

RESEARCH ARTICLE

Persistence of fish populations to longer, more intense, and more frequent mass mortality events

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Abstract

Over the last decades, mass mortality events have become increasingly common across taxa with sometimes devastating effects on population biomass. In the aquatic environment, fish are sensitive to mass mortality events, particularly at the early life stages that are crucial for population dynamics. However, it has recently been shown for fish, that a single mass mortality event in early life typically does not lead to population collapse. Moreover, the frequency and intensity of extreme events that can cause mass mortality, such as marine heatwaves, are increasing. Here, we show that increasing frequency and intensity of mass mortality events may lead to population collapse. Since the drivers of mass mortality events are diverse, and often linked to climate change, it is challenging to predict the frequency and severity of future mass mortality events. As an alternative, we quantify the probability of population collapse depending on the frequency and intensity as well as the duration of mass mortality events. Based on 39 fish species, we show that the probability of collapse typically increases with increasing frequency, intensity, and duration of the mortality events. In addition, we show that the collapse depends on key traits such as natural mortality, recruitment variation, and density dependence. The presented framework provides quantitative estimates of the sensitivity of fish species to these increasingly common extreme events, which paves the way for potential mitigation actions to alleviate adverse impacts on harvested fish populations across the globe.

KEYWORDS

duration, intensity, and frequency of events, early life, fish, marine heatwaves, mass mortality events, population level

1 | INTRODUCTION

The frequency and severity of extreme climatic events are increasing with anthropogenically caused climate change (Field et al., 2012; Laufkötter et al., 2020). For instance, marine heatwaves (MHWs) have been reported more frequently over the last century with increasing intensity and duration (Free et al., 2023;

Laufkötter et al., 2020; Oliver et al., 2018; Smith et al., 2023; White et al., 2023). Such extreme climatic events often cause extreme ecological events such as mass mortality events that rapidly remove a large proportion of individuals from many demographic classes over a relatively short period. An increased occurrence of mass mortality events has been reported globally and across taxa, including marine invertebrates and marine and

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freshwater fishes (Fey et al., 2015; Raymond et al., 2022; Tye et al., 2022). In the marine environment, mass mortality events are associated with a range of causes, including thermal and oxygen stress, biotoxicity, disease, and contaminants (Fey et al., 2015), that often can be directly or indirectly related to climate change. For example, the increasing prevalence and severity of diseases with climate change are affecting aquatic populations (Hoegh-Guldberg & Bruno, 2010), including fish (Genin et al., 2020; Tye et al., 2022). Harmful algal blooms (HABs) have increased in frequency over the last decades, partially linked to climate change (Gobler, 2020). HABs can cause mass mortality of fish (Karlson et al., 2021) including high mortality at the early life stages (Gjøsæter et al., 2000). For many marine organisms, and particularly for fish, survival through early life stages plays a key role in population dynamics (Gaillard et al., 2008; Moyano et al., 2023; Subbey et al., 2014). Early life stages of fish are known to have a relatively limited thermal tolerance (Dahlke et al., 2020), highlighting the link between MHWs and elevated mortality at these stages. For example, MHWs have been associated with loss of spawning habitat (Dahlke et al., 2018; Laurel & Rogers, 2020) and reduced egg or larval survival (Fiksen & Reglero, 2022; Laurel & Rogers, 2020; Rogers et al., 2021). Similar to increased temperature, oxygen stress (i.e., reduction of dissolved oxygen) may cause increased mortality in early-life fish (Köster et al., 2005, 2017). At the same time, areas of reduced oxygen (i.e., oxygen minimum zones) are projected to expand in the future (Stramma et al., 2012). In addition, non-climate-related human activities can lead to mass mortality in fish. For instance, a marine oil spill is a one-time event that can lead to mass mortality in the marine environment, including elevated mortality in the early life of fish (Hjermann et al., 2007; Langangen, Olsen, et al., 2017; Marris et al., 2020; Rooker et al., 2013). Another example is the adverse and potentially lethal effects in fish associated with cold shocks caused by industrial effluence (Ash et al., 1974; Szekeres et al., 2016). Taken together, this suggests that elevated mortality in the early life stages of fish, from now simply referred to as mass

mortality events in early life stages, will increase in frequency and intensity in the decades to come. Given the high sensitivity of early life stages to environmental perturbations, understanding how mass mortality at these stages affects population dynamics will improve the perception of how climate change will impact marine populations and biodiversity.

