Cascading effects of mass mortality events in Arctic marine communities

ØYSTEIN LANGANGEN[1], JAN OHLBERGER[1,2], LEIF C. STIGE[1], JOËL M. DURANT[1], ELISA RAVAGNAN[3], NILS C. STENSETH[1] and DAG Ø. HJERMANN[1,4]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway, [2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA, [3]International Research Institute of Stavanger, IRIS Environment, Postbox 8046, 4068 Stavanger, Norway, [4]Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, N-0349 Oslo, Norway

Abstract

Mass mortality events caused by pulse anthropogenic or environmental perturbations (e.g., extreme weather, toxic spills or epizootics) severely reduce the abundance of a population in a short time. The frequency and impact of these events are likely to increase across the globe. Studies on how such events may affect ecological communities of interacting species are scarce. By combining a multispecies Gompertz model with a Bayesian state-space framework, we quantify community-level effects of a mass mortality event in a single species. We present a case study on a community of fish and zooplankton in the Barents Sea to illustrate how a mass mortality event of different intensities affecting the lower trophic level (krill) may propagate to higher trophic levels (capelin and cod). This approach is especially valuable for assessing community-level effects of potential anthropogenic-driven mass mortality events, owing to the ability to account for uncertainty in the assessed impact due to uncertainty about the ecological dynamics. We hence quantify how the assessed impact of a mass mortality event depends on the degree of precaution considered. We suggest that this approach can be useful for assessing the possible detrimental outcomes of toxic spills, for example oil spills, in relatively simple communities such as often found in the Arctic, a region under increasing influence of human activities due to increased land and sea use.

Keywords: anthropogenic impacts, community-level effects, Gompertz model, mass mortality events, state-space modeling, uncertainty and assessment

Received 10 November 2015; revised version received 13 April 2016 and accepted 29 April 2016

Introduction

Catastrophic mass mortality events are known to occur throughout the animal kingdom and the frequency of such events is likely on the rise for many taxa across the globe (Fey *et al.*, 2015). Mass mortality events are often defined as rapidly occurring events causing elevated mortality that drastically reduce population abundance (Reed *et al.*, 2003), which can be an important factor in shaping the dynamics and persistence of populations (Mangel & Tier, 1994).

Mass mortality may be caused by natural abiotic events, for example, extreme weather such as storms and geological disaster such as volcanic eruptions and earthquakes, or natural biotic events, for example, species invasions, epizootics and toxic algal blooms (Fey *et al.*, 2015). Furthermore, human activity may directly or indirectly cause mass mortality events. Examples

include direct effects of toxic spills and indirect effects of increased disease caused by global transport of species. Such mass mortality events may have devastating effects not only on the impacted populations, but may also lead to large effects at the community level (Harvell *et al.*, 1999; Peterson *et al.*, 2003). Population fluctuations in animals are known to be driven by a plethora of processes including intrinsic density dependence, inter-specific interactions, climate forcing as well as possible interactions among the drivers (Bjørnstad & Grenfell, 2001). Predicting the responses to environmental perturbations in populations and even more so in communities and food webs is hence inherently difficult. Nevertheless, the demand for assessments of potential impacts of human activities is on the rise. Typically, models used to project environmental impacts of human activities have been based on single species, not accounting for species interactions (e.g., Peterson *et al.*, 2003; Hauge *et al.*, 2014). Hence, there is a strong need to improve our ability to project how anthropogenic effects may propagate in communities. Simple communities, as often found in the polar regions, may be especially vulnerable to changes in

Correspondence: Øystein Langangen, tel. +47 22854648, fax +47 22854001, e-mail: oysteol@ibv.uio.no

abundance or biomass in a single key species compared with more complex communities (cf. Paine, 1980). Human activities are likely to increase in the Arctic region, as large deposits of valuable natural resources such as oil and gas are expected to be found in this region (Bird *et al.*, 2008). As a result of the projected increase in land and sea use, a better understanding of possible outcomes of mass mortality events, in particular events associated with human activity in these relatively simple arctic communities, is needed.

Here, we demonstrate how a state-space framework can be used to quantify possible community-level effects of extreme pulse perturbations. To illustrate how the framework can be utilized to assess the impact of mass mortality events, in particular events caused by human activity, we present a case study where we investigate the impacts of a mass mortality event on an ecologically and economically important community of zooplankton and fish in the Barents Sea situated in the Arctic region.

Materials and methods

In this section, we first present the general modeling framework and how it can be applied to mass mortality events. Second, we present the Barents Sea ecosystem and the specific multispecies model representing the system. Third, we give an overview of the data and the model calibration method. Finally, we present the different mass mortality scenarios and how we include the degree of precaution in the assessed outcome.

Modeling the community response to mass mortality events

Most species are embedded in a community of interacting species resulting in a large number of potential interspecific interactions. In addition, as density-dependent regulation in the population dynamics is considered widespread in nature (Brook & Bradshaw, 2006), community models should be able to capture both the complexities of species interactions and density-dependent regulation. In order to account for density dependence, we use the Gompertz model (Gompertz, 1825) which has been successfully applied to empirical analyses of population dynamics (e.g., Saitoh *et al.*, 1997; Stenseth *et al.*, 1999, 2015). In addition, the Gompertz model can be expanded to account for dynamic multispecies interactions through the environmental term (Ives *et al.*, 2003; Hjermann *et al.*, 2007a; Mutshinda *et al.*, 2009, 2011). The Gompertz model can be expressed as

$$B_{t+1} = a'B_t e^{(b' \ln B_t + \Sigma_i E_{i,t})}$$

where B_t is the population biomass at time t, $a' > 0$ and b' are constants describing the productivity and degree of density dependence, respectively, and the E_t's are the environmental (biotic and abiotic, stochastic and/or deterministic) influences. On a logarithmic scale, the Gompertz model can be expressed as

$$X_{t+1} = a + bX_t + \Sigma_i E_{i,t}$$

where $X_t \equiv \ln B_t$, $a \equiv \ln a'$ and $b \equiv b' + 1$. The statistical properties of this equation are well known (e.g., Dennis *et al.*, 2006). Using a Bayesian state-space approach, we can include both process and observational error (Hilborn & Mangel, 1997; Clark, 2005) in the Gompertz model. The process errors, which account for environmental factors not included in the model (Clark & Bjørnstad, 2004; Dennis *et al.*, 2006), are assumed to be independent in time and to follow a multivariate normal distribution. With this approach, we account for both biotic effects such as predator–prey interactions and abiotic effects such as temperature and harvesting as well as uncertainty in the population dynamical processes. The output of such models is the posterior distributions of the model parameters. To evaluate the impact of mass mortality events at the community level, we run scenarios of biomass reduction of the focal species at different intensities occurring in different years. Due to the potential large uncertainties and often overconfidence in the output of forecasting approaches (Brander *et al.*, 2013), we base our scenarios on a hindcasting approach. Thus, we explore the impact of a perturbation occurring in a historical year assuming all other factors being equal.

