

**A Stochastic Dynamic Foodweb model for the Barents Sea ecosystem**

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Developing marine ecosystem models is inherently difficult because of the diversity and complexity of ecological processes to account for, the presence of non-linearities, and the broad range of spatial and temporal scales to cover. In general, the fundamental ecosystem processes involve several unknown components and parameters. Here, we adopt a parsimonious approach to model the dynamics of the Barents Sea ecosystem. By using a dynamic stochastic food web model (DSF), constrained by mass-balance, inertia and satiation, we simulate the foodweb dynamics of a simplified Barents Sea ecosystem. The aim is to generate realistic second order properties of the Barents Sea food web, such as temporal autocorrelation, functional responses, integrated diet fractions and covariation between tropho-species/groups. The tropho-species/groups included in the model are mammals, demersal and pelagic fish, benthos, euphausiids, copepods and phytoplankton. The model requires initial biomass values for each species and four species-specific parameters (satiation, inertia, metabolic efficiency and ecotrophic efficiency). These were either taken from literature or derived from existing models. Preliminary results from 100 years simulation show that the DSF model generates realistic species biomass trajectories, including pseudo cycles, and consumer-resource relationships. Interestingly, despite the fact that fluxes of biomass between trophospecies are modelled as being random - i.e., the consumption rates as a function of prey biomass are random - functional response relationships of some trophospecies emerge.

## Introduction

Natural living systems are characterised by a high level of complexity, which results from the diversity of biological components at many levels of organisation (molecules, cells, organs, individuals, species, communities) and from the diversity of possible interaction types (physical, chemical, trophic, behavioural, cognitive). In addition, many biological interactions are non-linear and biological systems display a remarkable ability to constantly adapt and reconfigure themselves. In addition, stochastic phenomena play an important role in real world physical and biological systems, and to the role of chance in shaping the dynamics of such systems. Natural systems are therefore complex and adaptive systems partially controlled by stochastic phenomena, which makes them difficult to analyse and even harder to predict.

The objective of this work is to construct a food web model which provides a realistic representation of food web dynamics based on a minimal set of constraints and stochastic trophic interactions. To our knowledge, only one example of such approach has been proposed by Mullon et al. (2009). Built on the principles of the model outlined by Mullon, we establish a set of equations which describe the transfer of mass within a foodweb given general stochasticity in trophic fluxes combined with constraints on species biomasses and fluxes. We term this model a stochastic dynamic foodweb model: SDF.

### The Stochastic Dynamic Foodweb model (SDF)

The purpose of SDF is to simulate food web dynamics based on a minimal set of constraints and a set of trophic interactions. The fundamental principle is that the flows of biomass between predators and preys are drawn randomly and trophic flows satisfy an ensemble of constraints that are set by physics, physiology and life-history. Physical constraints are set by the law of conservation of mass, i.e. the total biomass in the food web is maintained constant if the system is isolated (i.e. when there is no import, loss or export of biomass). Thus, fluctuations of total biomass in the food web are solely the result of the balance between import of biomass into the food web (e.g. new production) and export of biomass outside the food web (e.g. fishing and metabolic losses). The SDF share similarities with other mass-balanced models such as Ecopath with Ecosim (Ewe, Polovina, 1984, Christensen and Walters, 2004). Physiological constraints are set by the maximum rates of ingestion of individual organisms in a given population. The upper limit of ingestion rate by an individual species (i.e., the maximum *consumption over biomass* ratio) is termed *satiation*. In addition, the maximum growth rate of a population is limited, as a function of the species' lifespan, with population of short lived species growing potentially faster than populations of long-lived species. The relationship between life span and population growth rate has both theoretical and empirical support (Dulvy et al., 2004, Hoenig, 1983). The minimum biomass attainable by a population is set to be greater than zero and corresponds to a 'refuge' biomass below which the species is no longer accessible to predators. This is ecologically consistent with the existence of relict populations at low biomass.

