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RESEARCH ARTICLE

Management strategies can buffer the effect of mass mortality in early life stages of fish

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Abstract

1. Mass mortality (MM) events affecting early life stages of fish can have strong and long-term consequences for population abundance and demography as well as the economic activity supported by exploited stocks. Adaptive fishery management may help mitigate economic impacts and ensure sustainable resource use following a MM event.
2. Using a state-space life cycle model, we simulated 'what-if' scenarios of MM on Northeast Arctic cod (*Gadus morhua*) eggs and larvae. We compared the expected catches, total stock biomass (TSB), and interannual variability in catches over a period of 10 years after the simulated disturbance. We further evaluated a range of management mitigation strategies, namely reductions in fishing mortality of varying duration (1–10 years) and intensity (no fishing reduction to full ban).
3. A large range of reductions in fishing led to an increase in expected catches over 10 years compared to no reductions, especially when applied immediately after the perturbation and when the cod population was characterized by a high mean age and high TSB. Severe fishing reductions can increase catches substantially but are associated with high interannual variability. Fishing reductions of moderate intensity applied between 1 and 4 years would allow to increase catches with only a slight increase in interannual variability.
4. Our findings demonstrate the potential benefits of an adaptive approach to fisheries management and highlight that mitigation actions may ensure the sustainable exploitation of fish stocks in the wake of unexpected disturbances.
5. *Synthesis and application*. Mass mortality events during early life stages of fish can potentially have substantial and long-term effects on the population. Mitigation is more efficient when the affected population has a diverse age structure and when the mitigation strategy is applied immediately after the perturbation. Severe reduction in fishing mortality is an efficient measure to increase the expected average catch but is associated with high interannual variability. Fishing reduction of moderate intensity applied during 1–4 years after the event also increases the expected average catch with only slightly higher interannual variability in catches.

KEYWORDS
adaptive management, fishing, mass mortality events, mitigation, NEA cod

1 | INTRODUCTION

Extreme events are increasing in frequency, and natural populations are now threatened at an unprecedented rate (Fey et al., 2015; Ummenhofer & Meehl, 2017). Many natural and climatic events, such as heat waves and storms, are expected to increase in frequency and amplitude along with climate change (Bailey & van de Pol, 2016; Beniston et al., 2007; Jentsch et al., 2007). In parallel, direct anthropogenic pressure persists in the marine environment or can even increase, especially at high latitudes with an increase of shipping activities (Eguíluz et al., 2016) and petroleum activities (AMAP, 2007; Blanchard et al., 2014). Even if the nature and timing of extreme events are often unpredictable, there is an urgent need to develop potential management strategies to strengthen our ability to respond to such adverse events. In the case of exploited species, adaptive management actions may be critical to avoid severe population reduction and, at the same time, alleviate the effects on the economic activity supported by the stock (Walters, 1986). The Northeast Arctic stock of Atlantic cod (NEA cod, *Gadus morhua*) is a migratory stock of high commercial interest. This specific cod stock is, in contrast to most other cod stocks in the North Atlantic, described as sustainably exploited (Ottersen et al., 2014).

The early life stages (ELS) of fish are very sensitive stages and with the combined effects of climate change and the development of anthropogenic activities (e.g. shipping, petroleum activity, fish farming), the success of the NEA cod stock spawning may be at risk. Indeed, low concentrations of toxic compounds such as hydrocarbons or heavy metals can have dramatic effects on fish populations by affecting their survival (e.g. Boglione et al., 2013; Incardona et al., 2012; Sfakianakis et al., 2015). Moreover, storms can also be detrimental at some developmental stages by increasing their dispersal and modifying their drifting patterns (Lough et al., 1996). In a recent study, Rogers et al. (2021) showed the potential effect of heat waves on ELS of fish. Their work suggests that the heat wave observed in the North Pacific Ocean from winter 2013/14 through 2016 affected the ELS of a gadid (Walleye pollock, *Gadus chalcogrammus*) by modifying the energetic demand of the larvae as a direct effect of the increase in temperature on metabolism and at the same time indirectly through a modification of the quality of their prey, resulting in the near disappearance of the 2015-year class in the population.

Overall, the way populations are affected by a perturbation and the way they recover from it depends on many factors. Fishing has been described to alter the structure of populations by removing large and old individuals, which can in turn reduce their capacity to buffer perturbations (Planque et al., 2010). For instance, large and old females produce more and often larger eggs that may develop into larvae that grow faster and withstand starvation better (Hixon et al., 2014). Overall, the reproductive potential of the population is greater if larger/older individuals are proportionally more abundant and their offspring have potentially higher chances of survival and recruitment success (Marshall et al., 1998; Ohlberger et al., 2022) which could in turn allow buffering the effect of a perturbation affecting ELS.

Between a potential mass mortality (MM) event affecting egg and larval stages for the NEA cod, there is a time delay of approximately 3–6 years before the effects of the event can be detected in the fishery, as cod start recruiting to the fishery at age 3. As such, before the cohort potentially weakened by the MM event recruits into the fishery, there is a window of opportunity to implement management actions to alleviate potential long-term effects on catches and population abundance. However, details on how such actions should be implemented are less well explored. Using a life cycle model for NEA cod, Ohlberger and Langangen (2015) demonstrated that the stock is generally resilient to catastrophic events affecting ELS by measuring the duration of the impact. The effects were moderate because of density dependence in survival in later life stages and due to the broad population age structure, which buffers the loss of a single-year class. Although population recovery is relatively fast (less than 15 years), losses in harvest and economic value can nonetheless be substantial.

