

Population resilience to catastrophic mortality events during early life stages

JAN OHLBERGER¹ AND ØYSTEIN LANGANGEN

Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway

Abstract. Catastrophic mortality events that drastically reduce the abundance of a population or a particular life stage can have long-term ecological and economic effects, and are of great concern in species conservation and management. Severe die-offs may be caused by natural catastrophes such as disease outbreaks and extreme climates, or human-caused disturbances such as toxic spills. Forecasting potential impacts of such disturbances is difficult and highly uncertain due to unknown future conditions, including population status and environmental conditions at the time of impact. Here, we present a framework for quantifying the range of potential population-level effects of catastrophic events based on a hindcasting approach. A dynamic population model with Bayesian parameter estimation is used to simulate the impact of severe (50–99%) mortality events during the early life stages of Northeast Arctic cod (*Gadus morhua*), an abundant marine fish population of high economic value. We quantify the impact of such die-offs in terms of subsequent changes in population biomass and harvest through direct comparison of simulated and historical trends, and estimate the duration of the impact as a measure of population resilience. Our results demonstrate strong resilience to catastrophic events that affect early life stages owing to density dependence in survival and a broad population age structure. Yet, while population recovery is relatively fast, losses in harvest and economic value can be substantial. Future research efforts should focus on long-term and indirect effects via food web interactions in order to better understand the ecological and economic ramifications of catastrophic mortality events.

Key words: catastrophic events; density dependence; fishery; food web interactions; *Gadus morhua*; life stages; Northeast Arctic cod; Norwegian coast; population resilience.

INTRODUCTION

Extreme environmental perturbations that cause severe die-offs and drastically reduce the abundance of a population or a particular life stage of a population in a short time are referred to as catastrophic events (Mangel and Tier 1994, Reed et al. 2003). Such extreme perturbations can be important in determining population persistence and are of great concern for both conservation biologists and resource managers (Mangel and Tier 1994, Good et al. 2008). Severe die-offs may be caused by natural catastrophes such as disease outbreaks, biological invasions, or extreme climatic events (e.g., hurricanes, heat waves, floods, droughts), many of which are projected to increase in frequency due to climate change (IPCC 2014). In addition, human-caused perturbations such as toxic spills can cause massive mortalities with potentially long-term ecological consequences (Rice et al. 2001). Catastrophic events may

affect ecosystem function and cause economic loss, especially when harvested resources are affected. It is therefore essential to understand their ecological and economic repercussions; however, forecasting potential consequences of such events is difficult and highly uncertain due to unknown future conditions, including population status (e.g., total biomass, age structure) and environmental conditions at the time of an impact.

In the marine environment, human-caused oil spills can have particularly devastating ecological effects, as evidenced, for instance, by studies following the *Exxon Valdez* spill in 1989 (Rice et al. 2001, Peterson et al. 2003), the *Prestige* spill in 2002 (Barros et al. 2014), and the *Deepwater Horizon* spill in 2010 (Incardona et al. 2014). Acute oil spills can further have severe economic consequences if exploited resources are impacted. Marine fisheries provide important sources of food and economic income for many people worldwide. Many marine fisheries are overexploited, from a sustainable yield perspective. This may in turn increase their vulnerability to other stressors such as extreme climates or toxic spills. At the same time, exploitation of nonrenewable resources in habitats of major fish stocks is growing. For instance, it is debated whether or not to commence petroleum production in areas around the

Manuscript received 11 August 2014; revised 14 November 2014; accepted 18 November 2014; final version received 12 December 2014. Corresponding Editor: É. E. Plagányi-Lloyd.

¹ Present address: School of Aquatic and Fishery Sciences (SAFS), University of Washington, Box 355020, Seattle, Washington 98195-5020 USA. E-mail: janohl@uw.edu

Lofoten islands in Norway (Hauge et al. 2014), an area that is known for its key spawning and nursery habitats for several economically important fish species, including the world's most abundant stock of Atlantic cod (*Gadus morhua*).

The consequences of catastrophic events for population abundance and recovery depend on species' life history traits such as growth rate, fecundity, and life span, as well as the strength of density regulation in the population (Rice et al. 2001, Vincenzi et al. 2014). Massive mortality events that affect a single year class or generation can be expected to have weaker effects on long-lived than on short-lived species. Further, populations with strong compensatory density dependence, i.e., increased growth or survival at low abundance, may experience relatively weak effects, because density regulation partially offsets the loss of biomass from the population. Many populations show density regulation in that juvenile survival increases at low abundances, because the number of potential competitors for food and habitat is reduced (Arcese et al. 1992, Myers and Cadigan 1993, Gaillard et al. 1998, Rose et al. 2001). Density-dependent survival buffers population growth against perturbations, and can be seen as "ecological insurance" in populations experiencing variable and occasionally extreme environmental conditions.

