models, or minimally realistic models—is that there are mechanistic processes that connect different elements of the ecosystems and that these processes can be described and formalized by mathematical equations, for which parameters can be measured or estimated [see e.g. the review by Plagányi (2007)]. Regardless of their degree of complexity, most ecosystem models are tuned or optimized to describe the system state and dynamics in the best possible way.

The way in which observational and structural uncertainties can be dealt with by modellers, managers, and stakeholders is central to the modelling process, and given these uncertainties, it is not obvious that a *single best representation* of the system can be found. This has been recognized in the theoretical ecology literature and is well summarized by DeAngelis and Yurek (2015) who claim that there are no right models to describe ecological systems, only good approximations and that complex ecological models are so sensitive to structure and parameters that even the

most thoroughly and carefully developed model can hardly be expected to be predictive.

We explore a modelling tool for situations where it is not possible to fully and precisely observe a dynamic system, and where there is substantial irreducible uncertainty in our understanding of that system. The approach starts from few rules for which there is evidence and from existing observations. It explicitly recognizes our ignorance or incapacity to observe and model many ecological processes. A central element of this approach is that model outputs cover a range of possible ecosystem state and dynamics, rather than striving to deliver a best estimate. The existence of these multiple possibilities represents the starting point for discussions among modellers, managers, and stakeholders.

Communication and participatory management

As the use of algorithms and numerical models is increasingly prevalent in the studies and analyses that support management decisions, it is vital that these are well understood and trusted by all actors. Optimally all actors should be engaged in model building and interpretation. In practice, because models are often too complex, the exercise is left to specialists that are numerically competent. When non-specialists are left aside, they may perceive models as black boxes and can eventually develop some degree of distrust towards the models. As argued by [Saltelli and Funtowicz \(2014\)](#), in a multiple-actor context there is a need for models that are simple because

simpler models enable scientists and stakeholders alike to understand how assumptions and outputs are linked. Complex and often overparameterized mechanistic models should be used only for more speculative investigations outside of the policy realm.

The ongoing transition towards EBFM ([Browman et al., 2004](#)) and the development of integrated ecosystem assessments (IEAs) ([Dickey-Collas, 2014](#)) provide favourable conditions for scientists, managers, and actors of the fisheries sector to consider issues broader than individual fish stocks and fishing fleets. Nevertheless, most current quantitative modelling efforts are concerned either with single stock assessments, which do not address the broader issues, or with complex ecosystem models, which can address the broader issues but in a way that is often too complex for non-scientists to grasp or utilize. There is still a gap in the development of models that can serve EBFM efficiently. We contend that these would need to: be simple, transparent, and communicable, be trusted by scientists and non-scientists, recognize uncertainties in knowledge and observations, including irreducible Knightian uncertainties ([Schinckus, 2009](#); [Stirling, 2010](#)), recognize different perspectives and choices by different actors.

Principles of CaN modelling

We propose that the broad objectives of marine ecosystem models can be addressed in the following four steps.

First, express what is known in terms of constraints

Ecological constraints can be derived from physical and biological observations and theory and are often more easily defined than ecological laws ([Lawton, 1999](#)). For example, the constraints that population biomass is strictly positive, or that the trophic flow from a prey to a predator is strictly positive (otherwise the prey would regurgitate the predator alive) can be easily defined.

Similarly, there are upper limits to individual and population growth rates that can be derived from physiology and reproductive biology. Animal movements are also constrained by their swimming capabilities and the ocean circulation around them. Following ([Aubin et al., 2011](#)), we use the term *necessity* to define the ensemble of constraints operating on the modelled system.

Second, express what is not known in terms of sets of possibilities

Because ecological systems are complex and only partially observed, there is more out there that we do not know than we know. The existence of ecological laws that could underpin the equations used in numerical models has been questioned, in particular at the ecological community scale where most marine ecosystem models operate ([Lawton, 1999](#)). Instead, one can think of the processes and interactions operating in an ecosystem as a set of possibilities. For example, it is possible for a population to grow or decline, for an individual to survive or die, for a prey to be captured or not, or for a motile animal to move along certain trajectories. In the real-world, there is only one realization from this set of possibilities. Following ([Aubin et al., 2011](#)), we use the term *chance* to reflect the indeterminacy of this realization.

Third, explore the patterns emerging from the combination of chance and necessity

While chance, or randomness, makes predicting difficult, necessity constrains the possible state and dynamics of natural systems. In other words, “Nature may not be predictable, but it is not totally unpredictable either” ([Cury et al., 2005b](#)). The combination of chance and necessity provides a way to explore possible system dynamics when only partial knowledge of the system is available, as is the case for ecosystems. We use the acronym CaN for models that combined chance and necessity. The terminology originates from the influential work of [Monod \(1971\)](#).

Fourth, communicate knowledge in terms of CaN

CaN models explicitly recognize domains where processes are well understood and quantified, vs. those where randomness is a more acceptable way to account for lack of knowledge, uncertainties, or variability. This discrimination can help end users to better understand the scientific knowledge basis behind the model. In CaN models, it is the set of constraints that needs to be communicated and discussed rather than functional relationships. The former is often easier to grasp than the latter. Stochastic simulations provide dynamic illustrations of multiple plausible pasts and futures. Rather than focusing on the most likely ecosystem path, CaN models explore plausible trajectories of ecosystem dynamics providing a range of historical reconstructions or future scenarios.

A specific tool: polytope sampling

CaN model outputs consist of multiple solutions, and the main tool for implementing a CaN model is polytope sampling which can be summarized as follows ([Figure 1](#)):

- Mathematically, each system trajectory is represented by a point in a high-dimensional space. Each dimension of this space represents the state (or the variation in state) of one component of the system at a given time step. For example, if a system has 12 state variables and there are 8 time steps, the dimensions of the trajectories space is $96 = 8 \times 12$.

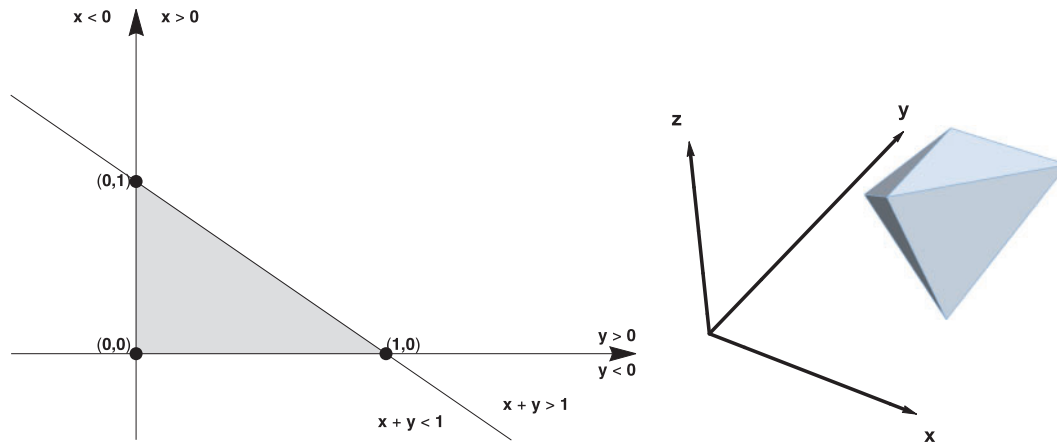


Figure 1. Left: a triangle is a simple example of a polytope; any edge determines a line in the plane, that is linear equality; the whole triangle is on one side of this line: its points satisfy a corresponding linear inequality; the three linear inequalities corresponding to edges, $x \geq 0$, $y \geq 0$, $x + y \leq 1$, determine the triangle. Right: polytope in $3 - d$; any face determines a plane in space, that is linear equality; the whole polytope is on one side of this plane: its points satisfy a corresponding linear inequality; the linear inequalities corresponding to faces determine the polytope.

- Using linear constraints, the ensemble of possible system trajectories is thus defined by a convex polytope (i.e. the equivalent of a convex polygon, but in higher dimensions).
- The polytope is then sampled uniformly to obtain a large set of possible solutions, i.e. an ensemble of possible system trajectories.