When evaluating the biological impacts of human activities, for example, toxic spills, it is often recommended to take a precautionary approach, such as stated in the *World Charter for Nature* (UN General Assembly, 1982). One important aspect of the proposed Bayesian state-space approach is the ability to assess the uncertainty in the outcome of perturbation scenarios, also accounting for uncertainties in the ecological processes. To further illustrate the suggested approach, we performed an evaluation of the possible, yet realistic, consequences of a lower trophic level single-species mass mortality event in a community of zooplankton and fish in the Barents Sea.

Study system

The Barents Sea is a high-latitude shallow sea situated to the north of Norway and Russia (Fig. 1) that supports a highly productive ecosystem. Human activity has been affecting the ecosystem for several hundred years, mainly through fishing and hunting (Shevelev *et al.*, 2011).

Recently, parts of these high-latitude marine areas have been opened for oil and gas exploration, accompanied by a heated scientific and political debate over the likely anthropogenic stress associated with these activities (Misund & Olsen, 2013). A major concern is the potential impact from a possible accidental oil spill on the ecologically and economically important fish populations, including the Barents Sea cod (*Gadus morhua*), Norwegian spring-spawning herring (*Clupea harengus*) and Barents Sea capelin (*Mallotus villosus*) (Hjermann *et al.*, 2007b). The debate has focused around the possible worst-case scenarios (i.e., the worst conceivable yet realistic event) and the large uncertainties in prospective studies of possible oil spills (Hauge *et al.*, 2014). Population-level impacts on the fish stocks may result from direct effects on the fish populations mainly through increased mortality of eggs and larvae (Hjermann *et al.*, 2007b; Vikebø *et al.*, 2014).

However, direct mortality effects on a single year-class of eggs and larvae of Barents Sea cod are likely to translate into a relatively small effect at the population level (Ohlberger & Langangen, 2015). Furthermore, fish stocks may be impacted by indirect ecosystem effects through, for example, loss of prey (Stige *et al.*, 2011).

The Barents Sea cod, capelin and Norwegian spring-spawning herring constitute a key interconnected fish community in the Barents Sea ecosystem (Hamre, 1994; Hjermann *et al.*, 2004b). The capelin in the Barents Sea feed extensively on zooplankton species, especially krill (*Euphausiids*, Dalpadado & Skjoldal, 1991; Eriksen & Dalpadado, 2011). Several process-based community and ecosystem models for the Barents Sea, including these and other species, exist (e.g., Bogstad *et al.*, 1997; Lindstrøm *et al.*, 2009). Here, we focus on the possible indirect effects at the population level that may be caused by loss of prey. In particular, we focus on how a catastrophic event affecting krill at the lower trophic level may propagate to other parts in the community, such as the two ecologically and economically important fish species, capelin and cod.

We construct a model for these key species in the Barents Sea ecosystem (Fig. 1), using the proposed Bayesian state-space framework to simultaneously account for observational noise and uncertainty in the processes. The model includes terms for all the interactions of Fig. 1, with the exception that we assume one-way interactions between young herring and the other species. The process equations for this system can be expressed as

$$\text{Krill}_{t+1} = a_{\text{Krill}} + b_{\text{Krill}}\text{Krill}_t + c_{\text{Krill,Cap}}\text{Cap}_t + d_{\text{Krill}}\text{Her}_t \\ + e_{\text{Krill}}T_t + \text{PE}_{\text{Krill},t} \tag{1}$$

$$\text{Cap}_{t+1} = a_{\text{Cap}} + b_{\text{Cap}}\text{Cap}_t + c_{\text{Cap,Krill}}\text{Krill}_t + c_{\text{Cap,Cod}}\text{Cod}_t \\ + c_{\text{Cap,Cal}}\text{Cal}_t + d_{\text{Cap}}\text{Her}_t + e_{\text{Cap}}T_t + f_{\text{Cap}}C_{\text{Cap},t} \\ + \text{PE}_{\text{Cap},t} \tag{2}$$

$$\text{Cod}_{t+1} = a_{\text{Cod}} + b_{\text{Cod}}\text{Cod}_t + c_{\text{Cod,Cap}}\text{Cap}_t + d_{\text{Cod}}\text{Her}_t \\ + e_{\text{Cod}}T_t + f_{\text{Cod}}C_{\text{Cod},t} + \text{PE}_{\text{Cod},t} \tag{3}$$

$$\text{Cal}_{t+1} = a_{\text{Cal}} + b_{\text{Cal}}\text{Cal}_t + c_{\text{Cal,Cap}}\text{Cap}_t + d_{\text{Cal}}\text{Her}_t + e_{\text{Cal}}T_t \\ + \text{PE}_{\text{Cal},t} \tag{4}$$

Specifically, the Krill_t, Cap_t, Cod_t, Cal_t and Her_t are the biomass indices on log scale in year t, the T_t is the annual average Kola section temperature in year t and $C_{\text{Cap},t}$ and $C_{\text{Cod},t}$ are the catch divided by the annual biomass in year t. The coefficients a are the productivity, b are the density dependence, c are the species interactions for the dynamically modeled species, d are the interactions with herring, e are the temperature effects, f are the fishing effects and the PEs are process errors to be estimated. We assume multivariate-normal-distributed (MVN) process errors. This means that the vector of process errors ($\text{PE}_t = (\text{PE}_{\text{Krill},t}, \text{PE}_{\text{Cap},t}, \text{PE}_{\text{Cod},t}, \text{PE}_{\text{Cal},t})$) (is given by $\text{PE}_t \sim \text{MVN}(0, \Sigma_t)$, where 0 is the zero vector and Σ_t is the covariance matrix. The covariance matrix can be split into two components representing environmental (C) and demographic (D) variance, that is, $\Sigma_t = C + D_t$. The demographic (D) part of the variance–covariance scales inversely with population size, which means that it is negligible for highly abundant species (e.g., May, 1973). As the abundances of these marine species

are high also under the most severe mass mortality scenarios (90% reduction in population biomass) considered here, we set the demographic component to zero ($D_t = 0$). Demographic stochasticity may be very important for population dynamics at low population levels and may lead to increased extinction risk. If more severe mass mortality events are considered, it may be necessary to estimate the demographic component of the covariance matrix.