In order to assess the sensitivity of a population to severe mortality events during the early life stages, one thus needs a population model that (1) accurately describes a species' life history, (2) includes density dependence due to ecological interactions such as competition, (3) propagates information and uncertainty from one year to the next, and (4) accounts for stochasticity in the modeled population dynamical processes (e.g., recruitment). Such models can be used for hindcasting population trends in response to catastrophic events (hindcasting refers to simulations of perturbations during past periods for which population status and environmental conditions are known). This approach avoids typical shortcomings of model forecasting, i.e., future projections, which can lead to inaccurate accounting of uncertainties and overconfidence in model projections (Brander et al. 2013). Using a hindcasting approach based on estimated parameter distributions from a dynamic population model, one can quantify the range of potential impacts of catastrophic events in terms of changes in population biomass through direct comparison of simulated and historical time series. Hindcasting thereby helps identify extrinsic and intrinsic factors that determine the impact of catastrophic events, and provides estimates of population resilience to such disturbances.

In this study, we use Bayesian parameter estimates from a full life cycle model for the population dynamics of Northeast Arctic (NEA) cod to simulate catastrophic die-offs of eggs or larvae. Eggs and larvae are particularly vulnerable to catastrophic events because they are the least mobile and most sensitive life stages

(Hjermann et al. 2007). We assess the consequences of severe mortality events in terms of changes in population biomass and estimate the impact duration as a measure of population resilience. We further calculate potential losses in fisheries catches and economic revenue.

METHODS

Northeast Arctic cod

The Northeast Arctic stock of Atlantic cod is distributed along the coast of Norway and throughout the Barents Sea. Mature cod spawn in March and April along the Norwegian coast, particularly around the Lofoten islands. Spawning eggs drift northeastward in the Norwegian Coastal Current and hatch into larvae less than a month after spawning and before reaching the feeding grounds in the Barents Sea. By late summer, the 0-group fish are distributed over large areas of the Barents Sea, where they settle to the bottom in late autumn to assume a demersal lifestyle. The fish remain in the Barents Sea as juveniles until they reach maturity, typically around 6–8 years old. Adult NEA cod perform annual migrations from the Barents Sea to the spawning grounds along the Norwegian coast (Olsen et al. 2010).

Life cycle model

We previously developed a life cycle model for NEA cod based on survey data for all life stages and fisheries landings (Ohlberger et al. 2014). Specifically, the model was fitted using survey indices of cod eggs, larvae, 0-group fish, and age classes 1–9, as well as commercial landings of age classes 4–12 (Fig. 1), covering a total time period of 54 years (1959–2012). In addition, we used annual data on age-specific mean body mass and age-specific probability of being mature. The model was implemented using a state-space approach, which accounts for both unexplained stochasticity in the population dynamics (process noise) and the inaccuracy of the survey data and landings (observation error). Bayesian inference was used to estimate the model parameters based on specified prior distributions (Fig. 1).

The process part of the model describes the population dynamics, i.e., the age- or stage-specific abundances over time, by modeling the survival from one life stage or age class to the next. The survival terms consist of a natural mortality and additional effects depending on life stage or age class, including a temperature effect on larval survival, intercohort cannibalism on the 0-group, intracohort density-dependent survival of age 1–3 juveniles, and fishing mortality on age 4+ fish (survival from eggs to larvae was modeled as a constant mortality term without additional effects). A linear relationship between spawning-stock biomass and egg numbers with stochastic variation was used to describe the recruitment process (lognormal error). A lognormal process error was also applied to the 0-group survival, the life stage at which NEA cod enter their feeding grounds in the Barents Sea and switch from pelagic to demersal