There are today efficient tools to extract samples from polytopes in high-dimensional space. These tools are used in many research areas, one of the most significant being for the study of steady states of metabolic equations (De Martino *et al.*, 2015). Details about polytopes and about the algorithm used to perform polytope uniform sampling are given in Appendix 1.

CaN modelling: a primer using the logistic equation

We illustrate the principles of CaN modelling using Verhulst’s problem as an example. The problem can be formulated in those terms: how to revise the Malthus exponential growth model so that it can account for limitation in population size (carrying capacity)? The classic solution to Verhulst’s problem is the logistic model of population dynamics illustrated in Figure 2a. An alternative solution is to express Verhulst’s problem in terms of trajectories and constraints. This was first proposed by Jean-Pierre Aubin as part of the viability theory (Aubin *et al.*, 2011).

Conventional approach

In the Verhulst approach, dynamics are expressed in continuous time. The formulation consists in a differential equation, expressing changes of population according to its intrinsic growth rate r and a carrying capacity K , the effect of which lies in constraining the solution in a given range.

$$x(0) = z_0 \text{ and } x'(t) = rx(t) \left(1 - \frac{x(t)}{K} \right). \tag{1}$$

The mathematical solution is given by:

$$x(t) = \frac{Kz_0e^{rt}}{K + z_0(e^{rt} - 1)}. \tag{2}$$

It results in typical population dynamics shown in Figure 2a, with first an increasing growth, then an inflexion and finally a decreasing growth. Population size increases asymptotically towards carrying capacity.

CaN approach

In the CaN approach, dynamics are expressed in discrete time. Formulation is in terms of constraints. These are of two types. The state (i.e. population size) is constrained:

$$x(0) = z_0 \text{ and } 0 \leq x(t) \leq K. \tag{3}$$

The variation of state (i.e. population growth) is constrained:

$$|x(t + 1) - x(t)| \leq rx(t). \tag{4}$$

Finding CaN solutions consists in sampling the dynamics of the system that satisfy the above constraints. This is done by expressing constraints as linear equalities or inequalities on trajectories, that is on vectors representing the succession of states: $X = (x_0, x_1, x_2, \dots, x_T) \in \mathbb{R}^{T+1}$. We use the elementary linear functions: I the identity function: $I(X) = X$, F the forward function: $F(x_0, x_1, \dots, x_T) = (x_1, x_2, \dots, x_T)$, H the truncation function: $H(x_0, x_1, \dots, x_T) = (x_0, x_1, \dots, x_{T-1})$, f the first term function: $f(x_0, x_1, \dots, x_T) = (x_0)$. Constraints are easily expressed in terms of these functions and thus are linear: constraint $x(0) = z_0$ becomes $f(X) \leq z_0$ and $f(X) \geq z_0$; constraint $0 \leq x(t) \leq K$ becomes $0 \leq I(X)$ and $I(X) \leq K$; constraint $|x(t + 1) - x(t)| \leq rx(t)$ becomes $(1 - r)H(X) - F(X) \leq 0$ and $(1 + r)H(X) - F(X) \geq 0$.

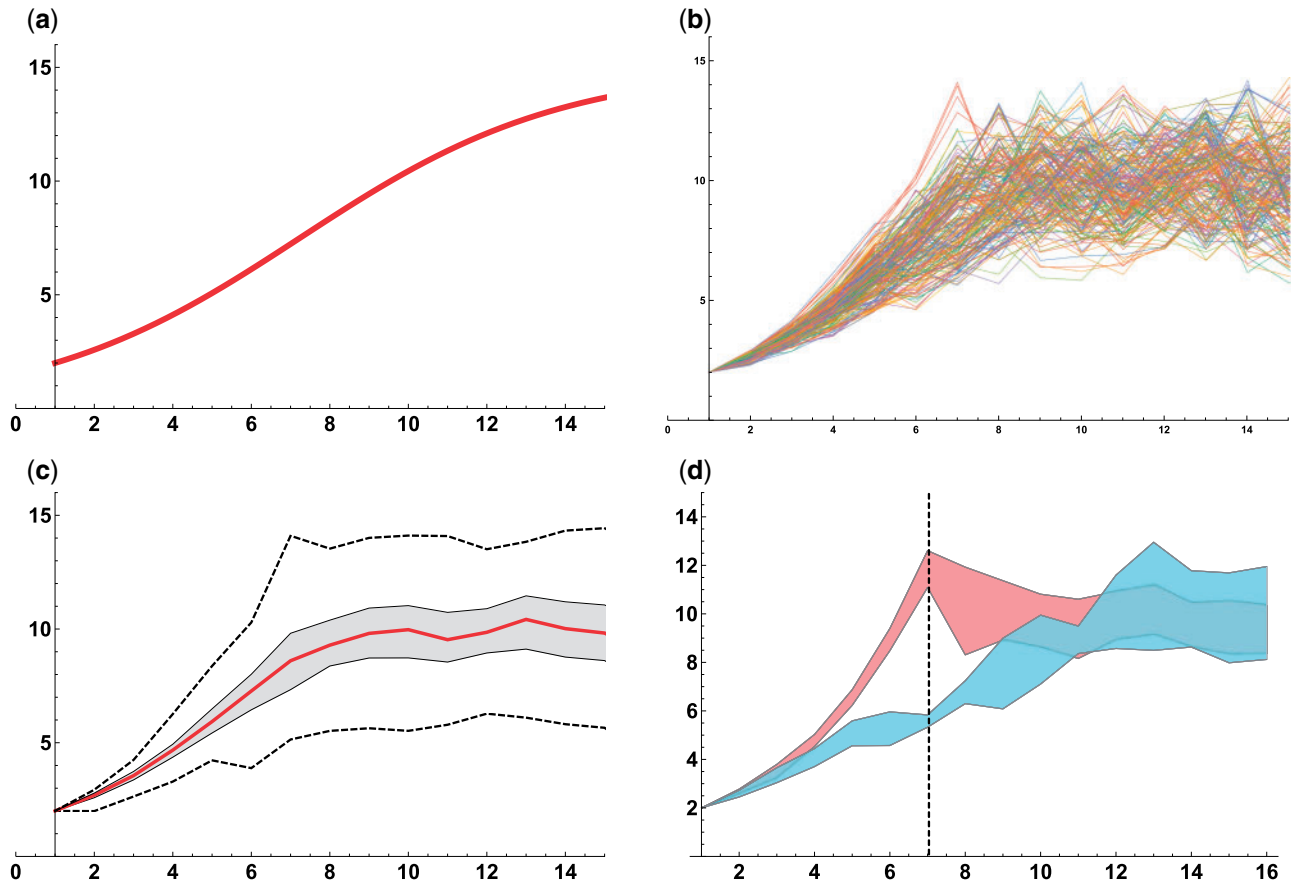


Figure 2. (a) The mathematical solution of the Verhulst model. (b) A set of trajectories from the CaN model of the Verhulst problem. (c) The 50% (thick line), 25–75% (grey ribbon) and 0–100% (dashed lines) percentiles of the trajectories of the CaN model. (d) Two sub-samples of CaN trajectories, with either high value (higher ribbon) or low value (lower ribbon) at time step 7. Parameters that have been used for both simulations are: $T = 10$, $z_0 = 2$, and $K = 15$. In the logistic model, intrinsic growth rate is $r = 0.5$; then effective growth rate in state x is $r(1 - x/K)$; in the CaN model, growth rates must be in the interval $[-r, r]$.

The set of linear inequalities above confines the set of possible population trajectories inside a convex polytope. The CaN solution is not a unique trajectory, but an ensemble of possible trajectories that can be obtained by sampling this polytope. The sampling method is provided in Appendix 1.

Results of CaN model are shown in Figure 2b. Interestingly, many of the trajectories sampled by CaN display an inflexion point, although this is not an immediate result of constraints. Assuming that all trajectories are equiprobable, the mean of the ensemble of trajectories can be derived (Figure 2c). Population growth trajectories that depart substantially from the sigmoid shape are possible, but it is extremely improbable to find such trajectories in the sample. If additional information about the population is available (e.g. measurement of population size at a particular time step), this information can be included in CaN as a new constraint and thereby reduce the set of possible trajectories (Figure 2d).