The model needs explicit prior specification for all parameters to be estimated. To impose an approximately uninformative prior, we assume an inverse Wishart distribution for the covariance matrix (Σ) with 4 degrees of freedom and we set the scale matrix to the 4 dimensional identity matrix. Furthermore, we assume that the biomass indices are observed with a temporally uncorrelated observation error. The observational errors are independent between species and normally distributed with a mean of zero and a uniformly distributed standard deviation between 0 and 10. Finally, all process parameters (a, b, c, d, e and f) are *a priori* assumed to be independent and are given a uniform prior distribution from -10 to 10.

Data

The data used in this study to calibrate the population model derive from several different sources. We have based this analysis on population biomass estimates (fish) or biomass indices (zooplankton). In addition, we have used landings for capelin and fishing mortality for cod to calculate indices of fishing pressure. The temporal coverage of the different time series is variable, but to obtain biologically reasonable parameter estimates, we have restricted the model to years when data on capelin are available (1972–2011), see Fig. 2 for an overview of the data.

The krill data were taken from Eriksen & Dalpadado (2011), using the standing stock biomass in the fall given in table 3 in that study. The data were log-transformed and normalized to zero mean and unit standard deviation.

To estimate *Calanus* dynamics, we adopted mesozooplankton indices from Stige *et al.* (2014). The main contribution to this index comes from *Calanus finmarchicus* in Atlantic water masses and *Calanus glacialis* and *Calnus hyperboreus* in arctic water masses (Orlova *et al.*, 2010a). We summed the total biomass indices derived for the southwest, central and northern Barents Sea from fall data on a linear scale, before we log-transformed and normalized the time series.

Capelin total stock biomass was derived from the joint Russian/Norwegian acoustic pelagic fish survey conducted annually in September and October since 1972 (ICES, 2013, table 9.6). The capelin biomass was measured in million metric tons and log-transformed. In addition, we use reported landings between the timing of the census in autumn as a proxy for catch of capelin. As a proxy for fishing pressure, we used the catch proxy divided by the observed biomass. Both the log-biomass and the fishing proxy were normalized.

Cod total stock biomass was derived from virtual population analysis (VPA) using mainly fisheries statistics and survey data (ICES, 2013, table 3.24). The time series goes back to 1946. The cod total biomass was measured in million metric
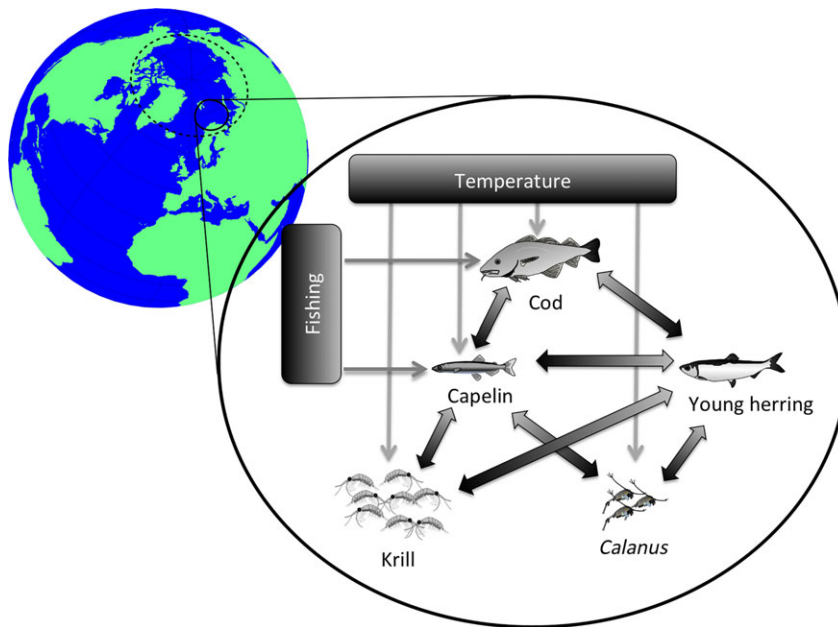
Fig. 1 The Barents Sea (solid circle) is situated to the north of the Arctic Circle (dashed circle). A schematic overview of the key Barents Sea community of fish and zooplankton as studied here is shown. Both biotic species interactions (thick two-head arrows) and other drivers (thin single headed arrows) are included in the model.
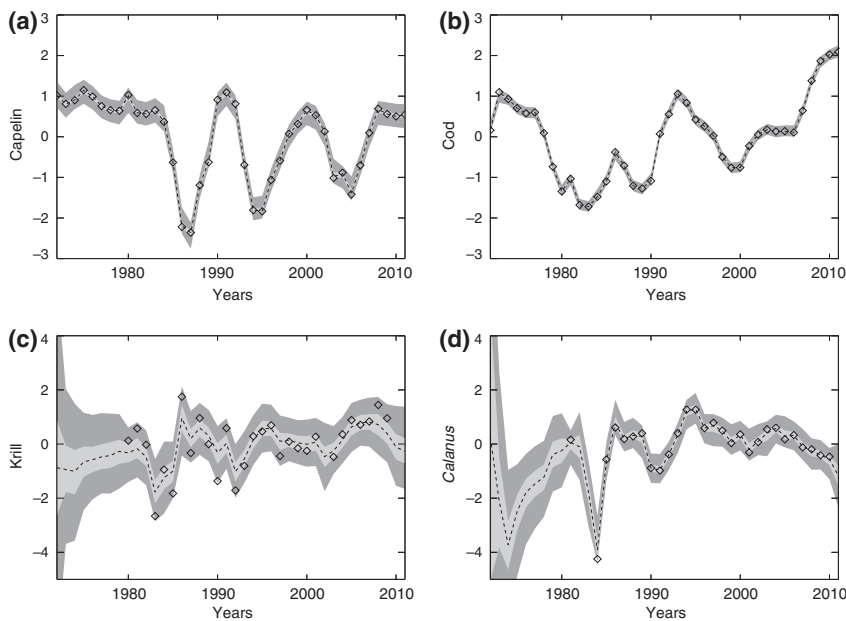
Fig. 2 The observed log-transformed and normalized biomass indices (diamonds) for capelin (a), cod (b), krill (c) and *Calanus* (d) are shown. The median model output (dashed lines) as well as 50% confidence limits (light gray) and 95% confidence limits (dark gray) are also shown.

tons and log-transformed. We used estimated instantaneous fishing mortality, for 5- to 10-year-olds (F_{5-10}), to calculate a proxy for the annual biomass removal due to fishing, $B_{\text{cod},t}(1 - e^{-F_{5-10}})$. As a proxy for fishing pressure in the model, we used the removed biomass divided by total biomass. As for capelin, both the log-biomass and the fishing pressure proxy were normalized.