Here, we aim to (1) evaluate the efficiency of various fishing reduction measures implemented after a MM event and (2) identify population characteristics that can be used to optimize decision-making. For this purpose, we focus on the NEA cod stock for which a life cycle model has been previously developed. We simulate MM events of different severity in ELS and compare the catches with and without mitigation. We then assess the impact of population characteristics such as mean age and spawning stock biomass on the efficiency of fishing reductions. Lastly, we quantify the trade-off between duration and intensity of fishing reductions in order to maximize mitigation efficiency (ME) while keeping the interannual variability in catch at acceptable levels for managers.

2 | MATERIALS AND METHODS

2.1 | The NEA cod

NEA cod is distributed along the coast of Norway and throughout the Barents Sea (Yaragina et al., 2011). Mature cod typically spawn in March and April along the Norwegian coast, particularly around the Lofoten Islands. The pelagic eggs drift northeastward mainly in the Norwegian coastal current. During the drift, the larvae hatch, develop and metamorphose into juveniles before reaching their 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 and start their demersal stage (Ottersen et al., 2014). The juveniles remain in the Barents Sea, and once they reach maturity, around 6–8 years old, they start performing their annual southbound migrations from the Barents Sea to the spawning grounds (Olsen et al., 2010).

NEA cod supports an economically highly valuable fishery. Individuals usually recruit to fisheries around the age of 3–6 and most of the catches are made during a short period that corresponds to the spawning season (ICES, 2019). In the mid-1970s, the catch was around 900,000 metric tons, but experienced a strong decrease over the next decade, reaching a minimum annual catch of 212,000 t in 1990. With the introduction of quotas in 1978 and 1989, for the trawler and coastal fleets, respectively, the catch increased from 1991 onwards remaining above 400,000 t. Other types of regulation are also implemented in order to alleviate the fishing pressure on young individuals (e.g. Minimum catch size, Minimum mesh size, and seasonal or area restriction; ICES, 2019).

Within the time period covered (1959–2012) by the model, the cod population has been fluctuating in both abundance and age-size structure (Hylen, 2002; Ohlberger et al., 2022). For example, in 1975 the population had a broad age structure and high mean age (3.57 years), and the total stock biomass (TSB) is larger than the time series average (2.22 million tons). In 1984, the population had a low mean age (1.33 years) and a low TSB (0.8 million tons). After the implementation of quotas, the stock recovered, and during the year 2000 the mean age of the population was around the mean of the time series (2.87 years), but TSB was still slightly lower than average (1.25 million tons). The time series of mean age of the population, estimated within the life cycle model is presented in Figure S1. The potential effects of a MM event have been described to vary with stock characteristics, with stronger impacts detected when the population had a low mean age among its spawners (Ohlberger & Langangen, 2015).

2.2 | The life cycle model

To evaluate the efficiency of fishing reduction after a MM event in the early stages of life, we employ a 'what if' scenario approach where we simulate MM events in the past followed by different types of fishing reductions. For this purpose, we used a life cycle model that was previously developed by Ohlberger et al. (2014) and was fitted to data from both scientific surveys and commercial landings of NEA cod. 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, covering a total period of 54 years (1959–2012). Furthermore, annual data on age-specific mean body mass and age-specific probability of being mature were used. This NEA cod model has been developed within a state-space approach which allows accounting for unexplained stochasticity in population dynamics (i.e. process noise) as well as for the inaccuracy of the observations (i.e. observation error). Bayesian inference was used to estimate the joint posterior distributions of all parameters in the model based on specified prior distributions. The process part of the model describes the population dynamics, that is, the age- or stage-specific abundances over time, by modelling the survival from one life stage or age class to the next. The survival terms consist of natural mortality and additional effects depending on life stage or age class, including a positive temperature effect on larval survival, intercohort cannibalism in the 0-group, intracohort density-dependent survival of age 1–3 juveniles, and fishing mortality on age 4 and older. Survival from eggs to larvae was modelled as a constant mortality term without additional effects, that is, a MM event on the egg or larval stages will have the same effect on the cohort. A log-normal 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 lifestyle. A linear relationship between spawning-stock biomass and egg numbers with stochastic lognormal process was used to describe egg production. To consider the thermal conditions in the Barents Sea, temperature records from the Kola meridian transect were used. A more complete description of the model is provided in Appendix S1 (see also Ohlberger et al., 2014 for details). The present study uses a modelling approach, as such no animal ethical approval was required.

2.3 | Simulation

The samples of the posterior parameter distributions from the NEA cod life cycle model were used in this study to simulate severe mortality of cod eggs or larvae in a single year and to evaluate the effect of different types of management actions (i.e. reduction of fishing of different strengths and duration) on population biomass and fisheries catches. We used the posterior distributions (750 samples) to describe the range of possible outcomes and not just an average.