The result is a mass balance model in which 1) trophic flows are drawn randomly, and for all species: 2) ingestion does not exceed satiation, 3) biomass increase does not exceed maximum growth rate and 4) biomass does not fall below the refuge level. The model principles are inspired from the work of Mullon *et al.* (2009). We present below the mathematical formulation of the model master equation and constraints as well as the definition of the model parameters and how these are related to ecologically meaningful quantities.

The state of the food-web at time  $t$  is described by the biomasses of the individual species ( $B_{i,t}$ ), the flows between them ( $F_{ij,t}$  = flow from species  $i$  to species  $j$  at time  $t$ ) and the eventual import ( $I_{i,t}$ ) or export of biomass ( $E_{i,t}$ ). For each time step, the new biomasses ( $B_{i,t}$ ) are calculated based on the following equation (1):

$$B_{i,t} = \psi_i(B_{i,t-1} + \gamma_i \sum_j F_{ji,t}) - \sum_j F_{ij,t} + I_{i,t} - E_{i,t} \quad (1)$$

The term  $\sum_j F_{ji,t}$  represents the total biomass of prey species consumed by species  $i$ ; the term  $\sum_j F_{ij,t}$  represents the total biomass of species  $i$  consumed by its predators.

The trophic flows are not defined by a deterministic equation but rather are drawn randomly, given that they satisfy the following set of constraints:

- flows are possible (i.e. species  $j$  is a predator of species  $i$ )
- flows are positive:  $F_{ij,t} \geq 0$
- resulting biomasses are not below 'refuge level':  $B_{i,t} \geq \beta_i$
- new biomass is limited by inertia:  $\mu_i B_{i,t-1} + I_{i,t} - E_{i,t} \leq B_{i,t} \leq \nu_i B_{i,t-1} + I_{i,t} - E_{i,t}$
- the total food intake of species  $i$  is limited by satiation:  $\sum_j F_{ji,t} \leq \sigma_i B_{i,t-1}$

At each time step a vector of random flows ( $\vec{F}$ ), which satisfies all the above constraints, is drawn.

- assimilation efficiency ( $\gamma$ ): the proportion of biomass ingested by species  $i$  which contributes to increase in biomass of species  $i$  ( $0 < \gamma < 1$ ).
- ecotrophic efficiency ( $\psi$ ): the proportion of a species biomass that is retained within the modelled food web. The quantity  $(1-\psi)$  represent the proportion of species biomass which is lost outside the modelled food web due to predation by species not explicitly included in the model, sedimentation, or other loss processes ( $0 < \psi < 1$ ),
- satiation ( $\sigma$ ): the maximum food consumption rate by species  $i$ , expressed as a proportion of the current biomass of species  $i$  ( $\sigma > 0$ ),
- inertia ( $\nu/\mu$ ): the maximum rates of biomass increase ( $\nu$ ) and decrease ( $\mu$ ) of species  $i$ .

Ecotrophic efficiency ( $\psi$ ), the proportion of a species biomass that is retained within the modeled food web, is both foodweb- and species-specific. The parameter value can vary from '0' (the biomass of species  $i$  is entirely removed from the food web at each time step) to '1' (the biomass of species  $i$  is fully retained within the food web, either by remaining in species  $i$  or by being transferred to predator species). Values of  $\psi$  can be established from expert knowledge or 'borrowed' from existing food web models such as Ecopath models in which ecotrophic efficiencies (usually termed  $EE$ 's) have been reported (e.g. Shannon et al., 2003). As a rule of thumb,  $\psi$  can be linked to mortality rate by assuming that the proportion of biomass lost outside of the model system cannot exceed twice the loss expressed in conventional population dynamics models:  $0 \leq \psi \leq (1 - e^{-2Z})$ , where  $Z$  is the population mortality coefficient.