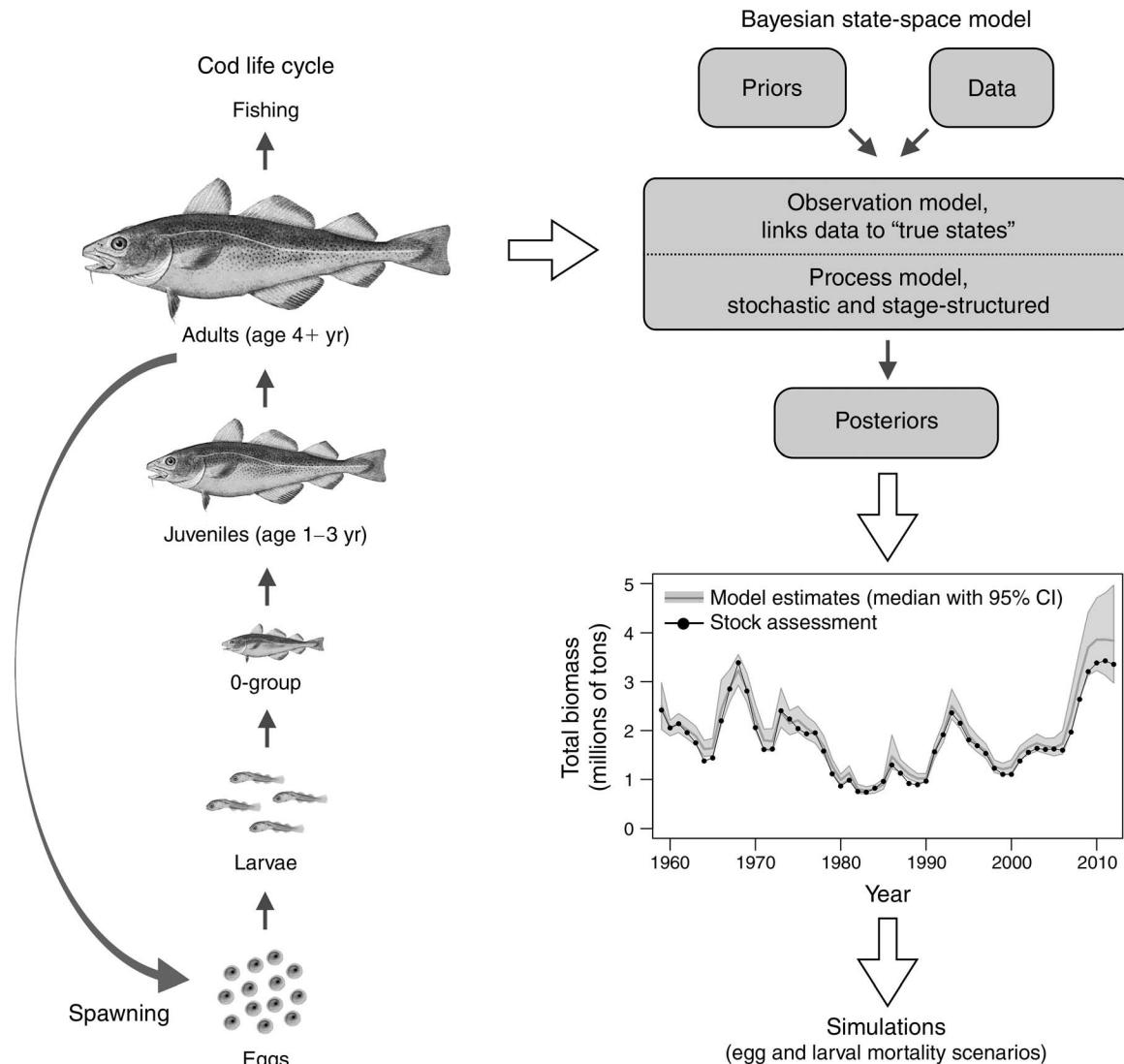


FIG. 1. Schematic illustration of the approach. In order to simulate the impact of catastrophic events, we used a previously developed life cycle model for Northeast Arctic (NEA) cod (*Gadus morhua*) that uses Bayesian inference to estimate the model parameters (Ohlberger et al. 2014). By using the parameter values from each sample of the estimated posterior distributions (750 samples), we simulate the impact of catastrophic events on population biomass and catch and directly compare them to the historical estimates on a sample-by-sample basis. For cod biomass and catch in all figures, 1 metric ton = 1 Mg; variation around the median model estimate is the 95% credible interval (CI).

lifestyle. The model-predicted temporal dynamics of age-specific abundances and population biomass are in close agreement with estimates from a virtual population analysis used in the NEA cod stock assessment (Fig. 1). A description of the model is provided in Appendix A (further details can be found in Ohlberger et al. 2014).

Simulations

The estimated parameters (posterior distributions) of the previously described model were used in this study to simulate the consequences of catastrophic events, i.e., a severe mortality of cod eggs or larvae in a single year, and to assess their impact on population biomass and fisheries

catches. Simulations were performed by sampling parameters from the estimated posterior distributions of the age-specific mortality rates, temperature effect, density dependence terms, fishing mortalities, and process errors (median values and standard deviations of key model parameters are provided in Appendix B: Table B1). This approach allowed us to directly compare simulated and estimated “true” biomass and catches (running simulations without any perturbation produces the same population abundances as with the original model). Median values as reported in the *Results* section, and credible intervals shown in figures, were obtained by running simulations for each set of parameter values (750 samples) from the model

posterior distributions in order to account for uncertainty in the population dynamical processes.

For each impact year, population biomass (accounting for age classes 3+) and annual catches (affecting age classes 4+) were simulated for all years following the impact. We then calculated the difference between simulated and historical values, and quantified harvest loss assuming the same fishing mortality rate as without the impact (“historical values” refers to the previously estimated “true” values from the original model). The duration of the impact at the population level was taken as the number of years during which population biomass was reduced to less than 90% of the historical biomass (using median values). This impact duration was used as a proxy for population resilience, i.e., the ability of the population to recover after a mortality event, which we note is just one of the many meanings of resilience that exist in the ecological literature (Gunderson 2000). Finally, we estimated maximum loss in economic value due to catch losses using historic data on the value of the NEA cod fishery (assuming that the price is a linear function of catch). The losses were calculated in real economic value by adjusting nominal values for the effect of inflation using the Norwegian consumer price index with 2013 as reference year (CPI data, converted from NOK to USD using an exchange rate of 0.16, are available online from Statistics Norway).²

Scenarios

We simulated impact scenarios of an additional 50% and 99% mortality on cod eggs or larvae (the scenarios are equivalent for the two life stages because survival from eggs to larvae is modeled using a constant natural mortality term). We focus on impacts on a single cohort of eggs or larvae, i.e., offspring of similar age from the same year, because catastrophic events are expected to affect a population over a short time. At the population level, acute mortality higher than 50% has previously been defined as *catastrophic* (Reed et al. 2003). Hence, by simulating 50% and 99% mortality during the early life stages, we cover the entire range of conceivable catastrophic mortality events.