Simulations were performed by sampling parameters from the estimated posterior distributions of the age-specific mortality rates, temperature effects, density dependence terms, fishing mortalities, and process errors. Those parameters remain the same as in the original model. MM events on ELS (i.e. eggs and larvae) were simulated for two different severities of events (50% and 99% mortality), in addition to scenarios without MM (0% mortality). In the year following the MM event, fishing reductions were applied for a duration of 1–10 years and an intensity from 0% to 100% (by steps of 10%). To compare the different scenario simulations, we focused on the total catches during the 10 years following the disturbance. The simulations were run for each possible year of the time series (1960–2001). Thus, this time span covers the immediate negative effects on catches due to implementing a fishing reduction, as well as the expected positive effects on population recovery. With 42 possible years of impact, three types of mortality, 10 fishing reduction intensities and 10 fishing reduction durations, a total of 12,600 different scenarios were tested. In addition, we tested the effect of a mitigation applied with a delay of 5 years (i.e. starting the year after the first MM effects are detectable in the catches).

2.3.1 | Mitigation efficiency

ME was calculated as the percentage change caused by a specific mitigation strategy on the total catches over a period of 10 years after the MM event:

$$\mathrm{ME} = \frac{\Delta C_{10\mathrm{yr}}}{Ci_{10\mathrm{yr}}} \times 100.$$

With Ci the 10 years total catch without applied fishing reduction and $\Delta C_{10\mathrm{yr}}$ the difference between Ci and the 10 years total catch with applied fishing reduction. We restricted our analysis to two main population descriptors that are routinely estimated: (1) TSB represents the biomass of all fish age 3+, including immatures, and (2) the mean age of the population, as an indicator of the relative contribution of old/large adults within the population. The relationship between the population descriptors and the mitigation efficiencies were explored using ordinary least squares regression on the mean of the parameter distribution.

3 | RESULTS

To evaluate the potential of different fishing reductions, we simulated the occurrence of a single-year MM event among ELS for each possible year of the time series (1960–2001) and for different severity levels. Fishing reductions of different intensity and duration were applied from the year following the MM event. An example of a severe MM event (99% mortality) for a single year (1970) is shown in Figure 1.

In comparison with the unperturbed time series, the decrease in catches in the scenario without fishing reduction (Figure 1a) is only noticeable 4 years after the perturbation, in 1974, when the affected cohort recruits into the fisheries. The impact of the MM event on biomass (Figure 1b) is moderate in the first years because the affected age class of juveniles contributes little to total biomass but between 1973 and 1977 it represents an annual loss of 0.57 million tones on average. A scenario of a single year total ban (no fishing for 1 year) is also represented in Figure 1. The immediate effect of a total ban is, naturally, absence of catches for that year but in the example presented in Figure 1a, the catches are considerably higher after the ban compared to the scenario where no mitigation was applied. As a result of the mitigation, annual losses in population biomass between 1973 and 1977 were reduced by more than a half (Figure 1b, annual loss of 0.23 million tones on average). There are noticeable differences in the dynamics of the catches between scenarios, especially in the short term, because the intense catch reduction due to the mitigation is often followed by a strong increase in catches (e.g. Figure 1). Therefore, to be better able to compare and evaluate the different scenarios, we computed the total catches over a period of 10 years following the perturbation.

As shown in Figure 2, which highlights three exemplary impact years, the catch loss over 10 years in absence of mitigation increases with the severity of the MM. It is worth noting that similar severity of MM events applied to those three impact years does not produce the same catch loss. For example, a MM event of 99% mortality in 1975 would imply, over the 10 years following the event and in the absence of any mitigation, a loss of 0.42 million tons (9% of the catches). The same MM event occurring in 1984 or 2000 would represent a loss of 0.27 and 0.46 million tons, respectively (representing 7% and 10% of catches).

Most of the mitigation actions presented in Figure 2 led to an improvement in the catches over a period of 10 years. One exception is a reduction by 10% for 10 years applied after an impact in 2000 which led to a reduction of the 10 years catch by 0.03 million tons.

The different measures of fishing reduction varied in efficiency. Over the four mitigation strategies presented, the total ban appears to be more efficient for the impact years 1975 and 2000 even if the differences with 50% reduction during 2 years and 25% reduction during 5 years are relatively small. In contrast, for the year 1984, a moderate fishing reduction of 25% applied during 5 years appears to be the most efficient mitigation, showing that the efficiency of a mitigation strategy can depend on the year of impact.

Figure 3 shows the ME for a 10% fishing reduction lasting 10 years and a total fishing ban for a single year representative of two types of mitigation: (i) long and moderate or (ii) short and intense. We represented the ME as a function of the mean age in the population (Figure 3a) and as a function of the TSB (Figure 3b), both at the time of impact. The efficiency of a 10% reduction in fishing for 10 years is not significantly related to the population's mean age (slope $= 0.004\,\mathrm{year}^{-1}$, p-value > 0.05). This has also been observed in all simulations that included a fishing reduction lasting 3 years or more. In contrast, the efficiency of a 1-year total ban is significantly associated with the population's mean age (slope $= 0.04\,\mathrm{year}^{-1}$, p-value < 0.05), showing that the potential of this type of mitigation is greater when the mean age of the population is high. The relationship between TSB and ME was found to be not significant for either long and moderate or short and intense mitigation strategies. However, it is worth noting that the increase in absolute catches depends on TSB, and fishing reductions applied when TSB is high lead to an increase in catches over the subsequent 10 years (Figure S2).