The abundance of Norwegian spring-spawning herring in the Barents Sea has been very variable, mainly depending on variable recruitment success (Krysov & Røttingen, 2011). When the Norwegian spring-spawning herring reach the age of 3–5 years, they tend to migrate out of the Barents Sea (Krysov & Røttingen, 2011). Therefore, we did not include herring dynamically in the model, but instead used the biomass of

juvenile herring growing in the Barents Sea as a covariate in Eqns 1–4. We used VPA estimates of the Norwegian spring-spawning herring in combination with average weight at age (ICES WGWIDE, 2012) to construct biomass indices for age 1 and 2 herring.

We used the annual average Kola transect temperature for the upper 200 m (Tereshchenko, 1996, retrieved from http://www.pinro.ru) as a proxy for the temperature experienced by the Barents Sea fish and zooplankton community.

Note that the biomass indices (predictors and response) are log-transformed and normalized to zero mean and unit standard deviation. As a result, all estimated parameters are dimensionless except the temperature effects (*e*) that have the dimension [1/°C].

Model estimation

We used a Bayesian Markov Chain Monte Carlo (MCMC) approach to estimate the parameters in the above-mentioned models. For this purpose, we used the JAGS (Just Another Gibbs Sampler, Plummer, 2003) software. The likelihood function was created based on the model and the data, and in combination with the prior distributions of the parameters, the posterior distributions were estimated. We used three independent chains with 1 400 000 iterations, where the first 700 000 iterations were used as 'burn-in' iterations to ensure that the chains have converged. In addition, we thinned the chains with a factor 700 to reduce autocorrelation in the posterior samples and to produce a reasonable amount of output, in this case resulting in 1000 samples from each chain, in total 3000. We used the Gelman and Rubin $\hat{R}$ convergence diagnostics (Gelman & Rubin, 1992) and visual inspection of the chains to ensure convergence.

Catastrophic mass mortality scenarios

In order to investigate the community response to a catastrophic mass mortality event affecting a single species at the lower trophic level, we took a hindcasting approach. Applying a pulse perturbation on the biomass of krill in a single historic year while keeping other conditions equal to the historic values (by drawing from the estimated posterior distribution), we evaluate possible community effects of mass mortality events on the two fish stocks (capelin and cod). To span the full range of likely catastrophic mortality events, we investigate how a loss of 10%, 50% and 90% in the krill population in a single year, starting in 1972 and ending in 2007, affects the community dynamics. To assess the possible outcomes of such events on the harvested fish population, we record the relative loss in the fish species in the years following a mass mortality event at the lower trophic level. We quantify the impact by estimating the maximum reduction in the biomass of each fish species and the duration of the impact by estimating the number of years the species' biomass remains below 95% of that of the unperturbed population in a given year. Here, we focus on bottom-up effects of mass mortality at the lower trophic level, and in this context, similar scenarios could be performed for mass mortality in *Calanus*. Due to the relatively weaker estimated effect of *Calanus* species on capelin compared to the

effect of krill (Fig. 3), such scenarios would most likely give less severe impact on the fish species at higher trophic levels. As a result, we decided to focus on mass mortality events on krill. However, to further illustrate the wide range of possible applications of the framework, we include scenarios of mass mortality in capelin and cod, as well as a scenario with mass mortality affecting both krill and *Calanus* simultaneously (see Appendix S1 and Movies S1–S4).

### Degree of precaution in the assessed impact

We also illustrate how the framework can be used to assess the possible impacts of an anthropogenic perturbation in a transparent precautionary way. As the strength of the interspecific interactions to a large extent determines how a community responds to a single-species mass mortality event, uncertainty in the estimated interactions will lead to uncertainty in the assessed community-level impact of a mass mortality event. We demonstrate how these uncertainties result in a different assessment of the risk of severe biomass loss at the community level. The assessed impact of a mortality event will significantly depend on which posterior parameter sample is used for the projection given (i) the data, (ii) the model and (iii) the mass mortality event. Here, we define the degree of precaution as the quantile of the probability distribution for the effect. This is estimated from the joint posterior distribution, by investigating the range of impact of all posterior parameter combinations, in total 3000 samples. This means, for example, that if we decide to take a 70% degree of precaution, we would calculate the impact at the population level for the target species (e.g., capelin or cod) for all posterior samples, and sort the impact from low to high. The impact at 70% degree of precaution would then be the 70th percentile of this impact, and the impact would be higher at higher degree of precaution.

Results

Model calibration

The models reproduce the observed temporal population fluctuations very well (Fig. 2). In general, the estimated confidence bands are narrower for the fish species (cod and capelin) than for the zooplankton species (krill and *Calanus*). The estimated marginal posterior distributions of the parameters are shown in Fig. 3.