Comparison

Using the conventional approach, the underlying determinism is evident while with the CaN approach uncertainty is evident. Both conventional and CaN models express the idea that population growth is negatively related to population size. In the conventional

approach this is translated into a differential equation which provides a unique (and therefore very restrictive) solution to the problem. This may result in overconfidence in the mathematical solution which relies on the assumption that there is adequate isomorphism between nature and the mathematical model. Using the logistic equation to describe population growth is a modeller’s choice, and the precise mathematical answer it provides reflects this choice rather than certainty in nature. The CaN approach relaxes the assumptions about the population growth determinism. The resulting outputs are not unique and the dispersion of the trajectories reflects our lack of precise knowledge about the control of population growth.

The logistic equation exhibits an inflexion point that can be analytically defined (it is found when population size reaches half of the carrying capacity and the when growth rate is maximum: $(1/r) \log(Kx_0)/x_0$). The population trajectories sampled from the CaN model also display inflexion points but highlight that there is a large range of possible values.

Application of CaN modelling to a marine system: the Barents Sea

Numerical models of ecosystem dynamics are part of the IEAs toolkit, which form an integral part of EBFM. These models are

potentially complex, often difficult to communicate and the assumptions and uncertainties associated with food-web models are a legitimate topic for debate among modellers, managers, and other parties. For these reasons, ecosystem models constitute an interesting case study to address the issue raised by Smith about the consideration of uncertainties and predictability by different actors.

Below, we develop an application of CaN modelling to the Barents Sea ecosystem. Our intention is to model the dynamics of this system using an approach that reflects shared knowledge and uncertainties about the ecosystem and that can favour the involvement of the different actors concerned with fisheries management. Perceptions of knowledge and uncertainties in ecosystem models may strongly differ between actors.

The aim of the Barents Sea ecosystem model is to provide a set of plausible past dynamics of the system, given few constraints, partial knowledge, and incomplete observations. This is particularly relevant to the work of the IEA group for this region which aims to describe the status and trends of the Barents Sea ecosystem (ICES, 2017).

The Barents Sea ecosystem

Located to the north of Norway and Russia, the Barents Sea is a wide continental shelf sea, seasonally ice covered and in which fisheries operate on several types of resources including demersal and pelagic fishes, macroplankton (krill), and benthic invertebrates (crabs and shrimps). There is an additional exploitation of marine mammals (whales and seals). The fisheries are co-managed by Russia and Norway. Fishing and landing data are well documented, and the ecosystem has been regularly monitored through series of surveys conducted on a yearly basis. There is a need for management to consider a number of ongoing ecosystem changes. The Barents Sea is warming (Lind *et al.*, 2018) with direct implications for species spatial distribution (borealization, Fossheim *et al.*, 2015). Invasive species (king and snow crabs) have spread in recent years. Key pelagic species (capelin) can fluctuate widely in response to and with effect on other species such as Atlantic cod and herring (Hjermann *et al.*, 2010).

For the purpose of this explorative model, we use the simplified representation of the Barents Sea food-web given in Lindström *et al.* (2017), Figure 3. This consists of eight species groups: phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, marine mammals, and birds. Species composition in each group is provided in the Supplementary Material. In the following we use the terms “species” and “species groups” interchangeably.

Several components of the Barents Sea ecosystem have been extensively monitored during ecosystem surveys (Olsen *et al.*, 2011). We use annual data on biomass estimates derived from surveys and stock assessment models, and landings for the major groups (ICES, 2017) for the period 1987–2013 (26 years, Figure 4). Satellite-derived estimates of annual primary production are available for the period 1998–2013 (Dalpadado *et al.*, 2014). Prior to 1998 we have assumed a fixed range of primary production. The details of data sources and uncertainties are provided in the Supplementary Material.

Modelling objectives

We use CaN modelling as a way to contribute to IEA by learning about the controls of the system while recognizing the limits to

our understanding and to our observational capabilities. We investigate how species and trophic interactions may have varied in the past and to which degree these variations can explain the changes in the Barents Sea ecosystem that have been observed. In addition to these general goals, we use CaN model outputs to explore the nature of predatory control (top-down vs. bottom-up) in the system.

Modelling steps

We construct the Barents Sea ecosystem CaN model as follows. First, we set the model structure and constraints based on our knowledge about the Barents Sea ecosystem and its components. We consider that (i) we know the food-web structure, (ii) we have estimates of primary production, (iii) we have estimates of biomasses for the different species groups, some of them quite precise, some of them imprecise, and (iv) we have accurate estimates of landings.

Second, we consider this imperfect knowledge in terms of chance and necessity can this knowledge be used to learn about trophic flows between species groups? Can it be used to reconstruct historical changes in trophic interactions and to understand the nature of the controls in this ecosystem?

To achieve this, we go through the following steps: (i) express ecosystem dynamics as a mass conservation equation, i.e. changes in biomass are the results of gains minus losses in each species group, (ii) express constraints on the system state (biomasses) and dynamics (trophic flows) and define the corresponding set of possible system trajectories (series of trophic flows) as a polytope, (iii) sample the polytope, and (iv) explore the samples. Steps (ii) and (iii) respectively reflect necessity and chance.

A mass conservation equation

The ecological process driving the dynamics of the system is expressed as a mass conservation equation, as done in most trophic models of marine ecosystems (Walters *et al.*, 1997). This equation describes the relationship between changes of biomasses and trophic flows: the change in biomass of a species is equal to gains provided by feeding minus losses due to predation and somatic maintenance. Prey assimilation and predation functionally depend on trophic flows, biological losses and previous biomasses. Fishing is expressed as a predatory loss. By iterating these stock–flow relationships across species, we conclude that the history of biomasses is a function of biomasses at initial step and of the history of trophic flows and fishing. The mathematical formulation is provided in Appendix 2. The derivation of mass conservation equation and the values of its parameters are detailed in the Supplementary Material.

Constraints

Several kinds of constraints are considered: (i) trophic flows are positive; (ii) biomasses must be in a given range, determined by observations; (iii) the relative annual variations of biomasses are bounded (inertia); (iv) feeding per unit time and per unit biomass is bounded (satiation); (v) flows to fisheries equate reported catches; and (vi) flows from primary production to trophic groups are limited by primary production itself. These constraints are detailed in Appendix 2.

As all of these constraints are linear, they define a polytope that can be sampled according to principles and algorithms given in Appendix 1.

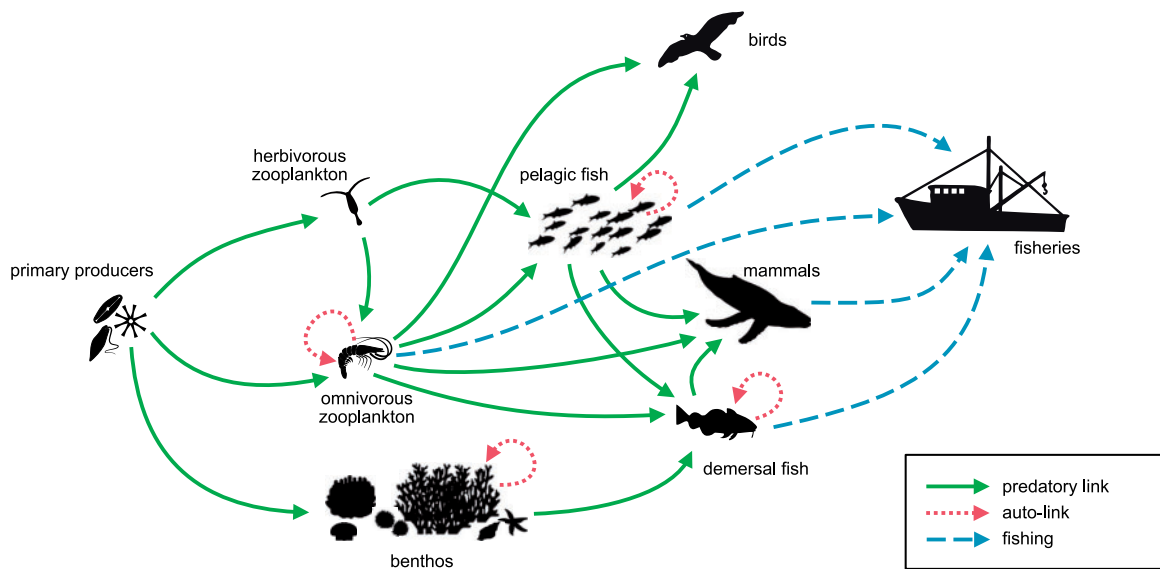


Figure 3. Simplified trophic structure of the Barents Sea ecosystem. Arrows indicate flow of biomass from prey to predators (plain, green), within the same trophic functional group (dotted, red) and towards fisheries (dashed, blue). The taxonomic composition of individual trophic groups is taken from Lindström *et al.* (2017) and detailed in the Supplementary Material.