Although intense fishing reductions over several years are efficient measures that can improve the catch over 10 years by more than 20% (Figure 4a) and lead to strong increases in the population total biomass (Figure S3), such mitigation measures are accompanied by higher interannual variability in catches. The interannual catch variability, computed as the standard deviation of the catches over the 10 years following the MM, is about 3–7 times higher compared to the interannual catch variability without mitigation (catch variability change from 200% up to almost 600%, Figure 4a). Additional years of fishing duration increase the ME by up to 4 years. Above 5 years of reduction, adding a year of fishing reduction would not increase the ME for the most intense fishing reduction (>60%) but will strongly increase interannual variability. The intense reduction applied for more than 7 years would lead to a negative efficiency on the 10-year catch. The uncertainty in ME and the change in catch variability associated with each mitigation, indicated by the wide

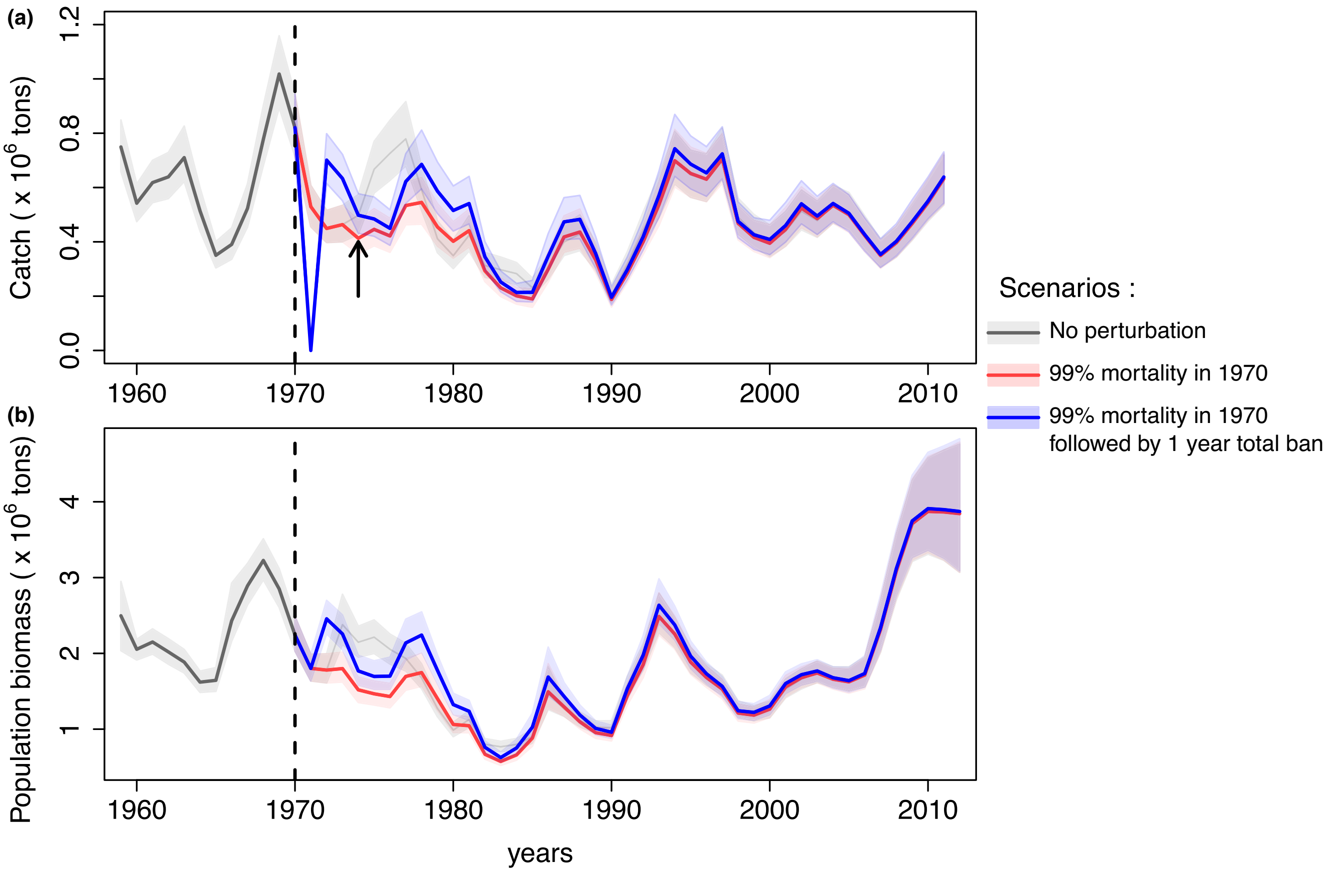

FIGURE 1 Time series of (a) annual catch from 1959 to 2012 and (b) total biomass of the population for three different scenarios. In both panels, the black line represents the median of the posterior distribution obtained from the unperturbed model, where no mass mortality or fishing reductions were applied. The red line corresponds to a scenario with 99% mortality on early life stages in 1970 without reduction in fishing. The blue line corresponds to a scenario with 99% mortality in 1970 followed by a total ban of 1 year. The shaded areas represent the 95% credible intervals of each time series. The black arrows point to the first noticeable effect of the 99% mortality event on the catch (1974).