In short, the estimated productivities (*a*) were mostly centered around zero; however, for *Calanus,* it was slightly negative. Compensatory density dependence (*b* < 1) was present in all species. The strength and sign of the estimated species interactions (*c*) depend on the specific interaction. For example, the effect of krill on capelin and the effect of capelin on cod were most likely positive. Temperature effects (*e*) were negative for *Calanus*, centered on zero for krill and capelin and positive for cod. Fishing effects (*f*) were negative for capelin and cod.
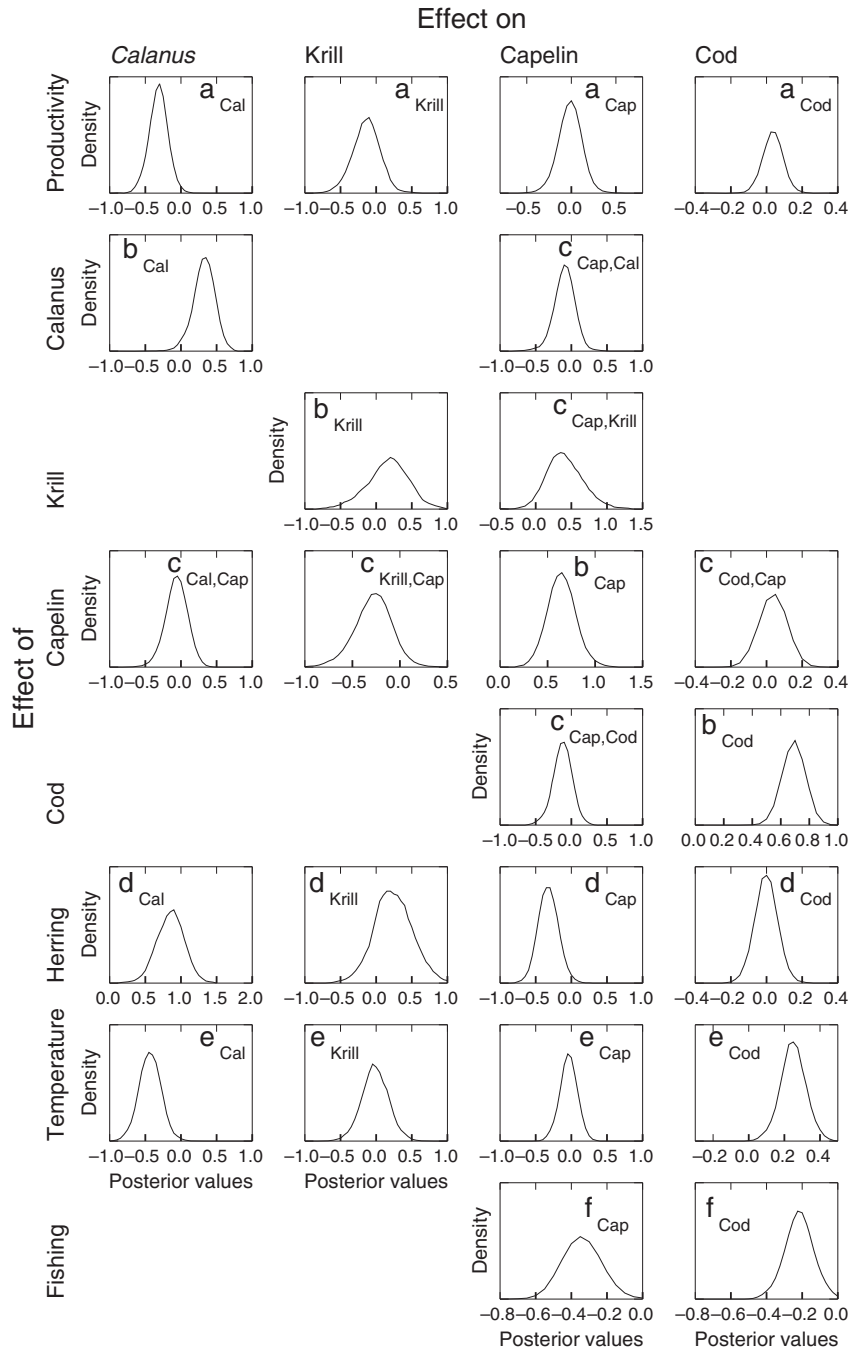
Fig. 3 Marginal posterior probability density distributions for the process model parameters are shown. Productivities are shown in the first row, while parameters describing species interactions are shown in row 2–6, temperature effects are shown in row 7 and the effects of fishing are shown in the last row. All parameter estimates are dimensionless except the *e* parameters which have the dimension 1/°C.

Correlations among the posterior distributions were present, but only five parameter pairs showed a higher absolute correlation than 0.5 and no higher than 0.59 (see Fig. S1). Note that by drawing the full parameter sample from the posterior distribution, we account for these correlations in the scenarios. The estimated standard deviation of the process errors was about 0.59 for krill, 0.45 for capelin, 0.31 for cod and 0.55 for *Calanus* (see Fig. S3). The correlation between modeled and observed biomass indices was in general high, with a correlation of 0.71 for krill, more than 0.99 for cod and capelin and 0.96 for *Calanus*.

Visual inspection of the chains and the $\hat{R}$-test (all individual parameters had an upper confidence value below 1.02 and the joint value was 1.01) strongly suggest convergence of the model. The posterior chains (after thinning) were at most marginally auto-correlated (about 0.1 or less, see Fig. S2). For a test of the sensitivity of our results to the observational model, see Figs S4 and S5.

*Assessed impact of catastrophic mass mortality events*

A pulse perturbation in single years affecting the krill population has a strong tendency to also impact the capelin population (Fig. 4 and Movie S1), and this may further propagate to the cod population. However, for the median outcome, the effect on the cod population is relatively minor, about 10% or less (Fig. 5).

In general, the projected effects of a pulse perturbation in one species may either lead to reduction or increase in the other species (see Fig. 4 and Movies S1–S3) depending on the sign and strength of the estimated interspecific interactions as well as the degree of precaution considered. For example, a mass mortality event affecting capelin is likely to lead to a decrease in the cod biomass and an increase in the krill biomass (Movie S2). A mass mortality event affecting cod is likely to lead to an increase in the capelin biomass, an effect that may propagate to the zooplankton level leading to, for example, a likely decrease in krill biomass (Movie S3). As the posterior parameter distributions are relatively wide (Fig. 3), the

assessed impact and duration of a mass mortality event may be significantly altered with the degree of precaution (Fig. 5). For example, the impact on capelin biomass due to a 50% reduction in krill may change from about 15% reduction at a 15% degree of precaution to about 25% reduction at 50% degree of precaution and to about 50% reduction at 95% degree of precaution (Fig. 5). The assessed duration of an impact also varies significantly depending on the degree of precaution, for example, for the 50% reduction in krill, the impact duration was 4 years for capelin at 50% degree of precaution and 10 years at 90% degree of precaution. Similarly, for cod, the impact on biomass is almost negligible at 50% degree of precaution, while it may be more than 10% at 95% degree of precaution (Fig. 5). Note that due to the log-linear nature of the Gompertz model, the biomass reduction relative to the unperturbed level is not changing between years.