While the impacts of mass mortality events on population dynamics have been investigated in detail over the years by ecologists (Commander & White, 2020; Kimbro et al., 2017; Lande, 1993; Mangel & Tier, 1994), climate change effect studies have largely focussed on short-term single events (Bailey & van de Pol, 2016); coined pulsed events (Bender et al., 1984; Clark-Wolf et al., 2023; Harris et al., 2018; Jentsch et al., 2007). Notwithstanding, some investigations of empirical systems have quantified the effects of multiple extreme events such as in coral populations (Fabina et al., 2015; Hughes et al., 2019). For instance, Fabina et al. (2015) found that infrequent but severe events had a higher impact at the population level than less severe and more frequent events. For fish, the population-level effects of pulsed mass mortality events in the early life stages are associated with the longevity of the species (Langangen et al., 2023; White et al., 2022). However, it remains to be investigated systematically how altered frequency, intensity, and duration of mass mortality events in early life stages affect fish at the population level. Since predicting and quantifying the future climate state and ecological consequences are associated with large uncertainty (Brander et al., 2013), we opted to reverse the question and ask how frequent and how severe mass mortality events can be before fish populations collapse. To address this question, we exposed 39 fish species (Table S1) described by statistical models to a range of mass mortality events of different intensities, durations, and frequencies (Figure 1), affecting early life stages and recorded the resulting probability of collapse. We quantify and describe the response of fish populations to increased occurrence and intensity of mass mortality in early life using the mass mortality characteristics and species-specific life-history traits describing mortality, recruitment, and size.

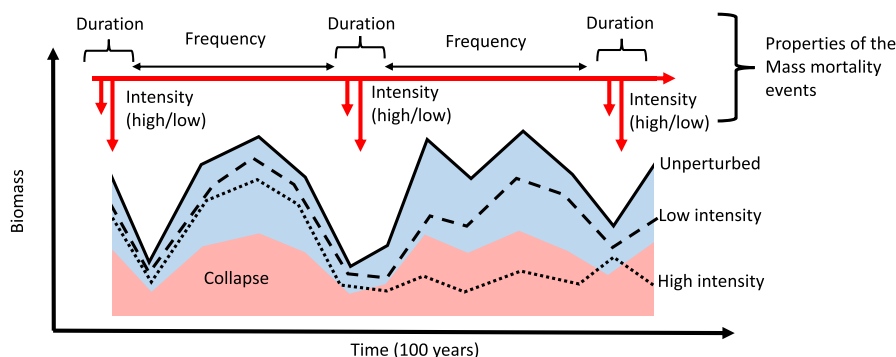


FIGURE 1 Overview of the modeling approach taken in this study. The period (shorter lead to a higher frequency) is the time between each mass mortality events (red downward pointing arrows), the intensity can vary (length of the arrows) as well as the duration of the events. The biomass trajectories for the perturbed cases (low-intensity mass mortality: dashed line and high-intensity mass mortality: dotted line) are compared with the unperturbed dynamics (solid line) to determine the probability of collapse for different frequency, duration, and intensity of mass mortality.