An experiment

In what follows, we explore an original method for ecosystem modelling rather than develop a fully functional ecosystem assessment model for the Barents Sea. We present how the method can be implemented for a system of intermediate complexity and show that computation is feasible. We then discuss the results and argue why these could improve the relationship between modellers and other actors in fisheries. Such modelling approach is best developed as an iterative exercise. In the first iteration presented here, there have been no adjustments of the model structure or input parameters, which are all derived from Lindström *et al.* (2017).

Sampling and exploring samples

Having expressed linear constraints, we extract a sample of 200 000 trajectories in the resulting polytope, and we plot and analyse this sample.

Results 1: historical changes in biomasses

Before modelling begins, variations in biomasses of some groups are known with some degree of certainty, while for other groups the only information available is the range of plausible biomass for the entire time period (Figure 4). The CaN model improves this prior knowledge by providing a set of coherent reconstructions of the past biomasses for all species groups (Figure 5).

A first observation is that there are solutions to the modelling problem, that is: it is possible to find ecosystem dynamics that can satisfy the model structure, constraints, and input data, for all species groups simultaneously. A second observation is that the simulated trajectories do not fill uniformly the “space” of available biomass trajectories for all species biomass, that is: the spread of sampled biomass trajectories is less than the uncertainty in the input biomass data. In other words, we have reduced our uncertainties about the history of the system. A third observation is that the results raise a number of questions regarding the functioning of the Barents Sea ecosystem and the construction of the

model. For example, modelled biomasses for many species are on the high side of the range of input data. Does this reflect that biomasses in the Barents Sea are higher than generally assumed? Does this arise from poor choice of input parameter values (e.g. assimilation efficiencies)? Does this reflect structural incorrectness of the model, such as missing species groups (e.g. bacteria, gelatinous plankton)?

Results 2: historical changes in trophic flows

In the Barents Sea, quantitative information about trophic interactions is available only for a restricted set of predators (mainly commercial species such as Atlantic cod, *Gadus morhua*), and for selected seasons (Dolgov *et al.*, 2011). There is no information available about temporal changes in trophic flows between most species groups studied here. The second important output of the model is that it can fill this gap by providing a set of possible histories of these flows (Figure 6).

A first observation is that there is a high year-to-year variability for almost all flows (trajectories are rugged), and that uncertainty is high for all trophic flow (large spread of sampled flows in individual years). A second observation is that the uncertainty is lower for flows between groups for which there are prior observations (primary production, zooplankton, fishes). A third observation is that trophic flows towards demersal and pelagic fishes, seem to reflect changes in the biomass of these groups. This can be interpreted as top-down control and is investigated further in the following section. A fourth observation is that the ratios of flow to biomass are generally high. This is particularly the case for flows operating within individual species groups, i.e. self-feeding links. This suggests that the production-to-biomass ratio is generally very high and also that a lot of energy is dissipated within trophic groups. It is unclear, at this point if these flow estimates are realistic. The estimated annual flows towards demersal fishes are generally much higher (17 million tons on average) than expected from stomach sampling programmes (~2.2 million tons, Dolgov *et al.*, 2011). The same applies for pelagic fishes with

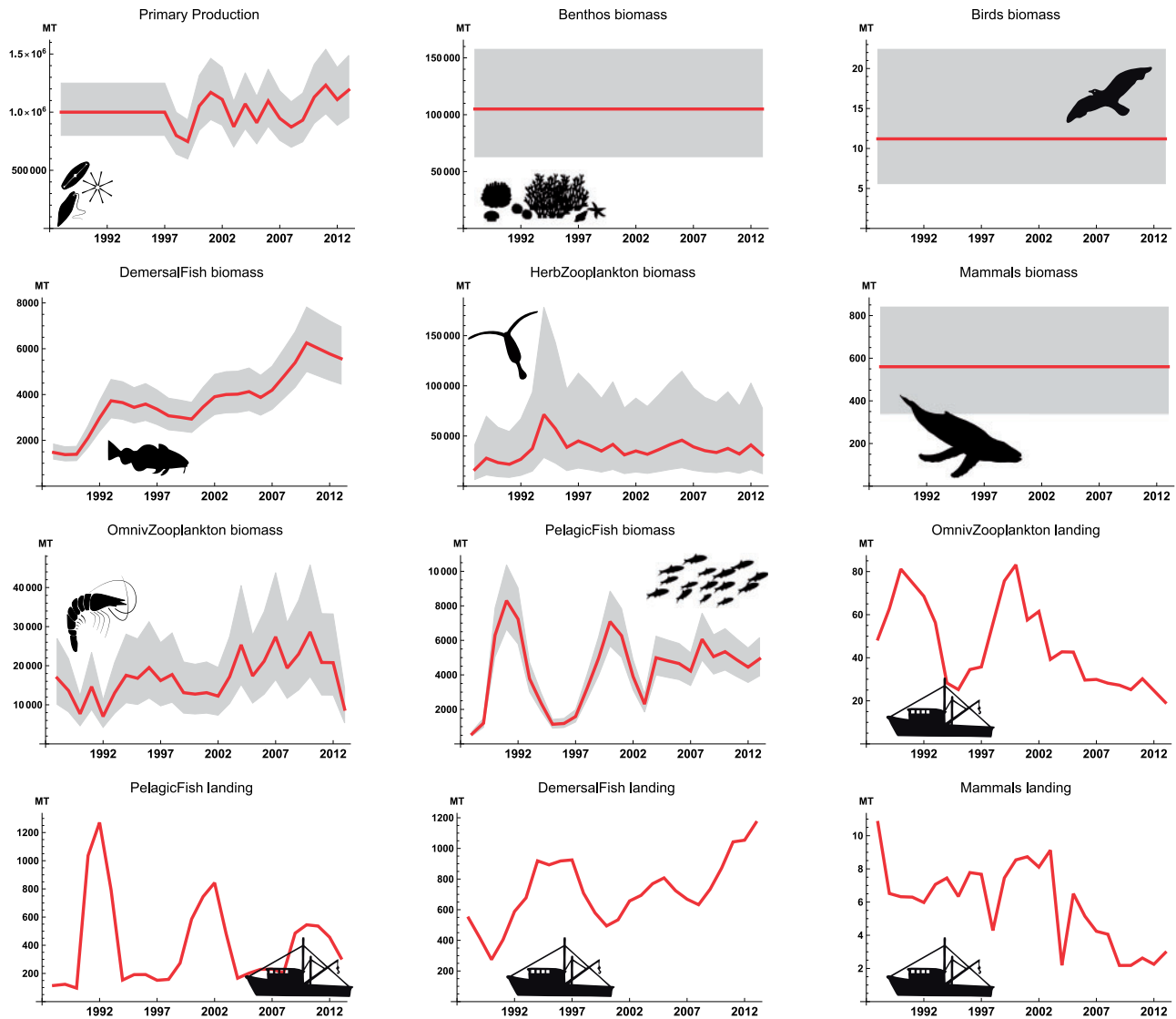


Figure 4. Primary production, estimated biomasses, and observed landings. Common unit is thousand metric tonnes. Thick red lines show the best estimates of biomass, production or landings reported in ICES (2017) or other relevant literature (see Supplementary Material). Grey ribbons illustrate the uncertainty around these estimates. Landings are assumed to be precisely known.