Discussion

We have illustrated how a multispecies Gompertz model can be combined with a flexible Bayesian state-space framework to assess possible effects of single-species mass mortality events on community dynamics. The approach is especially useful when assessing possible effects of anthropogenic-driven mass mortality events due to the ability to assess impacts at different degrees of precaution. For example, our results indicate that when
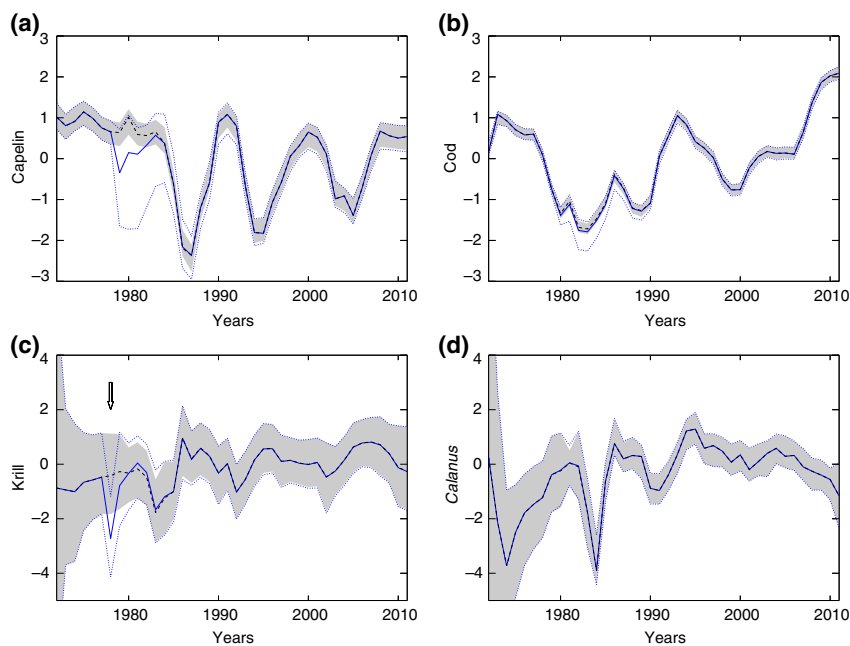
Fig. 4 Example of a pulse perturbation in 1979, killing 90% of the krill (arrow in panel c) in this particular year. The median unperturbed model output (dashed lines) and the 95% confidence limits (light gray) are shown. The median impact (solid blue lines) on the capelin (a), cod (b), krill (c) and calanus (d) are shown together with the 95% confidence limits of the perturbation (dotted blue lines).
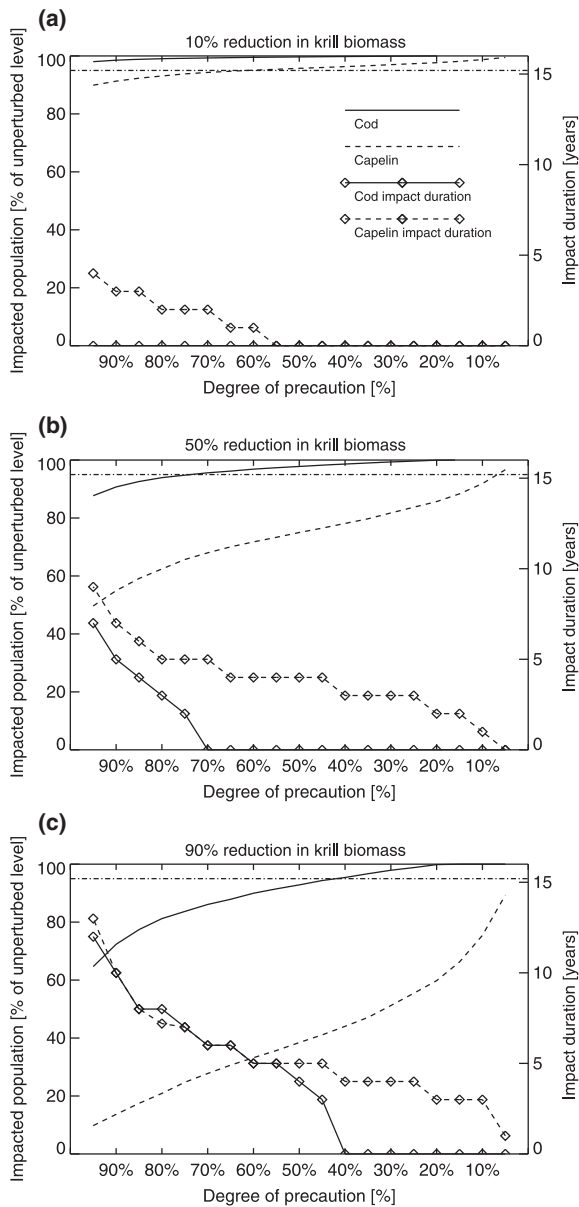
Fig. 5 An overview of the possible impact on the two fish populations, cod (solid lines) and capelin (dashed lines), of a mass mortality event killing 10% (a), 50% (b) or 90% (c) of the krill. The impact duration (diamonds) gives the number of years when the impacted population biomass is below 95% of that of the unperturbed population (dashed-dotted line). The assessed impact and the duration of a mass mortality event are given as a function of the degree of precaution, that is, the quantile of the posterior distribution.

only the median outcome (50% degree of precaution) is considered, relatively simple communities can be remarkably resilient to anthropogenic perturbations affecting a single species. However, this picture changes dramatically with the degree of precaution. The impact on species in the community increases with the degree

of precaution and may be large and ecologically highly significant. The reason for this increase in impact with the degree of precaution is the uncertainty about the strengths of the interspecific interactions, which largely determine, together with the intensity of the mass mortality event, how a community responds to a single-species mass mortality event. For example, in the Barents Sea, there may be large effects on the capelin stock if the krill stock is severely reduced; this reduction in capelin may further translate into a reduction in the cod biomass (Fig. 5). However, the strength and duration of the impact on both capelin and cod is highly dependent on both the intensity of the mortality event as well as the degree of precaution considered.

The estimated Barents Sea model captures the patterns in the empirical population biomass time series very well (Fig. 2). In general, the estimated fish stock dynamics are associated with narrower confidence bands compared to the krill and *Calanus* dynamics (Fig. 2). The estimated posterior parameter distributions (Fig. 3) are overall biologically reasonable. For example, for all four species, compensatory density dependence is present (*b*'s are <1), as is expected based on previous studies on zooplankton (Ohman & Hirche, 2001), cod (Ohlberger *et al.*, 2014) and capelin (Hjermann *et al.*, 2004a). Furthermore, most of the interspecific interactions (Fig. 3) are biologically reasonable and in line with previously reported interactions, such as the most likely positive effect of krill on capelin (e.g., Gjøsæter *et al.*, 2002; Orlova *et al.*, 2010b) and the reverse most likely negative effect of capelin on krill (e.g., Dalpadado *et al.*, 2002; Eriksen & Dalpadado, 2011). Similarly, the likely positive effect of capelin on cod was expected (e.g., Durant *et al.*, 2008), as was the reverse effect of cod on capelin (e.g., Bogstad & Gjøsæter, 2001). In addition, the negative effect of young herring on capelin (e.g., Huse & Toresen, 2000) and the absence of an effect of young herring on cod (e.g., Hjermann *et al.*, 2007a) are consistent with published interactions. A positive temperature effect on cod (e.g., Hjermann *et al.*, 2004b; Ottersen *et al.*, 2006; Ohlberger *et al.*, 2014) is in line with what has been reported in the literature, as is the absence of a direct temperature response in capelin (Hjermann *et al.*, 2004b). The effects of the fishing pressure indices were both negative as expected. Unexpectedly, the effect of herring biomass on zooplankton was estimated to be positive. However, this effect has also been previously reported and might be caused by herring predation on other zooplankton predators (Stige *et al.*, 2009). Interactions between capelin and *Calanus* may be weaker than expected (e.g., Stige *et al.*, 2014). The model captures the dynamics of the individual species well, and is mostly in line with our prior knowledge of the ecological interactions in

this system. We therefore argue that the model is performing satisfactory for the purpose of evaluating possible community dynamical responses to single-species mass mortality events.