RESULTS

Effect of density-dependent survival

Due to density dependence in juvenile survival, a severe mortality impact on early life stages does not directly translate into equivalent changes in cohort abundance at older life stages, i.e., a reduction in eggs or larval abundance results in a relatively smaller change at age 4 years, when the fish start to enter the adult life stage. We find that, depending on the year of impact (affected cohort), a simulated 50% early-life-stage mortality causes a reduction in the abundance of 4-year-olds of 20–48%, whereas a simulated 99% mortality causes a reduction in abundance at age 4 of

96–99%. These ranges refer to median values for all potential impact years (1960–2008; see Appendix C: Table C1).

Population response to catastrophic events

An illustration of the change in population biomass over time in response to a severe (99%) mortality event is shown in Fig. 2 (top panels) for the impact years 1963 and 1966, which caused the largest and smallest absolute biomass decline, respectively. The maximum decline occurs five years after the impact, which is when the affected cohort would have contributed most to population biomass. The biomass reduction propagates through time for many years, because an affected cohort produces fewer offspring and thus contributes less to future population biomass. This temporal echo of a catastrophic event is gradually dampened over time, and is reflected in the catch loss (Fig. 2, bottom panels).

Maximum annual decline in population biomass

The simulations showed large variation in the magnitude of reductions in population biomass depending on the year of impact. In general, the strongest biomass declines occurred when a large cohort was affected, i.e., in years with otherwise high recruitment. The largest annual declines typically occurred 4–6 years after a simulated mortality event, because 4–6 year olds contribute most to population biomass.

We used the year with the largest biomass decline following a simulated impact to assess the potential consequences of a catastrophic event (e.g., for the impact year 1963, the largest decline in population biomass occurred five years later in 1968; see Fig. 2). Maximum annual biomass declines were estimated between 0.05 and 0.26 million tons (1 metric ton = 1 Mg) in the case of 50% mortality (median values), and between 0.09 and 1.08 million tons in the case of 99% mortality (Fig. 3). For comparison, population biomass has fluctuated roughly between 0.7 and 3.9 million tons over the past 50 years, with a year-to-year variation of up to 0.8 million tons. The most severe absolute biomass declines were found for the early and late periods, when biomass was comparatively high. In contrast, the strongest relative declines in population biomass occurred during periods when population biomass was low, because the relative impact of a severe die-off during early life stages depends on the total biomass of all other cohorts. Even in the case of a catastrophic event that kills almost an entire cohort of eggs or larvae (99% mortality), most impact years produced maximum annual biomass declines of less than 30% (Fig. 3).

Impact duration

The impact duration of a catastrophic event at the population level was measured as the time at which that population biomass was reduced to less than 90% of historical values. The years of biomass reductions

² www.ssb.no

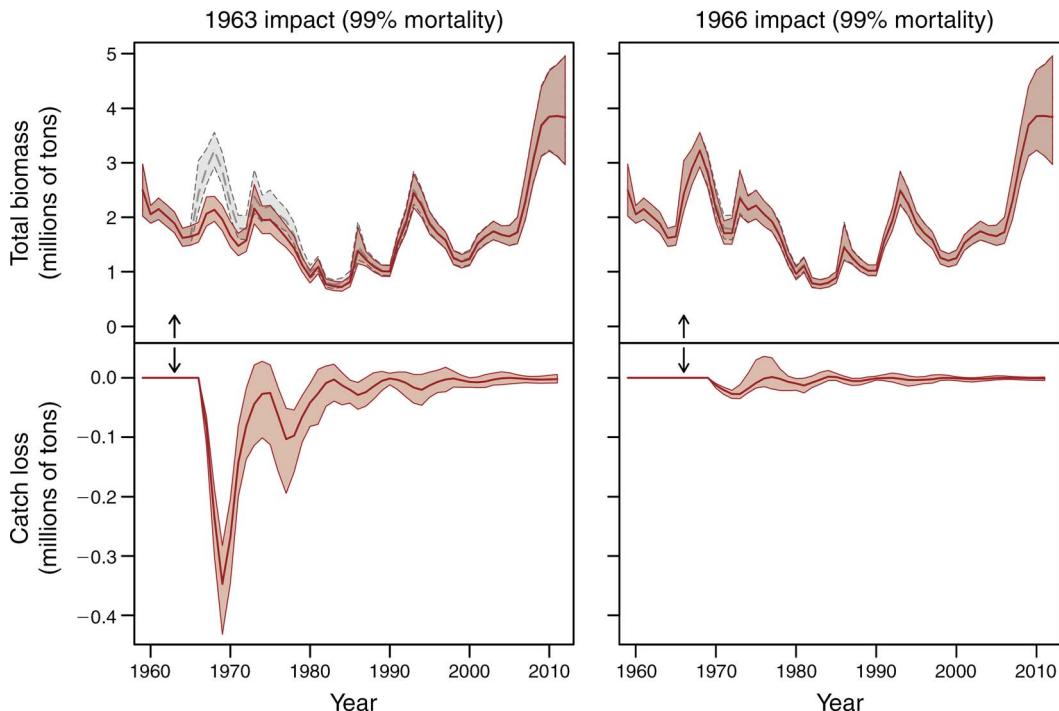


FIG. 2. Two examples of simulated catastrophic events (99% mortality) for impacts in 1963 and 1966, the years with the highest and lowest absolute declines in population biomass, respectively. Shown are medians and 95% credible intervals (CIs) for population biomass (upper panels) and catch loss (lower panels) for the original model estimates (gray, dashed lines) and the simulations (red, solid lines). Medians and CIs were obtained by running simulations for each set of parameter values from the model posterior distributions.