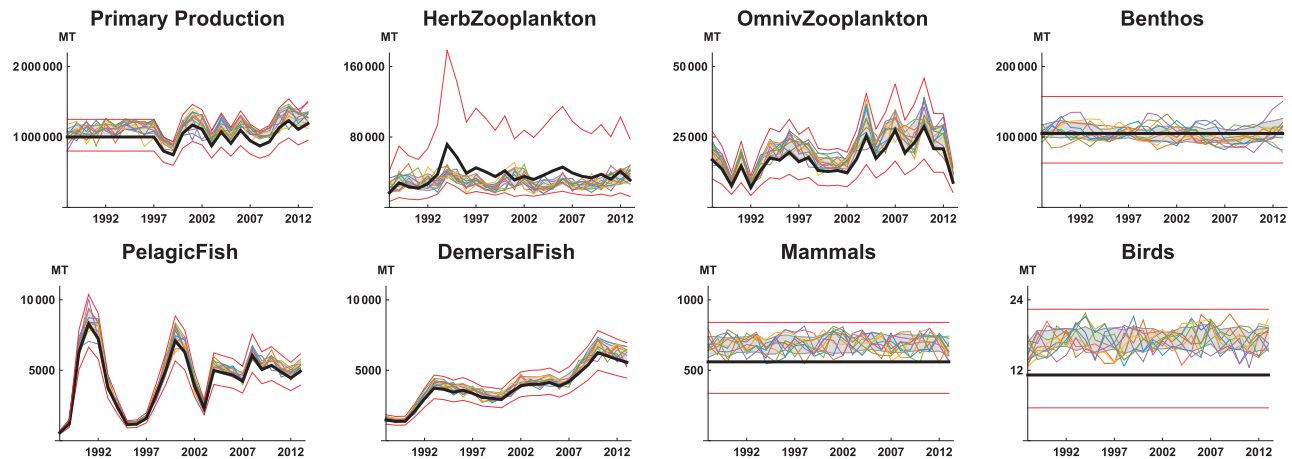


Figure 5. A representative set of sampled trajectories of biomasses. Thick (black) lines correspond to input trajectories shown in Figure 4. Thin upper and lower (red) lines indicate lower and upper biomass constraints. Grey ribbons encompass the 5–95% quantiles of all sampled trajectories. A subsample of ten trajectories is shown in thin (coloured) lines.

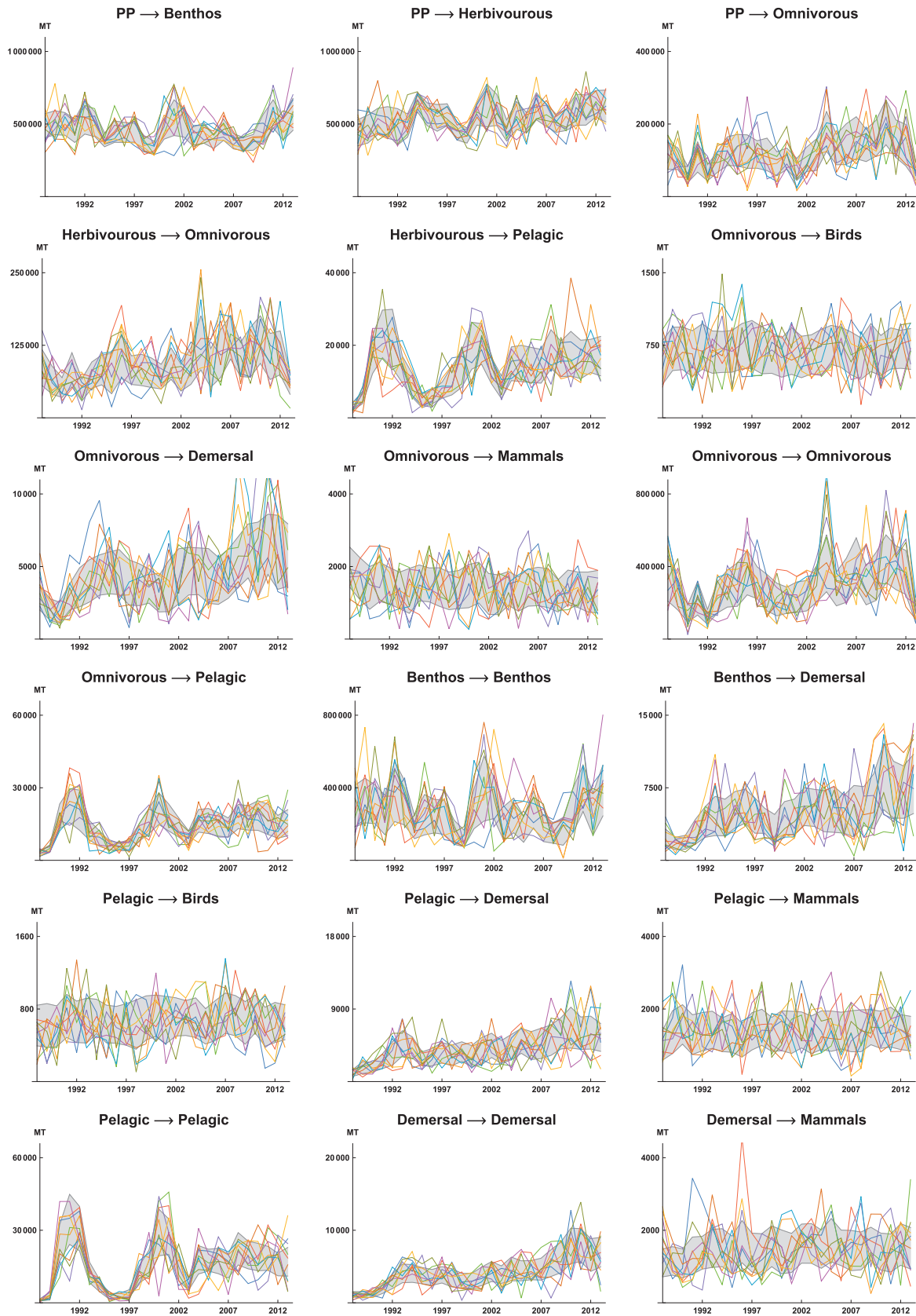


Figure 6. A representative set of sampled trajectories of trophic fluxes. Grey ribbons encompass the 5–95% quantiles of all sampled trajectories. A sub-sample of ten trajectories is shown in thin coloured lines.

an average of 43 million tons in the current model, vs. 29 million tons estimated from stomach sampling programmes (Dolgov *et al.*, 2011). Exposing the discrepancies between these estimates and discussing their origins will be an important step in the process of participatory modelling.

Results 3: trophic controls

Using model results on biomasses and trophic flows, it is possible to explore trophic controls between prey and predators. This can be done by looking at the correlation between individual prey–predator flows and the biomass of either the prey or the predator (Table 1). Positive and high correlation between the flow and prey suggest a bottom-up control. Positive and high correlation between flow and predator suggest a top-down control (Cury *et al.*, 2005a). This is observed, for example, for omnivorous zooplankton control on herbivorous zooplankton, or pelagic fish control on omnivorous zooplankton. High positive correlations in both directions suggest trophic interactions with feedbacks, as is the case for primary production and herbivorous zooplankton. High positive correlations for flows within a group (self-feeding link, e.g. pelagic fish or demersal fish) suggest that the group is mostly controlled by a high turnover rate and that the control by prey and predators may be of less importance.

Iterative model improvement

From this first attempt at modelling the dynamics of a simplified ecosystem, we can observe that uncertainties in model outputs reflect uncertainties in model inputs, i.e. model structure, input parameters, input data, and constraints. This can constitute the starting point of a deliberative exercise to investigate where model adjustments are necessary. Model structure assumptions, parameters, and data can be questioned in the following way: should the structure of the model (i.e. the structure of the food-web) be modified? Are the constraints sufficient and defined in an unambiguous manner? Are the input data reliable? Can the results of stomach sampling programmes be used to better constrain the model? Should one improve biomass estimates for benthos?, etc.

Table 1. Trophic flows (from prey to predator), their correlation with biomasses of prey and predator and the associated trophic controls.