In prospective studies, where the goal is often to assess how a hypothetical mass mortality event driven by human activity can affect ecosystem dynamics, a precautionary approach to assessing the possible impacts is recommended (UN General Assembly, 1982). Our results illustrate how the degree of precaution may alter the outcome of the assessment (Fig. 5). For example, in the 90% mortality scenario in krill, the maximum impact at the population level in cod may be about 5% of the population biomass if one follows the median estimated impact. This conclusion is significantly altered if one takes a more precautionary approach. According to the 95% quantile of the posterior distribution, the reduction in biomass of cod may in fact be about 35% (Fig. 5). Using the proposed framework, the effects of different degrees of precaution can be quantified in a transparent manner. In the face of potential increased land and sea use in the Arctic region, in particular increased activities associated with the recovery of potentially large oil and gas resources in the region (Bird *et al.*, 2008), reliable assessment of possible adverse environmental impact is needed. Such environmental assessments may be particularly important in the Arctic due to the relatively simple and hence potentially more vulnerable ecosystems (Paine, 1980; Hillebrand, 2004). The need for reliable and transparent environmental assessments is also demonstrated by the heated scientific and political debate over opening new areas in the Barents Sea for oil and gas extraction (Misund & Olsen, 2013), where the degree of precaution and defining the worst-case scenario has been in the center of the debate (Hauge *et al.*, 2014). While choosing the degree of precaution may be largely outside the realm of science, it is important to present and inform decision makers of the possibilities in a clear and concise manner.

In the current study, we have taken a hindcasting approach to avoid some of the problems associated with forecasting (Brander *et al.*, 2013). However, using a hindcasting approach to estimate possible outcomes of an event in the future has limitations. For example, we do not account for the effects of the projected changes in future climate (IPPC, 2013). Another aspect that is not accounted for are possible changes in species interactions that may occur in communities that experience perturbations in mortality. The effects of such altered species interactions have been suggested to be stronger than direct effects of climate change (Ockendon *et al.*, 2014). Hence, such unaccounted processes may be important, but hard to model in prospective

studies. Nevertheless, the presented method is useful for assessing how perturbations may propagate in a community, all other factors being equal.

With increased land and sea use across the globe including the Arctic region, accompanied by a potential increase in mass mortality events affecting natural populations, a better understanding of community-level dynamics and possible responses to human-induced perturbations is needed. Using a flexible Bayesian state-space modeling approach, we have illustrated how multispecies Gompertz models can be used to quantify possible community-level impacts of mass mortality events at different trophic levels. The flexibility of this modeling approach makes it suitable for assessing possible community-level responses to mass mortality events in a range of community structures, in particular in fairly simple communities. The flexibility of the approach, together with the ability to transparently illustrate the consequences of taking a precautionary approach, makes the framework highly useful for the quantification of ecological responses to human-induced mass mortality events at the community level.

Acknowledgments

References

Bird KJ, Charpentier RR, Gautier DL *et al.* (2008) *Circum-Arctic Resource Appraisal*. US Geological Survey, Menlo Park, CA.

Bjørnstad ON, Grenfell BT (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–643.

Bogstad B, Gjøsæter H (2001) Predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) in the Barents Sea: implications for capelin stock assessment. *Fisheries Research*, **53**, 197–209.

Bogstad B, Hauge KH, Ulltang Ø (1997) MULTSPEC–a multi-species model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, **22**, 317–341.

Brander K, Neuheimer A, Andersen KH, Hartvig M (2013) Overconfidence in model projections. *ICES Journal of Marine Science*, **70**, 1065–1068.

Brook BW, Bradshaw CJ (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**, 1445–1451.

Clark JS (2005) Why environmental scientists are becoming Bayesians. *Ecology Letters*, **8**, 2–14.

Clark JS, Bjørnstad ON (2004) Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology*, **85**, 3140–3150.

Dalpadado P, Skjoldal HR (1991) Distribution and life history of krill from the Barents Sea. *Polar Research*, **10**, 443–460.

Dalpadado P, Bogstad B, Gjøsæter H, Mehl S, Skjoldal HR (2002) Zooplankton-fish interactions in the Barents Sea. In: *Large Marine Ecosystems of the North Atlantic - Changing states and Sustainability* (eds Sherman K, Skjoldal HR), pp. 269–291. Elsevier Science B.V., Amsterdam.

Dennis B, Ponciano JM, Lele SR, Taper ML, Staples DF (2006) Estimating density dependence, process noise, and observation error. *Ecological Monographs*, **76**, 323–341.

Durant JM, Hjermann DØ, Sabarros PS, Stenseth NC (2008) Northeast arctic cod population persistence in the Lofoten-Barents Sea system under fishing. *Ecological Applications*, **18**, 662–669.

Eriksen E, 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.

Fey SB, Siepielski AM, Nusslé S *et al.* (2015) Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 1083–1088.

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–472.

Gjøsæter H, Dalpadado P, Hassel A (2002) Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. *ICES Journal of Marine Science*, **59**, 959–967.

Gompertz B (1825) On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, **115**, 513–583.

Hamre J (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodiversity and Conservation*, **3**, 473–492.

Harvell CD, Kim K, Burkholder JM *et al.* (1999) Emerging marine diseases - climate links and anthropogenic factors. *Science*, **285**, 1505–1510.

Hauge KH, Blanchard A, Andersen G *et al.* (2014) Inadequate risk assessments – A study on worst-case scenarios related to petroleum exploitation in the Lofoten area. *Marine Policy*, **44**, 82–89.

Hilborn R, Mangel M (1997) *The Ecological Detective*. Princeton University Press, Princeton, NJ.

Hillebrand H (2004) Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, **273**, 251–267.

Hjermann DØ, Ottersen G, Stenseth NC (2004a) Competition among fishermen and fish causes the collapse of Barents Sea capelin (ed Carpenter SR). *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 11679–11684.

Hjermann DØ, Stenseth NC, Ottersen G (2004b) Indirect climatic forcing of the Barents Sea capelin: a cohort effect. *Marine Ecology Progress Series*, **273**, 229–238.