standard deviation bars, is high (Figure 4b) and corresponds mainly to interannual variability as the ME varies between years (Figures 2 and 3). The response to a specific mitigation action depends on the year it is applied. Measures that respect the harvest control rules (Figure 4b), limiting the year-to-year change in quota to 20%, generally lead to an increase in average catch (ME between 1% and 6.8%) without substantially increasing the interannual variability (under 11.5%) (Figure S4). Interestingly, if the fishing reduction was applied 5 years after the perturbation (i.e. 1 year after the perturbation effects are detectable in the catches) instead of 1 year after the perturbation, the efficiency of any type of mitigation was lower. The only exception to this observation concerns short measures (i.e. applied during 3 years or less) applied after an impact in 1989 or 1990 (Figure S5).

4 | DISCUSSION

Extreme events with dramatic consequences for animal populations are rare but systematic and therefore should be taken into account when developing conservation strategies (Anderson et al., 2017). Over the last decade, examples such as the 2010 Deepwater Horizon oil blowout in the Gulf of Mexico (Safina, 2011) or the North Pacific heat wave that started during the winter of 2013–2014 (Cornwall, 2019) have emphasized the need to anticipate and evaluate mitigation strategies to be able to implement them when needed. Ohlberger and Langangen (2015) suggested that while populations of marine fish such as NEA cod can be resilient against catastrophic events that affect ELS, the resulting losses in catch and economic value can be substantial. In a recent study, Carroll et al. (2018) estimated that a long and moderate reduction in fishing can attenuate losses to the adult population, allowing a quick recovery after MM affecting a single age class. Whereas their estimates were based on a unique year of impact (1995) and for a unique type of mitigation (fishing reduced by 10% for 8 years), we evaluated the efficiency of fishing reduction applied to several years (i.e. all impact years between 1960 and 2001) and for a range of intensities and durations. We have shown that it is possible to attenuate the effect of MM events on catches, especially when mitigation actions are applied shortly after a MM event and when the population has a high mean

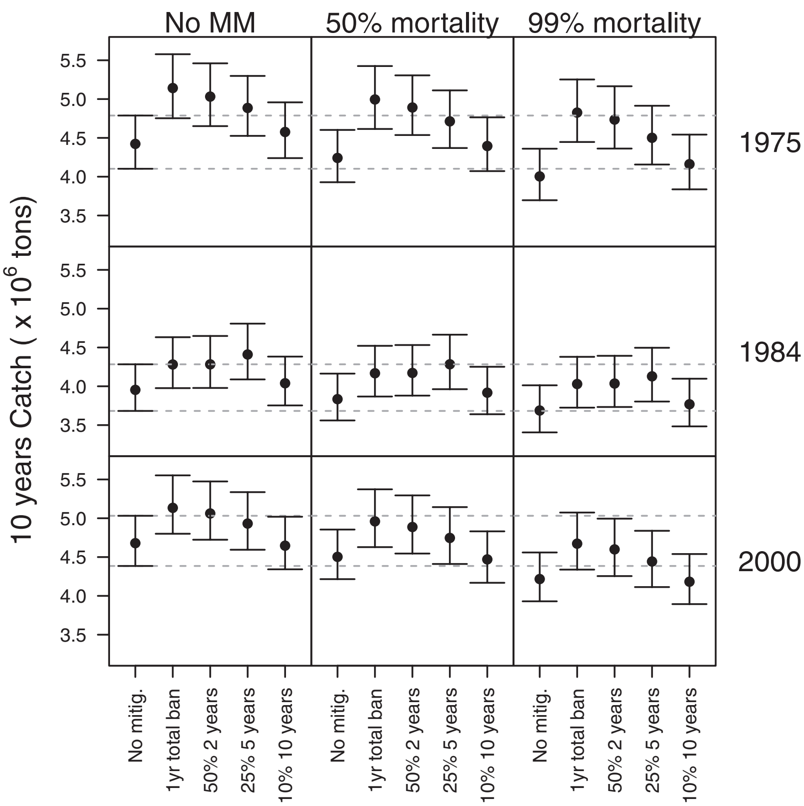

FIGURE 2 Total catches over the 10 years following no mass mortality (No MM, 1st column), a 50% mortality event during early life stages (ELS; 50% mortality, 2nd column) and a 99% mortality event during ELS (99% mortality, 3rd column) in 3 years 1975, 1984 and 2000. Catches were calculated as the sum of the 10 subsequent years after the MM event. The dots represent the median, and the error bars represent the 95% credible interval of the posterior parameter distribution. The dotted grey lines correspond to the 95% credible interval of the 10-year catch without MM event and mitigation action to serve as reference.

age. Intense fishing reductions are potentially more efficient, but also lead to greater interannual variability in catches, which can be an undesirable effect.