Satiation ( $\sigma$ ), which expresses the maximum food consumption per unit biomass of predators, can be derived from experimental studies or bioenergetic model results. It is common in the literature to report mean consumption ( $Q$ ) over biomass ( $B$ ) ratio and as a first approximation satiation can be estimated to twice this value:  $\sigma = 2(Q/B)$ .

Inertia ( $\nu$ ) is defined as the maximum population growth rate of a species. This can be approximated as twice the average population mortality rate (Norse et al., 2012). Natural mortality rates may not be readily available but for many taxonomic groups, this can be derived from data on species longevity. Hoenig (1983) provides empirical relationships between longevity and mortality rates for marine species. Using Hoenig's equation for fish leads to the following inertia estimates:  $\nu = 2e^{(1.46 - \log(L_s))}$ , where  $L_s$  is the longevity of the species, in years.

Assimilation efficiency ( $\gamma$ ), the proportion of prey consumed that contributes to biomass increase, can be derived from existing experimental or modelling work such as Dynamic Energy Budget (DEB) models (Kooijman, 2010). Alternatively, this can be approximated from Ecopath models, by the ratio of production over consumption ( $P/Q$ ).

The above formulation provides an update of the original formulation by Mullon et al (2009). In particular the main equation (1) which relates biomass at time  $t$  to biomass at time  $t-1$  has a solution even when ecotrophic efficiency is equal to one, which is the case when all the predators of a species are included in the modelled foodweb. The model parameters can all be interpreted biologically and can be estimated from already existing foodweb models (e.g. EwE) or dedicated empirical studies.

### Application to the Barents Sea ecosystem

We applied the SDF concept to a simplified foodweb of the Barents Sea. The model includes the following seven tropho-species: phytoplankton, copepods, euphausiids, benthic compartment, pelagic fishes, demersal fishes and marine mammals. These are connected through 14 trophic links which include cannibalistic links for pelagic and demersal fishes. The food web structure is illustrated in Figure 1.

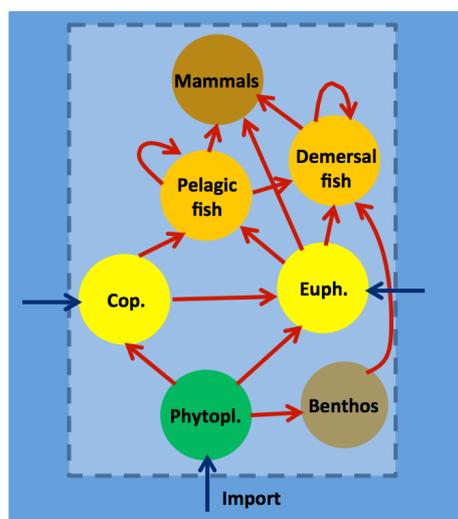


Figure 1. The foodweb topology used in the Barents Sea stochastic dynamic foodweb model. Each trophospecies is represented by a disc and trophic interactions are symbolised with red arrows. Import from outside the modelled system is symbolised with black arrows. The model boundaries are indicated by a dotted line

The model was run with constant import of phytoplankton, which served as a proxy for new primary production. In addition, import of copepods and euphausiids were included to represent the flow of individuals from the Norwegian Sea into the Barents Sea. Export was set to zero for all tropho-species.

The model parameter and starting values are given in Table 1, below:

*Table 1. the list of trophospecies and their associated parameter values, used in the SDF simulation of the Barents Sea ecosystem.*

	Phytoplankton	Copepods	Euphausiids	Benthos	Pelagic fishes	Demersal fishes	Marine mammals
Start biomass (t.km <sup>-2</sup> )	200	7	7	5	3	2	0.5
Assimilation efficiency	1.00	0.36	0.40	0.20	0.22	0.36	0.004
Ecotrophic efficiency	0.70	0.60	0.50	0.50	0.95	0.90	0.96
Lifespan (y)	0.06	1	2	40	3	15	30
Satiation	54	50	40	25	25	5	25
Import (t.km <sup>-2</sup> )	200	1	0.5	-	-	-	-
Export (t.km <sup>-2</sup> )	-	-	-	-	-	-	-

## Results and discussion

Because the SDF model is stochastic, each individual simulation provides a unique trajectory of the ecosystem. Analysing an individual trajectory is therefore of little interest but can be shown for illustrative purpose. Here, we follow a patterns orientated approach (Grimm et al., 2005), which primarily focuses on the statistical and emerging properties of the model.