below this threshold occurred with a delay of several years after the mortality event and do not necessarily occur in consecutive years. In the case of 50% mortality in the early life stage, the maximum impact duration was three years. In the case of 99% mortality, the

maximum impact duration was 15 years, while the median impact duration was three years (Fig. 4). Consequently, recovery time of the population was relatively fast, especially in the case of 50% egg or larval mortality.

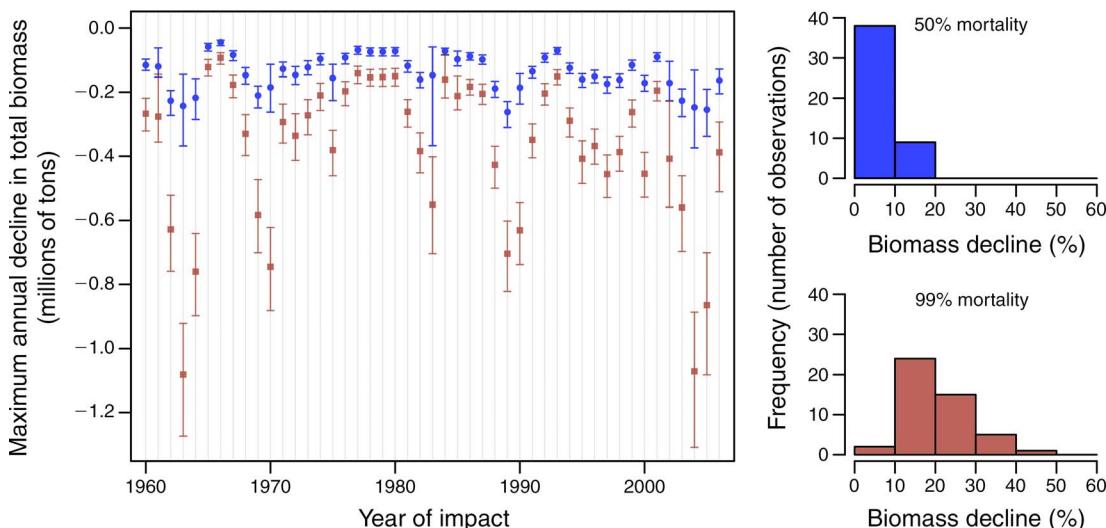


FIG. 3. Maximum annual biomass declines in response to 50% (blue/circles) and 99% (red/squares) egg or larval mortality events. Shown are medians and 95% credible intervals for each impact year (left), and the frequency distributions of the relative declines in population biomass (right). Medians and CIs were obtained by running simulations for each set of parameter values from the model posterior distributions.

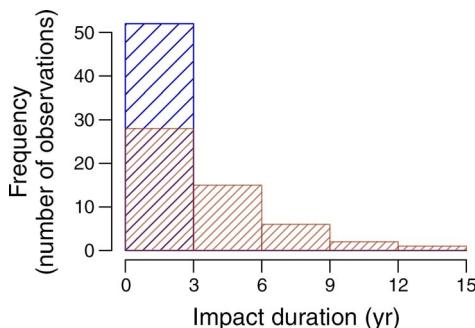


FIG. 4. Impact duration of catastrophic events, calculated as the number of years during which population biomass was reduced to less than 90% of historical values. Shown is the frequency distribution for the 50% (blue, low-density shading) and 99% (red, high-density shading) mortality scenarios.

Loss in catches and economic value

The maximum catch loss in a given year occurred 5–7 years after a simulated impact, because 5–7 year old cod contribute most to harvested biomass. Maximum annual catch losses were estimated between 0.01 and 0.08 million tons in the case of 50% mortality, and between 0.03 and 0.35 million tons in the case of 99% mortality (Fig. 5). The largest absolute losses were caused by an impact in 1963 (see Fig. 2) due to large declines in population biomass and relatively high fishing mortality in the late 1960s (~0.5–0.8 for ages 5–10 years). In relative terms, maximum annual catch losses were slightly higher than annual declines in population biomass (Figs. 3 and 5), because fishing mortality differs between age classes and is particularly high for intermediate ages.