We found that both the effect of MM events and the effect of specific mitigation strategies varied between years. The mean age of the population at the time of impact, one of the population descriptors that can typically be calculated based on stock assessment surveys, explained part of the variability in ME. A lower mean age of the population was associated with a lower ME, but also with a lower egg production (Figure S6). During the period covered by our model, the total biomass of the NEA cod stock declined from more than 2.5 million tons in the early 1970s to less than 1 million in the 1980s and the age structure of the population was strongly truncated. During this period, in addition to being more severely affected by potential MM of ELS (Ohlberger & Langangen, 2015), any mitigation strategy would have been less efficient. After the introduction of quotas, the stock started to recover and, from mid-1900, presents a relatively high biomass and mean age. Older and larger females are more fertile and produce eggs that are generally of better quality (Berkeley et al., 2004; Cardinale et al., 2000; Marteinsdottir & Thorarinsson, 1998) and tend to spawn for a longer period (Secor, 2007). They usually spawn over a larger area (e.g. Berkeley et al., 2004; Kjesbu et al., 1992, 1996), which is suggested to increase the survival of the offspring. Overall, the reproductive potential of the population is greater when older individuals are proportionally more abundant (Ohlberger et al., 2022), which in turn improves the capacity of the population to respond to perturbations. As fishing pressure is not random and targets older/larger fishes (Law, 2000), reduced fishing pressure itself leads to a recovery of the mean age of the population, and thus implies a higher capacity to buffer perturbations. Overall, most mitigation actions led to an improvement in catches over a 10-year period. All fishing reductions applied before the 2000s led to an increase in catch, including in scenarios without a MM event. This indicates that the stock was overexploited, from a sustainable yield perspective, for most of the period covered by the model.

It should be noted that the MM events simulated in this study affect eggs and larvae, while the reduction in fishing affects 4+ age classes. As such, only applying a fishing reduction for 4 years or more will reduce fishing mortality in the weak cohort, affected by MM. All the fishing reduction tested here decreased the fishing mortality on old and mature individuals that will contribute to the reproductive potential of the population. Our results show that fishing reductions applied with a 5-year delay are less efficient. This can be