We present below a summary of the model output based on:

- selected time series of biomass
- the dominant temporal frequency of individual trophospecies (pseudo-cycles),
- the statistical distributions of trophospecies biomasses
- the proportion of various preys taken by individual predators (an equivalent to stomach content integrated over the whole simulation period),
- the biomass, consumption and production for the different trophospecies,
- the trophic functional relationships for each prey-predator couple.

The temporal dynamics of the tropho-species during a 100y simulation, illustrated in Figure 2, shows that the DSF generate realistic temporal patterns, i.e. the frequency and amplitude of the biomass observed during this 100y run are similar to real data. For example, two recent studies (Johannesen et al., 2012b, Eriksen and Dalpadado, 2011) suggests that that biomass of euphausiids, pelagic and demersal fishes varied between 1-20, 0.75-6 and 0.9-2.9 t/km<sup>2</sup> respectively whereas in our simulations the biomass ranged between 0.5-27, 0.05-2.2 and 0.4-5.4 t/km<sup>2</sup>.

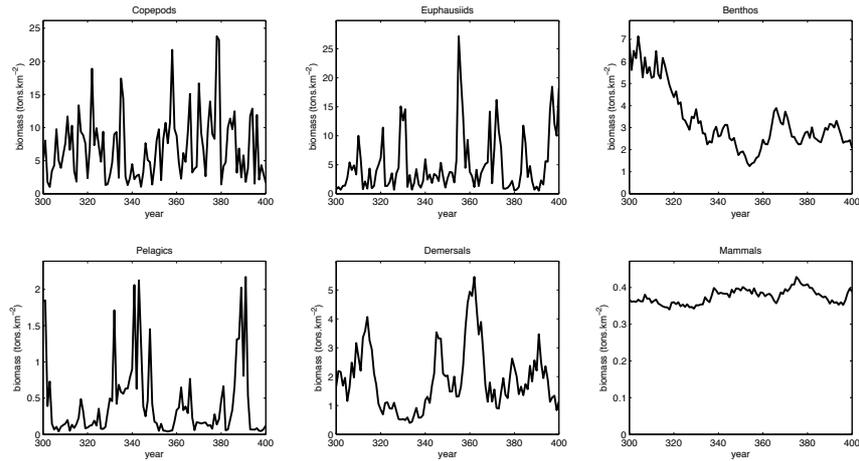


Figure 2. An illustration of the temporal dynamics of biomass of copepods, euphausiids, benthos, pelagic fishes, demersal fishes and marine mammals for 100y.

The power spectrum analysis (Figure 3) shows that the dominant frequencies vary between trophic groups. Most trophospecies display high power at low frequencies, indicating long-term (>300y) fluctuations. Fluctuations in biomass at higher frequencies are observed the middle and lower trophic levels, i.e. copepods (all wavelengths), euphausiids (30-50y wavelength) and pelagic fishes (50y wavelength).