Flow	Prey	Predator	Control
PrimaryProduction → Benthos	0.52	0.32	
PrimaryProduction → HerbZooplankton	0.59	0.83	Feedback
PrimaryProduction → OmnivZooplankton	0.14	0.62	Top-down
HerbZooplankton → OmnivZooplankton	−0.12	0.59	Top-down
HerbZooplankton → PelagicFish	0.01	0.70	Top-down
OmnivZooplankton → Birds	−0.01	0.32	
OmnivZooplankton → DemersalFish	0.26	0.53	Top-down
OmnivZooplankton → Mammals	−0.01	0.22	
OmnivZooplankton → OmnivZooplankton	0.64	0.64	Turnover
OmnivZooplankton → PelagicFish	−0.05	0.70	Top-down
Benthos → Benthos	0.02	0.02	
Benthos → DemersalFish	0.00	0.56	Top-down
PelagicFish → Birds	0.07	0.31	
PelagicFish → DemersalFish	0.17	0.60	Top-down
PelagicFish → Mammals	0.07	0.24	
PelagicFish → PelagicFish	0.82	0.82	Turnover
DemersalFish → DemersalFish	0.76	0.76	Turnover
DemersalFish → Mammals	0.14	0.23	

Asking these questions is a first step to refine the model and work towards less uncertain outputs. In a context of participatory modelling, this questioning should be conducted jointly by modellers and other actors and modelling-questioning cycle should be repeated to converge towards better-constructed, less-ambiguous, and less-uncertain models.

Discussion

Nonlinearity is at the heart of the chaos theory paradigm. With nonlinearity comes sensitivity to initial conditions, feedback loops, strange attractors, limited predictability, and high uncertainties. In fisheries research, the application of chaos theory has mainly been inspired by the work of Sugihara and May (1990) with further developments by Hsieh *et al.* (2005), Liu *et al.* (2012) by Ye *et al.* (2015) or Munch *et al.* (2018). These studies have shown that it is possible to use nonlinear chaotic system theory to improve the forecasting of complex ecological systems without requiring complicated mechanistic ecological models (DeAngelis and Yurek, 2015).

Here, we purposely stepped out of this track and, starting from the same initial point, we primarily focused on the relationship between different actors involved in fisheries management. We looked at how models could be used to reconcile scientists, managers, and other actors' perspectives about uncertainty and predictability of fisheries systems.

To illustrate the key points of the CaN approach, we have compared a conventional and a CaN approach to the logistic problem. While the conventional mathematical solution is elegant and easily accessible to modellers trained in the use of differential equations, it may appear a little too elegant to non-modellers who think that it does not correspond to what they are experiencing. For them, understanding that population size and growth are constrained might be more intuitive than manipulating differential equations. Non-modellers may also be sceptical towards the exact solution provided by the mathematical model and rather accept as more realistic premises that population size in the future (or even in the present) is uncertain. CaN modelling reflects this second attitude.

The CaN modelling approach we have sketched here consists of (i) defining the conceptual model of the system (here, the food-web and fisheries), (ii) identifying available observations (fisheries and biological time-series), (iii) defining important constraints and quantifying them (e.g. satiation), (iv) recognizing uncertainty in observations and lack of knowledge, and (v) jointly exploring the diversity of model outputs.

By applying the CaN approach to a trophic model of the Barents Sea, we attempted to present modelling choices in a simple and transparent way. These choices include modelling principles (such as a mass conservation equation that reflects transfer of energy in the food-web), model assumptions, lack of knowledge, or observation uncertainties. We presented here a specific application of CaN to the Barents Sea but these principles are general enough to be applied in other areas and for building models with different structure and objectives.

CaN modelling is closely related to the viability theory (Aubin *et al.*, 2011), from which it borrows the emphasis on chance and necessity. A common key point between viability theory and CaN modelling has to be underlined: both consider the set of possible trajectories (“histories”) of a system as a way to deal with the question of indeterminism. Viability theory goes far beyond the

example developed in this paper and applies the ideas of CaN to several research fields (evolution, robotic, finance, etc.).

In CaN modelling, trajectories are said possible if they agree with physical laws, ecological theories (e.g. life history theory or metabolic theory of ecology) and are compatible with observations. When CaN models are constrained by observed historical trajectories of the system, CaN modelling is part of inverse modelling (Vézina and Piatt, 1988).

Outputs of CaN models are comparable to outputs from ensemble models, without the cost of running a collection of models. Ensemble modelling has been advocated as a strategy to embrace structural and parameter uncertainties in ecological models and to allow for different ways of representing reality (Spence *et al.*, 2017). Because CaN does not rely on strong assumptions regarding functional relationships (trophic functional relationships in the present case), it encompasses a range of dynamics that could be produced by multiple deterministic models relying on different assumptions.

An interesting feature of CaN models is that more knowledge about the ecological system almost always lead to less uncertainties in the model outputs. Since ecological knowledge is expressed primarily in terms of constraints, increased knowledge translates into a more constrained system, that is a reduced space for the model dynamics to operate.

Modelling assumptions often remain unchallenged because they are drowned in technical narratives. For example, the definition of functional groups, their number and the data available to parameterize them in a model are most often left to modellers. When choosing these functional groups scientists can be constrained by data availability and computing time, or may simply borrow from earlier models. When other actors have different representations of the groups interacting in the ecosystem, can these be shared through joint modelling exercises? Equations can also be very difficult to communicate outside the scientific community. The mass conservation equation used in this example is relatively simple but more importantly, it can easily be presented and interpreted in plain language (all coefficients have a biological meaning). Observation uncertainty and lack of knowledge lead to uncertainty in the model outputs. After each modelling step, patterns and uncertainties can be summarized and discussed by all actors. Each of the above points is critical for the model outputs to be understood and shared by different actors. They can constitute the starting point for constructive discussions among scientists, managers, and other actors. Based on past experience, one can anticipate that the proposed method will promote better conditions for participative modelling. At this stage, the proposed CaN modelling approach has not been tested directly with stakeholders and this remains to be done, to move from concept to proof-of-concept. The ICES IEA groups provide an ideal platform for such test in an operational context.

In participatory modelling (Röckmann *et al.*, 2012), the first step usually consists in reaching an agreement on a common objective. This objective is then translated into a corresponding objective function in an optimization programme. Because of the correspondence between the management objective and the objective function, it can be problematic for various actors to challenge the optimization output, even when they do not have a clear understanding of the how the underlying model functions. Strategies can be adopted by modellers and stakeholders alike to favour an optimization criteria that serves best their particular needs (Hämäläinen, 2015). The approach proposed here differs

from the above by recognizing that different actors have different perspectives and preferences and may not share a common objective. For example, some may favour conservation of resource while other promote maximization of income; some may favour one type of resource over another, etc. These different positions can lead to different interpretation of the model results. As CaN provides multiple outputs, it is possible for different actors to highlight different fisheries-ecosystem trajectories that best illustrate their personal view of the system or best serve their needs. Each actor can use their preferred trajectories to identify a sequence of events and build an associated narrative. Once this is achieved, actors can confront their interpretations of model results. In this way, every actor learns from the model, while considering the disparity of the objectives and interpretations of all others actors. Instead of the modelling results and their interpretation—being delivered from the expert modellers to the other actors, this provides a framework for the appropriation of the modelling results by all actors.

The proposed CaN modelling approach combines simplicity and the recognition of irreducible uncertainties. This is in line with Saltelli and Funtowicz (2014), and Manski (n.d.) who advocate for the use of simple models and efficient communication of scientific uncertainty [although convincing modellers to engage into transparent and participatory modelling remains a challenge (At this point, we may recall one of the well-known Nasreddin's short stories. Nasreddin is a well-respected authority. His wife remarks that the gap between rich and poor in the village is becoming intolerable and she asks Nasreddin to convince people that they must share wealth. Nasreddin leave his house in the morning to talk to the people in the village. At the end of a long day, he returns home exhausted and says to his wife: It was difficult. I only half succeeded. I convinced the poor.)]. Our proposition is also in line with the position taken by Stirling (2010) to “keep it complex” by acknowledging knowledge gaps and uncertainties throughout the expert process. CaN offers a way to deliver plural and conditional advice, rather than forcing consensus and producing definitive science-based advice that may simply reflect the ignorance of fundamental uncertainties about the natural system during the modelling process.