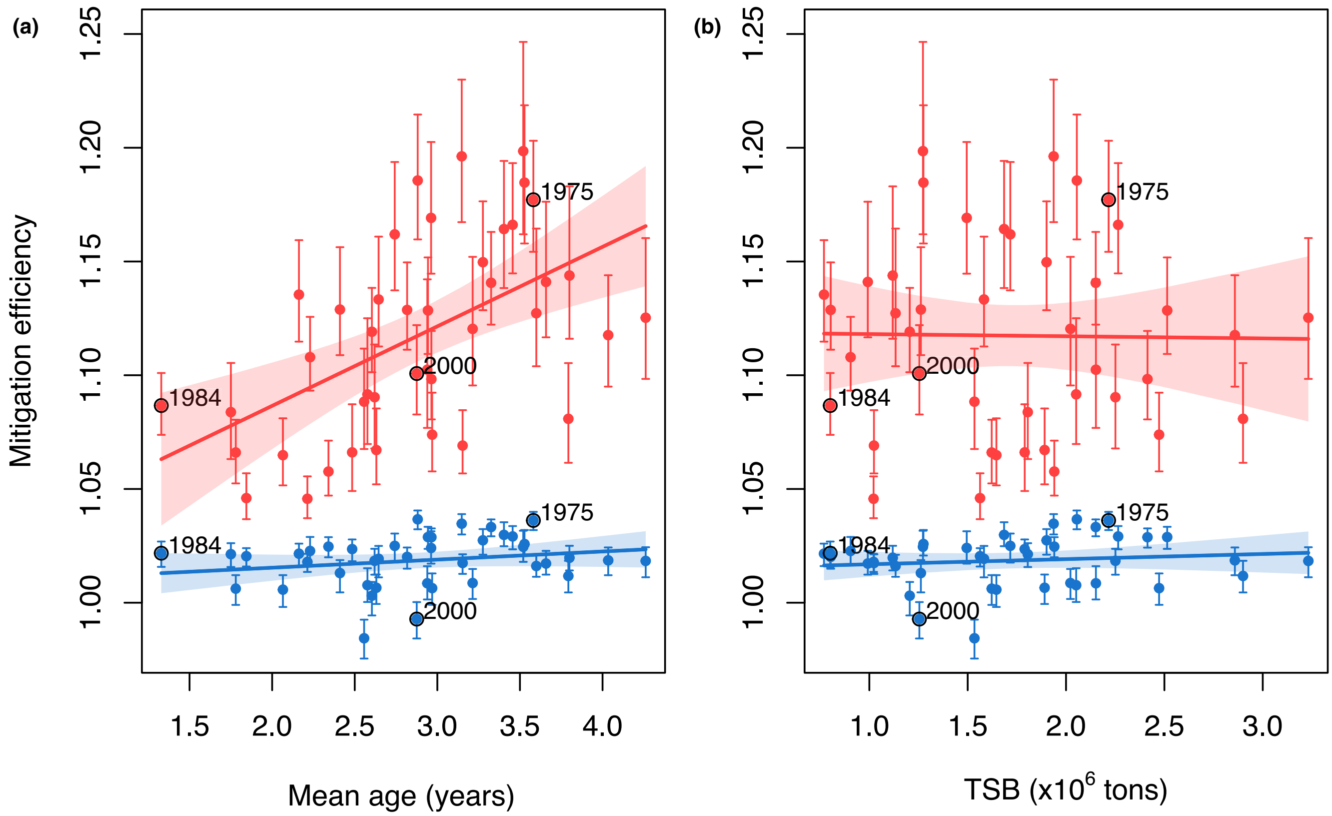

FIGURE 3 Mitigation efficiency (ME), calculated as the 10-year catch ratio between scenarios with and without reduction of fishing, in relation to (a) the mean age of the population and (b) the total biomass of the stock. In both panels, each dot represents the median ME for each year of impact, and the bars correspond to the 95% credible interval from the posterior distribution. The red dots correspond to a strong and short fishing reduction (total ban for a single year); the blue dots correspond to a moderate and long-lasting fishing reduction (10% reduction lasting for 10 years).

explained by the fact that the reproductive potential of the population decreases when the weak cohort enters the spawning stock, from age 6. Applying the reduction as soon as possible, potentially even during the MM event, will likely improve the efficiency of any mitigation.

Sustained management of fish stocks promotes greater stability both in biomass and catches (Worm et al., 2009), and it also allows more mitigation alternatives in order to buffer extreme events, as moderate fishing reduction can be efficient. It would also be important to evaluate the potential of mitigation strategies for fish with shorter lifespans (e.g. capelin), more variable recruitment (e.g. herring or haddock) or low degree of compensatory density dependence, which are expected to be more vulnerable to losses in a single recruitment event (Botsford et al., 2014; Langangen et al., 2023; White et al., 2022). MM events may also last for more than a single year (White et al., 2022), with potentially higher cumulative impacts such that mitigation strategies may need to be more drastic. More detailed studies that simulate such long-lasting MM events are needed to identify the best mitigation strategies in such cases. The age structure is an important aspect of the resilience of the population, and it will be important to consider the effect of mitigation strategies on the population age structure as it could affect its capacity to endure long-term disturbances.

Effects of a MM event on eggs and larvae would be detectable in catches only 3–6 years later when the cohort affected by the MM event has recruited into the fishery. Consequently, management actions that alleviate the long-term effects on catches and ensure sustainable use of the stock can be implemented before catches are affected. An important feature that our analysis revealed is that mitigation actions must be taken as soon as possible to maximize ME. This implies the need to strengthen our ability to assess the mortality caused by perturbations and to adopt appropriate measures quickly. Within this study we focused on MM occurring in a single year and hence affecting one unique cohort, but other kinds of disturbance can occur over several years. One of the most striking examples is the North Pacific heat wave (called 'the blob') that lasted more than 4 years starting in winter 2013–2014, leading to a reduction in the population of Pacific cod (*Gadus macrocephalus Tilesius*) by more than 70% in 2017 (Cornwall, 2019). Subsequently, strong quotas were implemented that limit fishing on Pacific cod by 80%, but the stock has not recovered so far (Peterson Williams et al., 2021).

Intense fishing reductions are on average the most effective to obtain high catches over the 10 years following a MM event. Drastically reducing fishing mortality for a year allows more fish to survive, grow and eventually reproduce, and these fish can be