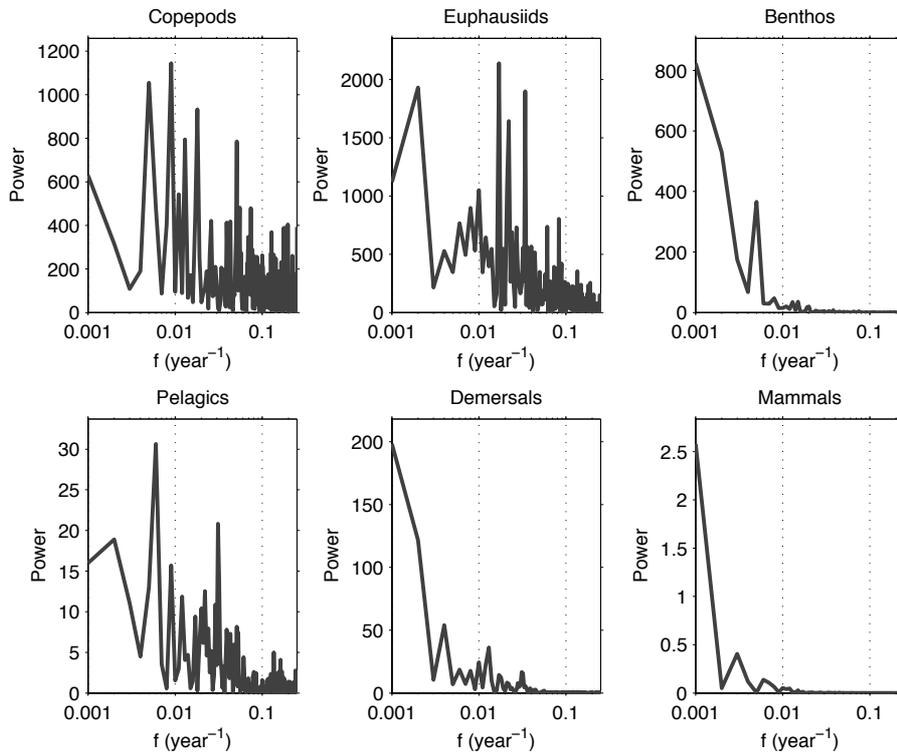


Figure 3. Power spectra showing the dominant frequencies of biomass temporal fluctuations for copepods, euphausiids, benthos, pelagic fishes, demersal fishes and marine mammals.

The density-distributions of the tropho-species biomasses are asymmetrical (Figure 4). For copepods, euphausiids, pelagic and demersal fishes these distributions are highly skewed, indicating dynamics with extremely high biomasses in only few years. Unfortunately, there are very few empirical data with which such distributions could be compared and it is therefore difficult to evaluate if the distributions emerging from the model simulation display a sufficient degree of realism.

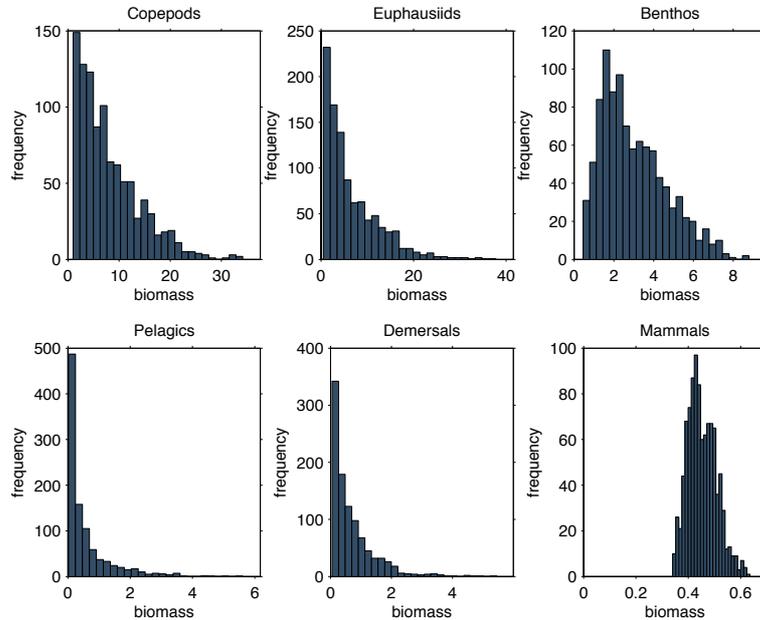


Figure 4. Empirical frequency distributions of biomass for copepods, euphausiids, benthos, pelagic fishes, demersal fishes and marine mammals.