Conclusion

Our proposition is that CaN modelling constitutes a useful contribution to the ecosystem modelling toolkit required to support EBFM. CaN modelling tool strives to support communication and deliberation among scientists, decision makers, and other actors. It is a way to explore together datasets (the example here) or to explore the possible futures of a natural system. It relies on the concepts of chance and necessity that should be easy to grasp by all actors and on relatively light modelling tools (short computer code that can be implemented in various programming languages without requiring heavy computing power). CaN models are simple, transparent, explicit about knowns and unknowns and the interpretation of the results is simple enough to be used in a context of participatory management. Three decades after Smith (1990), CaN can be a practical step to realize her proposition that chaos theory could reconcile scientists and non-scientists.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Appendices

Appendix 1: A short introduction to polytopes and polytope sampling

Our proposition relies strongly upon polytope sampling, as a tool to explore and communicate uncertainty. As exemplified in Figure 1, polytopes are related to linear constraints. In a general setting, a convex polytope \mathcal{P} is defined by linear inequalities: $\mathcal{P} = \{X \in \mathbb{R}^n | A.X \leq B\}$, where $A \in \mathbb{R}^{nc \times n}$ is a matrix and $B \in \mathbb{R}^{nc}$ vector, nc being the number of constraints. Despite their apparent simplicity, polytopes have very interesting mathematical properties, have been characterized by significant theorems and are still the object of an intense theoretical research (Brondsted, 2012).

Sampling a polytope consists in finding a representative set of its points. The algorithmic issue is how to proceed when the ambient space is high dimensional (several hundreds of dimensions) and the number of constraints is very high. Polytope sampling has many applications, for example in the computation of steady state of metabolic equations (De Martino *et al.*, 2015). While in most applications, it is the state of the system that is explored with polytope sampling, in the present model, it is the set of system trajectories that is sampled.

Several algorithms exist to sample polytopes; a simple and nevertheless efficient method is the Hit and Run algorithm (Kannan and Narayanan, 2012). The sample is the result of a walk inside the polytope. The steps of the algorithm consist in: (i) Set, at step $t = 0$, the current point to be a randomly drawn point in the interior of the polytope X_0 , (ii) (a) from the current step X_t , randomly draw a direction in the underlying space; and (b) randomly draw a point on the interval that is inside the polytope and on the line passing by the current point and is according to the selected direction; (c) set the current point X_t being this point, set $t := t + 1$ and (d) go to (a). This algorithm becomes less efficient when there are large differences in the size of the polytope along the different dimensions. The walk can stay very long in some sharp vertices.

In this paper, we use a variant of this algorithm, the Dikin algorithm (Kannan and Narayanan, 2012; Sachdeva and Vishnoi, 2016; Chen *et al.*, 2018), which allows to deal with this issue, and results in a Metropolis–Hastings walk. It is a Monte Carlo

Markov chain algorithm and its mixing properties can be theoretically studied (Chen *et al.*, 2018). It relies on the idea of a barrier function, a function that becomes infinite on the faces of the polytope. If the polytope is defined by inequalities: $\sum_j m_{c_j} x_j \geq b_c$, one usually uses as a barrier function $L(x) = -\sum_c \log(\sum_j m_{c_j} x_j - b_c)$ and the ellipsoid defined by the barrier function at a point X depends on its second derivatives: if $H(X)$ is the Hessian of L at X : $H(X)_{ij} = \partial^2 L / \partial x_i \partial x_j(X)$, then the ellipsoid is defined as the set of points Z such that $t(Z - X).H(X).(Z - X) \leq 1$. The algorithm, illustrated in Figure A1, is the following. (i) Set, at step $t = 0$, the current point to be a randomly drawn point in the interior of the polytope X_0 , (ii) (a) from the current step X_t , randomly draw a direction D according to the ellipsoid defined by the barrier function at X_t , (b) randomly draw a point Y inside the polytope on the line starting from X_t with direction D , (c) compute the volumes of ellipsoids at X_t and Y : $v(X_t)$, $v(Y)$, and (d) randomly draw $p \in [0, 1]$; if $p \leq v(X_t)/v(Y)$, let $X_{t+1} = X_t$, else $X_{t+1} = Y$; set $t := t + 1$ and (d) go to (a).

Appendix 2: Constraints and polyhedron sampling for trophic systems

Method

The principles of CaN modelling are: (i) there is a mass conservation equation: biomasses linearly depend on trophic flows, (ii) constraints on biomasses and flows can all be expressed linearly, which results in linear constraints on flows trajectories, and (iii) the set of possible flows trajectories constitutes a polytope. This can be expressed in matrix notation.

In what follows, we provide details about the definition of linear constraints on trajectories, given that the system is described in discrete time. Using linear algebra, we formulate relationships in terms of trajectories (each trajectory is an element in $\mathbb{R}^{n \times T}$, T being the number of time steps).

Mass conservation principle

The principle of a mass conservation equation (Vasconcellos *et al.*, 1997) is to relate changes in biomasses to trophic flows, trophic losses and export or import of biomass. Here we consider a simplified situation, without import or export of biomass.

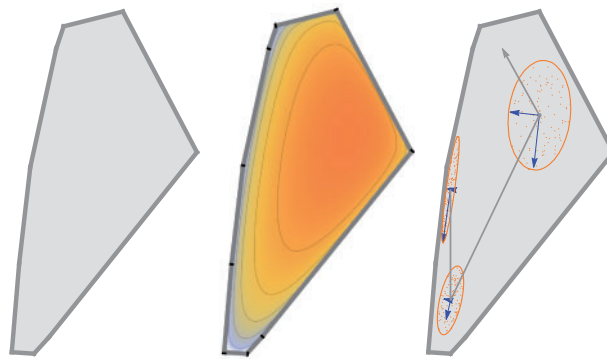


Figure A1. Principles of the Dikin sampling algorithm. Left: a polytope. Middle: density plot of the barrier function. Right: a walk among three points; at each step, the random direction is selected according to the directions of the ellipsoids at current point.

We consider a trophic system with E species. Fishery is represented as a predatory species. Biomass of species i at time t is noted $B_{i,t}$. In this system, there are P trophic flows. Each flow f has an origin $o(f)$, the prey, and an end $e(f)$, the predator. Flows during time interval $[t, t + 1]$ are noted $F_{f,t}$. In Section 2.1 of the [Supplementary Material](#), we show how to derive a mass conservation equation, using a previous modelling attempt for the Barents Sea food-web ([Lindström et al., 2017](#)):

$$B_{i,t+1} - B_{i,t} = \sum_f N_{if} F_{f,t} - H_i B_{i,t}. \tag{A1}$$

This is a linear equation:

$$\mathbf{B}_{t+1} = (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{B}_t + \mathbf{N} \cdot \mathbf{F}_t, \tag{A2}$$

involving: (i) the vector of biomasses at year t , $\mathbf{B}_t = (B_{i,t}) \in \mathbb{R}^E$; (ii) the vector of trophic flows at year t , $\mathbf{F}_t = (F_{f,t}) \in \mathbb{R}^P$; (iii) $\mathbf{H} \in \mathbb{R}^{E \times E}$, the matrix with diagonal terms H_i ; (iv) $\mathbf{I}_E \in \mathbb{R}^{E \times E}$, the identity matrix; and (v) $\mathbf{N} = (N_{if}) \in \mathbb{R}^{E \times P}$, a matrix related to the impact of flows on biomasses.