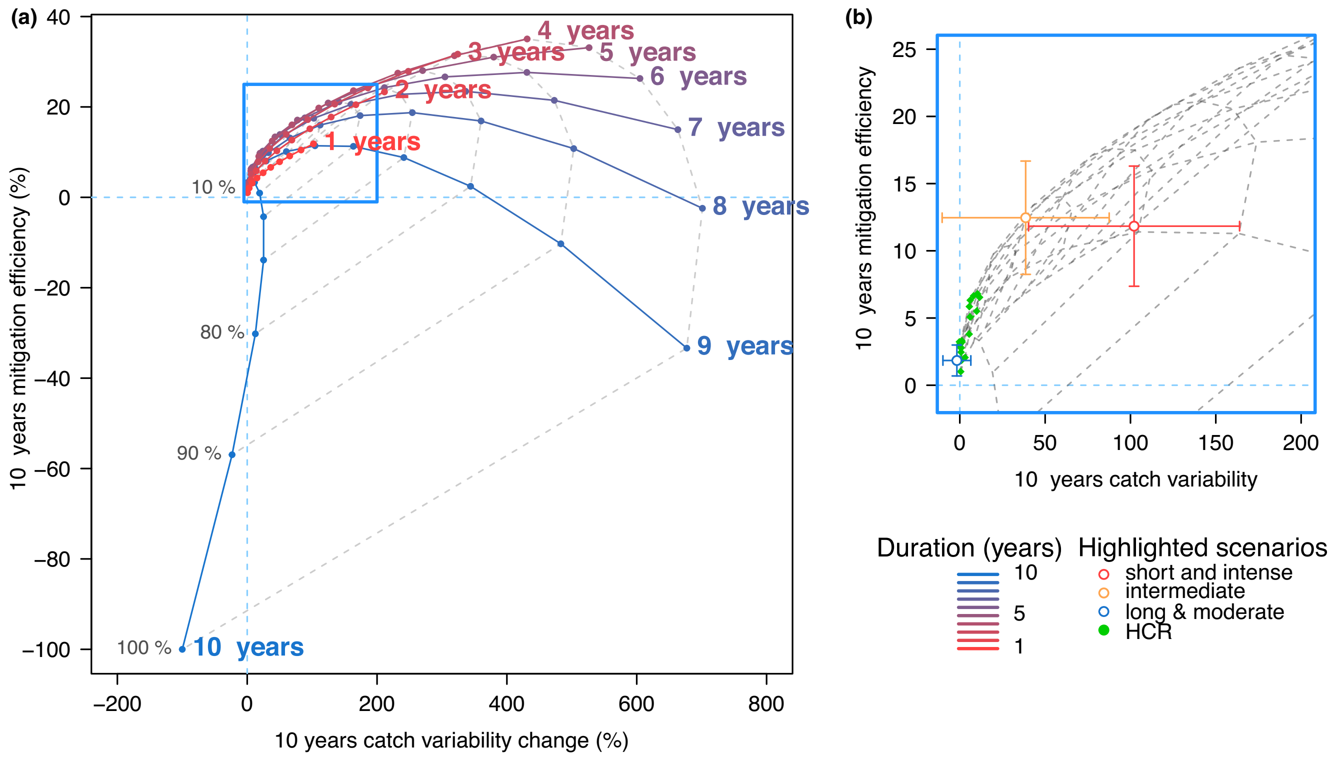

FIGURE 4 Mitigation efficiency (ME) and catch variability associated with each mitigation strategy tested. (a) Each dot represents the average for each mitigation strategy over all possible impact years. Isoclines of fishing reduction intensity are represented by the grey dotted lines (10%, …, 80%, 90%, 100%), and isoclines for duration of the fishing reduction are represented by solid lines in a colour gradient from red (1 year duration) to blue (10 years duration). The blue square represents the area shown in (b). In (b) three scenarios, representative of short and intense (red), intermediate (orange), and long and moderate (blue) fishing reductions. The vertical and horizontal bars represent the standard deviation in both ME and change in catch variability. Green dots represent scenarios that comply with the harvest control rules for Northeast Arctic cod (ICES, 2019).

caught in the following years as older heavier individuals. Their offspring will recruit 3–6 year later, contributing to the catch over the 10-year period (Figure S7).

However, intense fishing reductions tend to strongly increase the interannual variability of catches, which can have economic consequences for fishermen (Sethi, 2010). Measures that respect the harvest control rule, which limits the year-to-year change in quotas by 20%, allow to increase catches without substantially increasing the interannual variability. Severe MM events may, however, require a more intense fishing reduction. Although the present work did not include socio-economic aspects, it is likely that the acceptance of any mitigation among fishermen will depend on the nature of the perturbation itself. Natural extreme conditions, toxic spills or a disease outbreak may have a different effect on consumer behaviour and consequently on the market value. As an example, Safina (2011) suggested that consumer perceptions affected fisheries economic value after the Deepwater Horizon blowout. In addition, our model focuses on a single species but other components of the ecosystem should ideally be accounted for to choose a proper management strategy, because the implementation of a quota on a single species can have consequences for other exploited species. For example, strong fishing quotas are often associated with an increase in discards (Crean & Symes, 1994). When simulating MM events and subsequent mitigation strategies, we assume that all the relationships between parameters, fitted to the observational data, will remain unchanged. However, catastrophic events may produce unexpected changes in ecosystem dynamics and structure that may affect natural mortality, and cannot be accounted for using our modelling approach. Within the range of observed temperatures during the period covered by the model, there is a positive relationship between temperature and larval survival (Ohlberger et al., 2014). We can hypothesize that with higher temperatures, the recovery after a catastrophic event will be faster. However, the relationship between larval survival and temperature may change above a certain temperature threshold such that we cannot extrapolate outside the range of observed temperatures.

Despite these limitations, our findings demonstrate the potential benefits of an adaptive approach to fisheries management. They highlight that mitigation actions can ensure the sustainable exploitation of fish stocks in the wake of an unexpected disturbance. Management actions, consisting of reducing fishing effort during one or several years, can alleviate the adverse effect of MM events that affect ELS of fish on expected catches over a period of 10 years. Nevertheless, the trade-off between ME, interannual variability in catch and other socioeconomic factors will have to be carefully weighted by decision makers. To maximize their efficiency, it is crucial to promptly implement fishing reductions when a MM event is detected. Furthermore, populations with a more diverse and older age structures are expected to exhibit greater resilience to MM events, and thus require lower intensity intervention in the wake of MM events.

AUTHOR CONTRIBUTIONS

Øystein Langangen and Jan Ohlberger conceived the study. All authors contributed to the study design. Lucie Buttay performed modelling, analyses and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The present study uses the data available in supplement to Ohlberger et al., 2014 and can be accessed here https://figshare.com/articles/dataset/_Stochasticity_and_Determinism_How_Density_Independent_and_Density_Dependent_Processes_Affect_Population_Variability_/1044345 and directly downloaded through Figshare here https://doi.org/10.1371/journal.pone.0098940.s001 (Ohlberger et al., 2014).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Description of the process model for NEA cod age-structured population dynamics.

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