The proportions of various preys eaten by predators are illustrated in Figure 5. These correspond to integrated diet over the whole simulation period. The diet fractions appear realistic with e.g. Mammals predominantly feeding on euphausiids (krill) and to a small extent on demersal and pelagic fishes; demersal fishes feeding on average on circa 1/3<sup>rd</sup> euphausiids, 1/3<sup>rd</sup> benthos and 1/3<sup>rd</sup> fish; pelagic fishes feeding on 50% copepods, 40% euphausiids and 10% pelagic fishes.

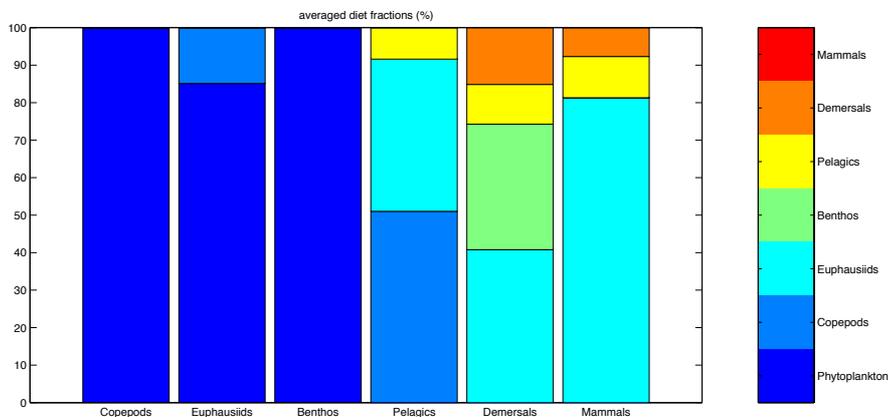


Figure 5. Mean proportion of preys eaten by each predator group.

The mean biomass, consumption and production simulated of each group are illustrated in Figure 6. Current available estimates of biomass for zooplankton, pelagic and demersal fishes are 130, 9.2 and 1.5 t.km<sup>-2</sup> respectively for the Norwegian and Barents Sea combined (Gaichas et al., 2009). In the Barents Sea alone these estimates are 14.6, 2.8 and 1.5 t.km<sup>-2</sup> (Johannesen et al., 2012a). The simulated biomasses for the same groups are respectively 14.5, 0.6 and 0.7 t.km<sup>-2</sup>. The model is therefore capable of simulating realistic biomasses for zooplankton and demersal fishes but the pelagic component is underestimated. The mean benthic biomass is estimated to 3 t.km<sup>-2</sup>, which is likely to be an underestimate. The mean biomass of marine mammals is 0.45 t.km<sup>-2</sup>, a value close to the starting biomass of the simulation, estimated from previous Ecopath modeling work (Blanchard et al., 2002). The simulated levels of consumption and production will need to be compared to existing empirical estimates for the Barents Sea.