Hjermann DØ, Bogstad B, Eikeset AM, Ottersen G, Gjøsæter H, Stenseth NC (2007a) Food web dynamics affect Northeast Arctic cod recruitment. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 661–669.

Hjermann DØ, Melsom A, Dingsør GE *et al.* (2007b) Fish and oil in the Lofoten-Barents Sea system: synoptic review of the effect of oil spills on fish populations. *Marine Ecology Progress Series*, **339**, 283–299.

Huse G, Toresen R (2000) Juvenile herring prey on Barents Sea capelin larvae. *Sarsia*, **85**, 385–391.

ICES (2013) *Report of the Arctic Fisheries Working Group*. ICES CM 2013/ACOM:05, Copenhagen, 18-24 April 2013, 682 p.

ICES WGWIDE (2012) *Report of the Working Group on Widely Distributed Stocks (WGWIDE)*. 75 p.

IPPC WG2 (2013) *IPCC Fifth Assessment Report*. 153 p.

Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, **73**, 301–330.

Krysov AI, Røttingen I (2011) Herring. In: *The Barents Sea - Ecosystem, Resources, Management. Half a Century of Russian - Norwegian Cooperation* (eds Jakobsen T, Ozhigin VK), pp. 215–224. Tapir Academic Press, Trondheim, Norway.

Lindstrøm U, Smout S, Howell D, Bogstad B (2009) Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. *Deep-Sea Research Part II*, **56**, 2068–2079.

Mangel M, Tier C (1994) Four facts every conservation biologists should know about persistence. *Ecology*, **75**, 607–614.

May RM (1973) Stability in randomly fluctuating versus deterministic environments. *American Naturalist*, **107**, 621–650.

Misund OA, Olsen E (2013) Lofoten–Vesterålen: for cod and cod fisheries, but not for oil? *ICES Journal of Marine Science*, **70**, 722–725.

Mutshinda CM, O'Hara RB, Woiwod IP (2009) What drives community dynamics? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **276**, 2923–2929.

Mutshinda CM, O'Hara RB, Woiwod IP (2011) A multispecies perspective on ecological impacts of climatic forcing. *Journal of Animal Ecology*, **80**, 101–107.

Ockendon N, Baker DJ, Carr JA *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology*, **20**, 2221–2229.

Ohlberger J, Langangen Ø (2015) Population resilience to catastrophic mortality events during early life stages. *Ecological Applications*, **25**, 1348–1356.

Ohlberger J, Rogers LA, Stenseth NC (2014) Stochasticity and determinism: how density-independent and density-dependent processes affect population variability. *PLoS ONE*, **9**, e98940.

Ohman MD, Hirche HJ (2001) Density-dependent mortality in an oceanic copepod population. *Nature*, **412**, 638–641.

Orlova E, Boitsov VD, Nesterova VN (2010a) *The Influence of Hydrographic Conditions on the Structure and Functioning of the Trophic Complex Plankton – Pelagic Fishes – Cod*. Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk.

Orlova EL, Rudneva GB, Renaud PE, Eiane K, Savinov V, Yurko AS (2010b) Climate impacts on feeding and condition of capelin *Mallotus villosus* in the Barents Sea: evidence and mechanisms from a data set spanning 30 years. *Aquatic Biology*, **10**, 105–118.

Ottersen G, Hjermann DØ, Stenseth NC (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, **15**, 230–243.

Paine RT (1980) Food webs - linkage, interaction strength and community infrastructure - the 3rd tansley lecture. *Journal of Animal Ecology*, **49**, 667–685.

Peterson CH, Rice SD, Short JW, Esler D, Bodkin JL, Ballachey BE, Irons DB (2003) Long-term ecosystem response to the Exxon Valdez oil spill. *Science*, **302**, 2082–2086.

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

Reed DH, O'Grady JJ, Ballou JD, Frankham R (2003) The frequency and severity of catastrophic die-offs in vertebrates. *Animal Conservation*, **6**, 109–114.

Saitoh T, Stenseth NC, Bjørnstad ON (1997) Density dependence in fluctuating grey-sided vole populations. *Journal of Animal Ecology*, **66**, 14–24.

Shevelev MS, Sunnaná K, Gusev EY (2011) Fisheries and hunting in the Barents Sea. In: *The Barents Sea - Ecosystem, Resources, Management. Half a Century of Russian - Norwegian Cooperation* (eds Jakobsen T, Ozhigin VK), pp. 495–514. Tapir Academic Press, Trondheim.

Stenseth NC, Bjørnstad ON, Falck W, Fromentin JM, Gjøsæter H, Gray JS (1999) Dynamics of coastal cod populations: intra-and intercohort density dependence and stochastic processes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 1645–1654.

Stenseth NC, Durant JM, Fowler MS *et al.* (2015) Testing for effects of climate change on competitive relationships and coexistence between two bird species. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20141958.

Stige LC, Lajus DL, Chan K-S, Dalpadado P, Basedow SL, Berchenko I, Stenseth NC (2009) Climatic forcing of zooplankton dynamics is stronger during low densities of planktivorous fish. *Limnology and Oceanography*, **54**, 1025–1036.

Stige LC, Ottersen G, Hjermann DØ, Dalpadado P, Jensen LK, Stenseth NC (2011) Environmental toxicology: population modeling of cod larvae shows high sensitivity to loss of zooplankton prey. *Marine Pollution Bulletin*, **62**, 395–398.

Stige LC, Dalpadado P, Orlova E, Boulay A-C, Durant JM, Ottersen G, Stenseth NC (2014) Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in the Barents Sea. *Progress in Oceanography*, **120**, 243–253.

Tereshchenko VV (1996) Seasonal and year-to-year variations of temperature and salinity along the Kola meridian transect. *ICES CM*, **1996/C:11**, 24.

UN General Assembly (1982) *World Charter for Nature*. 28 October 1982, A/RES/37/7, New York.

Vikebø FB, Rønningen P, Lien VS, Meier S, Reed M, Ådlandsvik B, Kristiansen T (2014) Spatio-temporal overlap of oil spills and early life stages of fish. *ICES Journal of Marine Science*, **71**, 970–981.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Cross-correlation in between parameters.
Figure S2. Auto-correlation in the chains.
Figure S3. Process errors.
Figure S4. Posterior distributions from model with fixed small observation error.
Figure S5. Posterior distributions from model with fixed large observation error.
Movie S1. Effects of 90% krill mortality.
Movie S2. Effects of 90% capelin mortality.
Movie S3. Effects of 90% cod mortality.
Movie S4. Effects of 50% krill and Calanus mortality.
Appendix S1. Additional mortality scenarios.