We further estimated total catch loss for the period 4–8 years after the impact (Fig. 6). This period includes all

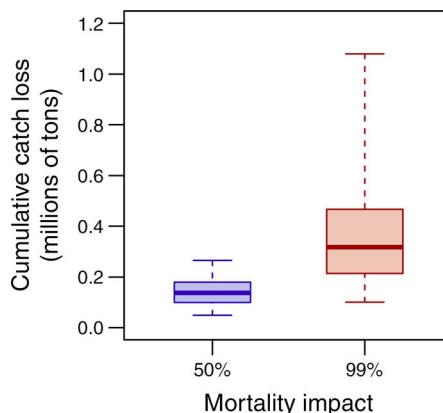


FIG. 6. Cumulative catch loss in millions of tons in response to 50% (blue) and 99% (red) mortality events. Cumulative catch loss was calculated for the 5-year period four to eight years after an impact (see *Results* for further details). Thick lines represent median values, boxes represent the 25th and 75th quartiles, and whiskers extend to the most extreme data points.

years when the affected cohort would have contributed significantly to the catches, but excludes long-term effects due to low recruitment as a consequence of the decline in population biomass. According to this metric, a catastrophic event can cause a maximum catch loss over five years of up to 0.3 million tons in the case of 50% mortality, and up to 1.1 million tons in the case of 99% mortality (impact year 1963, losses in years 1967–1971). These are considerable losses when compared to the long-term average annual catch of the NEA cod fishery, which amounts to about 0.5 million tons for the period 1959–2012.

Maximum annual losses in economic value were estimated as US\$26–167 million in the case of 50%

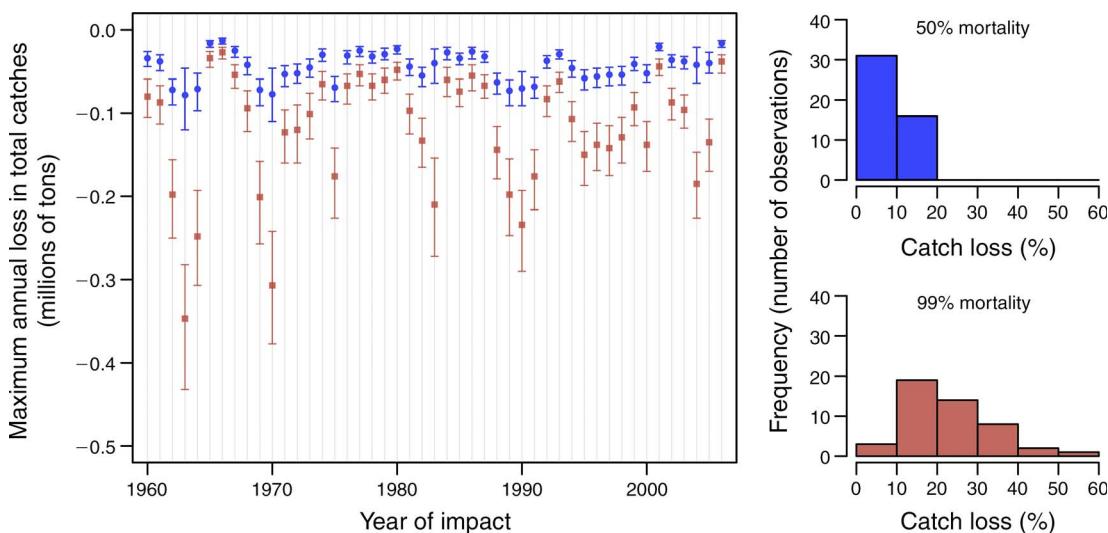


FIG. 5. Maximum annual catch loss in response to 50% (blue/circles) and 99% (red/squares) mortality events. Shown are medians and 95% credible intervals for each impact year (left), as well as the frequency distributions of relative catch loss (right). Medians and CIs were obtained by running simulations for each set of parameter values from the model posterior distributions.

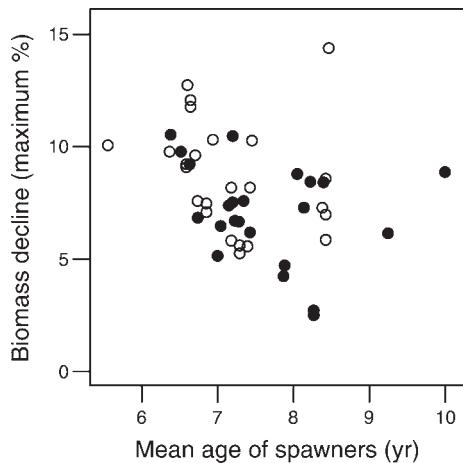


FIG. 7. Maximum relative decline in population biomass vs. mean age of spawners in response to 50% egg or larval mortality. The figure illustrates that the impact of a catastrophic event on population biomass tends to increase as the mean age of spawners decreases. Circles represent high (solid) and low (open) population biomass relative to the median value, indicating that this trend exists at both high and low levels of population biomass.

mortality and US\$53–594 million in the case of 99% mortality, depending on the overall effect on harvestable biomass and the value of the fish in the years following a simulated impact. This corresponds to relative annual economic losses of 3–16% and 6–52%, respectively. It should be noted that this approach assumes the same constant net value per unit biomass of simulated and actual catch. This approximation could potentially over- or underestimate economic loss, depending on how the market value of the fish would change in response to a catastrophic event, for instance when caused by a toxic spill.