Matrix formulation of dynamics

Starting with an initial state of biomass \mathbf{B}_0 , we iterate Equation (A2):

$$\mathbf{B}_1 = (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{B}_0 + \mathbf{N} \cdot \mathbf{F}_0, \tag{A3}$$

$$\mathbf{B}_2 = (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{B}_1 + \mathbf{N} \cdot \mathbf{F}_1, \tag{A4}$$

$$= (\mathbf{I}_E - \mathbf{H})^2 \cdot \mathbf{B}_0 + (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{N} \cdot \mathbf{F}_0 + \mathbf{N} \cdot \mathbf{F}_1, \tag{A5}$$

$$\dots, \tag{A6}$$

$$\mathbf{B}_t = (\mathbf{I}_E - \mathbf{H})^t \cdot \mathbf{B}_0 + \sum_{u=0}^{t-1} (\mathbf{I}_E - \mathbf{H})^{t-u-1} \cdot \mathbf{N} \cdot \mathbf{F}_u. \tag{A7}$$

We collect all states in a same vector. We put:

$$\mathbf{F} = (\mathbf{F}_0, \mathbf{F}_1, \mathbf{F}_2, \dots, \mathbf{F}_{T-1}) \in \mathbb{R}^{P \times T}, \tag{A8}$$

$$\mathbf{B} = (\mathbf{B}_1, \mathbf{B}_2, \dots, \mathbf{B}_T) \in \mathbb{R}^{E \times T}. \tag{A9}$$

We have a linear relationship:

$$\mathbf{B} = \mathbf{L} \cdot \mathbf{F} + \mathbf{M} \tag{A10}$$

with:

$$\mathbf{L} = \begin{pmatrix} \mathbf{N} & 0 & 0 & \dots & 0 \\ (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{N} & \mathbf{N} & 0 & \dots & 0 \\ (\mathbf{I}_E - \mathbf{H})^2 \cdot \mathbf{N} & (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{N} & \mathbf{N} & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ (\mathbf{I}_E - \mathbf{H})^{T-1} \cdot \mathbf{N} & (\mathbf{I}_E - \mathbf{H})^{T-2} \cdot \mathbf{N} & (\mathbf{I}_E - \mathbf{H})^{T-3} \cdot \mathbf{N} & \dots & \mathbf{N} \end{pmatrix}, \tag{A11}$$

$$\mathbf{M} = \begin{pmatrix} (\mathbf{I}_E - \mathbf{H}) \cdot \mathbf{B}_0 \\ (\mathbf{I}_E - \mathbf{H})^2 \cdot \mathbf{B}_0 \\ (\mathbf{I}_E - \mathbf{H})^3 \cdot \mathbf{B}_0 \\ \dots \\ (\mathbf{I}_E - \mathbf{H})^T \cdot \mathbf{B}_0 \end{pmatrix}. \tag{A12}$$

This is a single linear equation relating the trajectory of biomasses to the trajectory of flows.

Matrix formulation of constraints

The constraints we have introduced in Section 5.3.2 are linear functions of the vector of flows trajectories \mathbf{F} .

1. Trophic flows are positive. Biomasses are positive. Using Equation (A10), we get:

$$\begin{aligned} \mathbf{F} &\geq 0 \\ \mathbf{L} \cdot \mathbf{F} &\geq -\mathbf{M}. \end{aligned} \tag{A13}$$

2. Some biomasses $B_{i,t}$ must be in a given range, determined by observations $B_{i,t}^O$; see [Figure 4](#). We have: $B_{i,t} \in [\lambda_i B_{i,t}^O, \nu_i B_{i,t}^O]$. Using Equation (A10), we get matrix equations:

$$-\mathbf{L} \cdot \mathbf{F} \geq -\nu \mathbf{B}^O + \mathbf{M}, \tag{A14}$$

$$\mathbf{L} \cdot \mathbf{F} \geq \lambda \mathbf{B}^O - \mathbf{M}. \tag{A15}$$

3. The relative annual variation of biomasses is bounded: $e^{-\rho_i} B_{i,t} \leq B_{i,t+1} \leq e^{\rho_i} B_{i,t}$. In matrix terms:

$$\begin{pmatrix} -\mathbf{I}_E & 0 & 0 & \dots & 0 \\ \mathbf{e}^{\rho} & -\mathbf{I}_E & 0 & \dots & 0 \\ 0 & \mathbf{e}^{\rho} & -\mathbf{I}_E & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & -\mathbf{I}_E \\ \mathbf{I}_E & 0 & 0 & \dots & 0 \\ -\mathbf{e}^{-\rho} & \mathbf{I}_E & 0 & \dots & 0 \\ 0 & -\mathbf{e}^{-\rho} & \mathbf{I}_E & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & \mathbf{I}_E \end{pmatrix} \cdot \begin{pmatrix} \mathbf{B}_1 \\ \mathbf{B}_2 \\ \mathbf{B}_3 \\ \dots \\ \mathbf{B}_T \end{pmatrix} \geq \begin{pmatrix} -\mathbf{e}^{\rho} \mathbf{B}_0 \\ 0 \\ 0 \\ \dots \\ 0 \\ \mathbf{e}^{-\rho} \mathbf{B}_0 \\ 0 \\ 0 \\ \dots \\ 0 \end{pmatrix}.$$

That is, in matrix notation:

$$\mathbf{D} \cdot \mathbf{B} \geq \mathbf{B}_0^{\rho}. \tag{A16}$$

Using [Equation \(A10\)](#), it comes:

$$\mathbf{D} \cdot \mathbf{L} \cdot \mathbf{F} \geq \mathbf{B}_0^{\rho} - \mathbf{D} \cdot \mathbf{M}. \tag{A17}$$

4. Inflow is limited by biomass according to a satiation principle. Let $I_{i,t}$ be the sum of incoming flows to species i . Then: $I_{i,t} \leq \sigma_i B_{i,t}$. We denote $S: \mathbb{R}^{P \times T} \rightarrow \mathbb{R}^{E \times T}$ the incidence matrix: $S(S_{ft,kt}^i)$ is 1 if $o(f) = i$ and $t = t'$, else is 0) and σ be the diagonal matrix obtained with T repetitions of $(\sigma_1, \sigma_2, \dots, \sigma_e)$. We express satiation principle as:

$$\mathbf{S} \cdot \mathbf{F} \leq \sigma \cdot \mathbf{B}. \tag{A18}$$

Using Equation (A10), it comes:

$$(\boldsymbol{\sigma} \cdot \mathbf{L} - \mathbf{S}) \cdot \mathbf{F} \geq \boldsymbol{\sigma} \cdot \mathbf{M}. \quad (\text{A19})$$

5. Real landings are equal to their observed values; we have: $F_{f,t} = F_{f,t}^O$ if f is a landing (see Figure 4). \mathbf{Q} being the restriction of the whole set of flows to the set of landings, we get a matrix equation:

$$\mathbf{Q} \cdot \mathbf{F} = \mathbf{Q} \cdot \mathbf{F}^O. \quad (\text{A20})$$

6. Flows from primary production to herbivory plankton and benthos are limited by primary production itself. We have estimates of primary production: $P^O(t)$. The constraint is:

$$\lambda_p P^O(t) \leq \sum_{f|o(f)=P} F_f(t) \leq \mu_p P^O(t)$$

\mathbf{R} being the restriction of the whole set of flows to the set of flows from matrix production, we get a matrix equation:

$$\mathbf{R} \cdot \mathbf{F} \geq \lambda_p \mathbf{P}^O, \quad (\text{A21})$$

$$-\mathbf{R} \cdot \mathbf{F} \geq -\mu_p \mathbf{P}^O. \quad (\text{A22})$$

Putting altogether previous inequalities, all constraints result in multiple linear inequalities involving vector \mathbf{F} , which get be expressed in the form:

$$\mathbf{A} \cdot \mathbf{F} \geq \mathbf{b}. \quad (\text{A23})$$

Parameterization for the Barents Sea

The parameters we use for building a CaN model come from a previous modelling experiment of the Barents Sea by Lindström *et al.* (2017). In the [Supplementary Material](#), we provide:

- (1) The species composition of trophic groups (Section 1.1).
- (2) The estimated values of biomass and landings for the 1988–2015 period (Section 1.2).
- (3) The parameters used in the Lindström's modelling experiment (Section 1.3).
- (4) The derivation of the mass conservation equation (Section 2.1). The parameters of the mass conservation equation appear in Table 4.
- (5) The parameters of the constraints equations, their values and the assumptions for using these values (Section 2.2).

The complete set of parameters is reported in Tables 4 and 5. Given that this is a relatively small set of parameters, we can speak of a simple model.