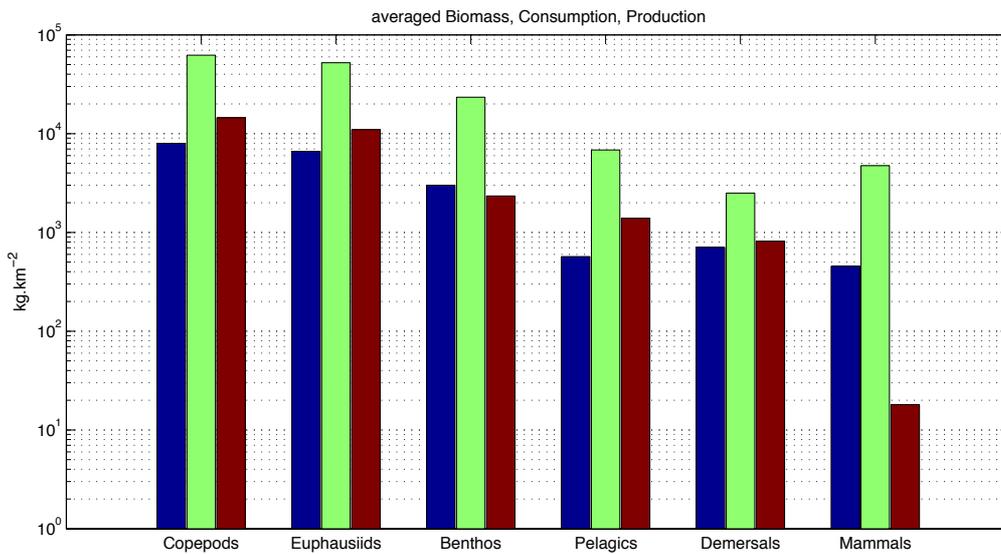


Figure 6. Mean biomass (blue), consumption (green) and production (red) of copepods, euphausiids, benthos, pelagic fishes, demersal fishes and marine mammals.

The SDF model does not explicitly include trophic functional relationships. Rather, these are emerging properties of the model. Various types of trophic functional relationships emerge from the simulation (Figure 7). These include: 1) absence of functional relationships, e.g. for benthos feeding on phytoplankton or demersals feeding on euphausiids; 2) linear relationships, e.g. for euphausiids feeding on copepods and mammals feeding on pelagics; and 3) non-linear relationships, e.g. for euphausiids feeding on phytoplankton and pelagics feeding on euphausiids. How much these features resemble actual trophic functional relationships is difficult to evaluate and predominantly depends on appropriate field data.

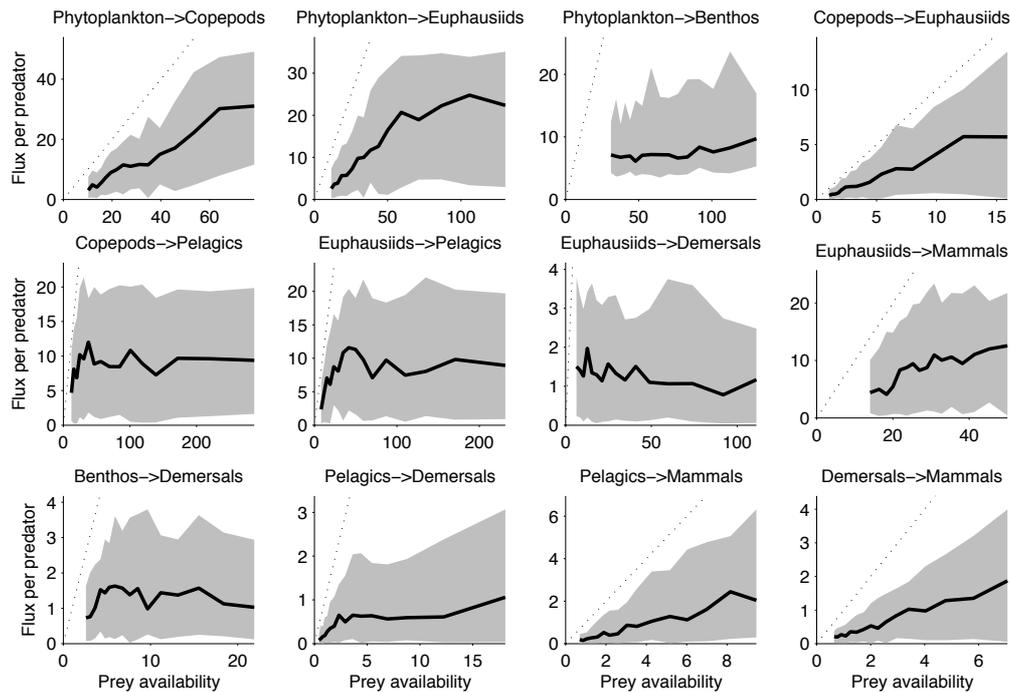


Figure 7. Trophic functional relationships for each prey-predator couple. The thick black line indicate the median flux per predator. The shaded surfaces represent the 5-95% percentile distributions. The thin dotted line shows theoretical maximum flux (i.e. when all available preys are consumed). Availability and fluxes are expressed in tonnes of prey per tonnes of predator.