DISCUSSION

In this study, we present a framework for quantifying potential effects of catastrophic events at the population level. Using a life cycle model with Bayesian parameter estimation, we simulate catastrophic mortality events during early life stages and assess their consequences for population biomass and harvest in an exploited resource through direct comparison to historical time series. Our simulations demonstrate that marine fish populations can be remarkably resilient against catastrophic events that affect early life stages, owing to density-dependent survival of juveniles and a diverse age structure, with several age classes that constitute population biomass and contribute to future reproduction. Although recovery is generally fast, losses in catch and economic value can be substantial. Our results further suggest that research efforts should focus on long-term and indirect effects via food web interactions, as well as possible sublethal effects, in order to better understand the ecological and economic ramifications of catastrophic events such as oils spills in the marine realm.

Although survival probability over the first year of life is generally low in NEA cod, with typically less than one in a thousand larvae surviving to age 1, interannual variability in survival is high (Langangen et al. 2014). The ratio of maximum to minimum survival from hatching to age 1 year for the modeled time period is about one order of magnitude (factor 10). Hence, an additional mortality of 50% (factor 2) is small, but an additional mortality of 99% (factor 100) is large compared to the natural variation in mortality during the first year of life. As a consequence of the natural variation, few cohorts typically dominate the population biomass, and the simulated impact of a catastrophic event at the population level strongly varies between years.

In addition to the strength of the affected cohort, longevity and the number of reproducing age classes determine the impact of catastrophic events. In a population that consists of many age classes, a partial loss of a cohort has little effect on population biomass and future reproduction. The population-level effects are only considerable when the affected cohort is particularly large and thus is a strong contributor to overall population biomass compared to the preceding cohorts. Therefore, long-lived species are expected to show weaker impacts of severe die-offs that affect a single generation of individuals. Likewise, within populations, catastrophic events can be expected to show stronger impacts when the population is composed of relatively fewer age classes, for instance as a consequence of harvesting. Our simulation analysis suggests that a decrease in the mean age of spawners indeed increases the relative impact of a catastrophic event on population biomass (Fig. 7). Accordingly, it has been shown that generation time affects the relative contribution of recruitment to population growth (Durant et al. 2013). Therefore, changes in the population age structure can increase the sensitivity of a population to extreme events (Perry et al. 2010). Further, massive mortality events during early life stages of long-lived species such as cod have a delayed effect on population biomass, because individuals mature relatively late and grow substantially in body mass in the first few years of life. Year classes thus contribute most to population biomass and harvest after several years, which implies that mitigating management actions such as reducing fishing pressure might be applied successfully during the years following a catastrophic event.

Population resilience to perturbations such as severe egg or larval die-offs is further enhanced by population-intrinsic regulation such as density-dependent survival. Our model incorporates density dependence within and between cohorts. Both mechanisms have been suggested by previous studies on NEA cod (Myers and Cadigan 1993, Bogstad et al. 1994, Hjermmann et al. 2004, Dingsør et al. 2007), and both contribute to population resilience to catastrophic events. First, cannibalism by older cod affects the survival of the 0-group, i.e., post-larval fish

that are a few months to one year old. This *intercohort* density dependence has a delayed compensatory or overcompensatory effect, because a diminished cohort increases the survival of cohorts that follow a few years later. Second, the survival rate of juveniles at age 1–3 years increases at low cohort abundances. This *intra-cohort* density dependence has a compensatory effect. Thus, a cohort that suffers from severe mortality during early life stages experiences higher juvenile survival, which alleviates the impact of the egg or larval die-off as the cohort ages. Our results show that density-dependent juvenile survival due to reduced competition is particularly important for population recovery when the mortality impact is moderate.

In this study, we use a full life cycle model that dynamically links multiple effects of extrinsic and intrinsic factors on the different cod life stages, from eggs to spawners. Specifically, the model incorporates environmental stochasticity through process errors, accounts for the inaccuracy of the scientific survey and landings data, and includes important population-intrinsic processes such as density dependence (Ohlberger et al. 2014). Several processes that could affect the impact of a catastrophic event have not been considered and thus add uncertainty that is not accounted for in the model. Most importantly, we do not account for indirect effects of catastrophic events via food web interactions. Indirect effects via adverse impacts on other components of the food web such as prey species are likely, and may cause delayed and long-term impacts (Peterson et al. 2003). Like most species, NEA cod are embedded in a complex web of interspecific interactions such as predation and competition. Furthermore, we do not consider potential depensatory dynamics at low abundances, because such dynamics have not been observed within the range of historic stock levels in NEA cod (Keith and Hutchings 2012). Catastrophic events may further cause unexpected shifts in ecosystem structure that have not occurred in the past and are thus not represented in the observational data used to fit the model. Such shifts may also occur in the future due to changes in environmental conditions.

Finally, the presented model does not account for potential sublethal effects of natural or human-caused catastrophes, which could be particularly important in the case of toxic spills in the marine environment. Although it is generally recognized that acute exposure to toxic substances, e.g., due to an oil spill, can have devastating impacts on affected populations in very short time, it is also increasingly appreciated that chronic exposure due to the persistence of toxins in the environment can have lasting impacts via indirect effects on behavior, reproduction, or food web interactions (Peterson et al. 2003). Such long-term impacts cannot be modeled via direct effects in a single impact year as done in the present study. However, it is impossible to improve projections of long-term and ecosystem-wide impacts of catastrophic events such as toxic spills

without understanding the consequences of acute mortality. Irrespective of the ultimate cause of the mortality, our results suggest that severe die-offs during early life stages can be buffered by density dependence in vital rates and a broad age structure in long-lived marine species.

ACKNOWLEDGMENTS

We thank staff and scientists at the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) for collecting data on cod eggs and larvae as well as the temperature records of the Kola section. This work was supported by VISTA, a basic research program funded by Statoil and conducted in collaboration with The Norwegian Academy of Science and Letters.

LITERATURE CITED

- Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular Song Sparrow population. *Ecology* 73:805–822.
- Barros, A., D. Álvarez, and A. Velando. 2014. Long-term reproductive impairment in a seabird after the Prestige oil spill. *Biology Letters* 10:20131041.
- Bogstad, B., G. R. Lilly, S. Mehl, O. K. Pálsson, and G. Stefánsson. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). *ICES Marine Science Symposia* 198:576–599.
- Brander, K., A. Neuheimer, K. H. Andersen, and M. Hartvig. 2013. Overconfidence in model projections. *ICES Journal of Marine Science* 70:1065–1068.
- Dingsør, G., L. Ciannelli, K.-S. Chan, G. Ottersen, and N. C. Stenseth. 2007. Density dependence and density independence during the early life stages of four marine fish stocks. *Ecology* 88:625–634.
- Durant, J. M., M. Hidalgo, T. Rouyer, D. Ø. Hjermann, L. Ciannelli, A. M. Eikeset, N. Yaragina, and N. C. Stenseth. 2013. Population growth across heterogeneous environments: effects of harvesting and age structure. *Marine Ecology Progress Series* 480:277–287.
- Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- Good, T. P., J. Davies, B. J. Burke, and M. H. Ruckelshaus. 2008. Incorporating catastrophic risk assessments into setting conservation goals for threatened Pacific salmon. *Ecological Applications* 18:246–257.
- Gunderson, L. H. 2000. Ecological resilience—in theory and application. *Annual Review of Ecology and Systematics* 31:425–439.
- Hauge, K. H., A. Blanchard, G. Andersen, R. Bolland, B. E. Grøsvik, D. Howell, S. Meier, E. Olsen, and F. Vikebø. 2014. Inadequate risk assessments—a study on worst-case scenarios related to petroleum exploitation in the Lofoten area. *Marine Policy* 44:82–89.
- Hjermann, D. Ø., A. Melsom, G. Dingsør, M. Durant, A. Eikeset, L. Røed, G. Ottersen, G. Storvik, and N. C. Stenseth. 2007. 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.
- Hjermann, D. Ø., N. C. Stenseth, and G. Ottersen. 2004. The population dynamics of Northeast Arctic cod (*Gadus morhua*) through two decades: an analysis based on survey data. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1747–1755.
- Incardona, J. P., et al. 2014. *Deepwater Horizon* crude oil impacts the developing hearts of large predatory pelagic fish.

- Proceedings of the National Academy of Sciences USA 111:E1510–E1518.
- IPCC. 2014. Climate Change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Keith, D. M., and J. A. Hutchings. 2012. Population dynamics of marine fishes at low abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1150–1163.
- Langangen, Ø., L. C. Stige, N. A. Yaragina, F. B. Vikebø, B. Bogstad, and Y. Gusdal. 2014. Egg mortality of northeast Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *ICES Journal of Marine Science* 71:1129–1136.
- Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614.
- Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1576–1590.
- Ohlberger, J., L. A. Rogers, and N. C. Stenseth. 2014. Stochasticity and determinism: How density-independent and density-dependent processes affect population variability. *PLoS ONE* 9:e98940.
- Olsen, E., S. Aanes, S. Mehl, J. C. Holst, A. Aglen, and H. Gjøsæter. 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. *ICES Journal of Marine Science* 67:87–101.
- Perry, R. I., P. Cury, K. Brander, S. Jennings, C. Möllmann, and B. Planque. 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *Journal of Marine Systems* 79:427–435.
- Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B. Irons. 2003. Long-term ecosystem response to the *Exxon Valdez* oil spill. *Science* 302:2082–2086.
- Reed, D. H., J. J. O'Grady, J. D. Ballou, and R. Frankham. 2003. The frequency and severity of catastrophic die-offs in vertebrates. *Animal Conservation* 6:109–114.
- Rice, S. D., R. E. Thomas, M. G. Carls, R. A. Heintz, A. C. Wertheimer, M. L. Murphy, J. W. Short, and A. Moles. 2001. Impacts to pink salmon following the *Exxon Valdez* oil spill: persistence, toxicity, sensitivity, and controversy. *Reviews in Fisheries Science* 9:165–211.
- Rose, K. A., J. H. Cowan, Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2:293–327.
- Vincenzi, S., A. J. Crivelli, W. H. Satterthwaite, and M. Mangel. 2014. Eco-evolutionary dynamics induced by massive mortality events. *Journal of Fish Biology* 85:8–30.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-1534.1.sm>