## Conclusions

The SDF model is one of the most simple formulations of a dynamic food web model. Despite its great simplicity and its potentially high variability due to its stochastic nature, this model is able to capture a wide range of features observed in the Barents Sea ecosystem. As such, it can serve as a reference against which more complex ecosystem models can be evaluated. This is in line with the original idea of Mullon et al (2009) who defined this model as a *null* model, in the sense of *null* hypothesis. This would however require the definition of quantitative and objective evaluation criteria to evaluate various model's ability to reproduce real ecosystem patterns. Approaches based on statistical evaluation of second order properties (also called summary statistics) should be developed to achieve this objective (Grimm et al., 2005, Hartig et al., 2011). There is currently no objective way of optimizing parameter values in this model, and although there is a limited number of parameters (at least in comparison with most other ecosystem models), exploring the parameter space remains a challenging task.

Developments in model evaluation and optimisation techniques will allow for quantitative comparisons of the SDF with other ecosystem models currently being developed for the Barents Sea (e.g. Atlantis and Ecopath with Ecosim).

## References

- Blanchard, J. L., Pinnegar, J. K., and Mackinson, S. 2002. Exploring marine mammal-fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea Ecosystem. 117. 52 pp.
- Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities, and limitations. *Ecological Modelling*, 172: 109-139.

- Dulvy, N. K., Ellis, J. R., Goodwin, N. B., Grant, A., Reynolds, B., and Jennings, S. 2004. Methods of assessing extinction risk in marine fishes. *Fish and Fisheries*, 5: 255-276.
- Eriksen, E., and Dalpadado, P. 2011. Long-term changes in Krill biomass and distribution in the Barents Sea: are the changes mainly related to capelin stock size and temperature conditions? *Polar Biology*, 34: 1399-1409.
- Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J. S., Overholtz, W., Megrey, B. A., Gjøsæter, H., et al. 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. *Progress in Oceanography*, 81: 47-62.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., et al. 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. *Science*, 310: 987-991.
- Hartig, F., Calabrese, J. M., Reineking, B., Wiegand, T., and Huth, A. 2011. Statistical inference for stochastic simulation models – theory and application. *Ecology Letters*, 14: 816-827.
- Hoening, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fisheries Bulletin U.S.*, 81: 898-903.
- Johannesen, E., Høines, Å. S., Dolgov, A. V., and Fossheim, M. 2012a. Demersal Fish Assemblages and Spatial Diversity Patterns in the Arctic-Atlantic Transition Zone in the Barents Sea. *PLoS ONE*, 7: e34924.
- Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., Knutsen, T., et al. 2012b. Changes in Barents Sea ecosystem state, 1970-2009: climate fluctuations, human impact, and trophic interactions. *ICES Journal of Marine Science*, 69: 880-889.
- Kooijman, S. A. L. M. 2010. *Dynamic Energy Budget Theory for Metabolic Organisation*, Cambridge University Press, Cambridge, UK.
- Mullon, C., Fréon, P., Cury, P., Shannon, L., and Roy, C. 2009. A minimal model of the variability of marine ecosystems. *Fish and Fisheries*, 10: 115-131.
- Norse, E. A., Brooke, S., Cheung, W. W. L., Clark, M. R., Ekeland, I., Froese, R., Gjerde, K. M., et al. 2012. Sustainability of deep-sea fisheries. *Marine Policy*, 36: 307-320.
- Polovina, J. J. 1984. An overview of the Ecopath model. *Fishbyte*, 2: 5-7.
- Shannon, L. J., Moloney, C. L., Jarre, A., and Field, J. G. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems*, 39: 83-116.