2 | MATERIALS AND METHODS

We classified scenarios of mass mortality according to frequency (expressed through the number of years between events, that is, the periodicity, instead of the number of events per year), duration (number of years with increased mortality per event), and intensity (level of increased mortality) of the events (Figure 1). We investigated how changes in these three variables affect the population dynamics of fish. For this purpose, we used species-specific population models that account for density dependence in early life, stochastic recruitment, natural and fishing mortality, age structure, length-specific growth, and weight-specific reproductive output (Langangen et al., 2023). In short, the Stock–recruitment relationship was modeled as a linearized Ricker model (Ricker, 1954):

$$\log\left(\frac{R_t}{S_t}\right) = \beta_0 + \beta_1 S_t + \epsilon_t, \quad (1)$$

where R_t and S_t are recruitment and spawner biomass respectively adjusted to the appropriate time-lag. β_0 and β_1 represent density-independent and density-dependent processes and ϵ_t is an error term. The error term accounts for lag 1 autocorrelation according to $\epsilon_t = \varphi\epsilon_{t-1} + \omega_t$, where φ is the autocorrelation coefficient and ω_t is normally distributed with mean zero and standard deviation σ . The models were parameterized for 39 different species (Table S1) with stock-specific stock–recruitment data (i.e. age at recruitment a_R and time series of recruitment and spawner biomass; Myers et al., 1995) using the software Just Another Gibbs Sampler (JAGS) (Plummer, 2003). Post-recruit survival was modeled with a standard cohort relationship:

$$N_{a,t} = \begin{cases} R_t & \text{for } a = a_R \\ N_{a-1,t-1} \exp(-(M+F)) & \text{for } a > a_R \end{cases}, \quad (2)$$

where $N_{a,t}$ is the abundance at age a at year t and M and F are the natural and fishing mortalities. In the model, the spawner biomass was calculated using:

$$S_t = \sum_{a=a_{\text{mat}}}^{\text{max-age}} W_a \times N_{a,t}, \quad (3)$$

where a_{mat} is the age at maturity and max-age is the maximum age set to 50 (100 for the long-lived Greenland halibut). Note that the maximum age estimated based on Hoenig (1983) was less than 40 years for all species (except Greenland halibut, Langangen et al., 2023). Growth in weight was modeled with a von Bertalanffy growth curve:

$$W_a = W_\infty (1 - \exp(-k(a - t_0)))^b, \quad (4)$$

where W_a is the weight at age a , while W_∞ and k are the asymptotic weight and the growth coefficient, respectively. The t_0 scales the size at age zero and b is the power coefficient in the length–weight relationship. Species-specific parameter values for a_{mat} , M , W_∞ , k , t_0 , and b were taken from FishBase (Table S1; Froese & Pauly, 2000). The fishing

mortality F (see Table S1) was used to scale the average biomass, and values were used as in Langangen et al. (2023).

The above models were used to simulate population dynamics over a century under different mass mortality scenarios to quantify the potential population-level impact of different duration (*dur*, three levels), frequency (*fre*, six levels), and intensities (*int*, four levels) of early life mass mortality (Table 1; Figure 1). The different combinations of the three variables gave in total 72 different scenarios applied to each of the 39 species. Note that differences in intensity could be due to both the strength of the extreme events as well as the degree of spatiotemporal overlap between the events and the early life stages. For each scenario and species, we performed 100 simulations to reduce the risk of results being driven by randomness. The early life mass mortality was simulated by reducing the S_t (a proxy for egg numbers) over the duration and by the intensity and periodicity as described in the scenarios (Table 1). We compared the population dynamics of the perturbed with the unperturbed population dynamics over the 100-year simulation period (from the first year of impact). The time frame of 100 years was used to enable the investigation of long periodicities (Table 1). We considered the species to collapse, or persist if not, if the population biomass was reduced to 50% or less compared with the unperturbed population biomass, often called a baseline normalized approach (Ingrisch & Bahn, 2018), at any time during the 100 years simulated (Figure 1). We used the median persistence (*persist*, 0 or 1) across simulations for further analysis. For visualization and summarizing our results, we applied a regression model to the median simulated persistence (White et al., 2014) with impact, duration, and frequency as interacting covariates. In addition, we included the species-specific life-history parameters in the regression, that is, natural mortality (M), recruitment age (a_R), asymptotic weight (W_∞), maturation age (a_{mat}), recruitment variation (σ), and degree of density dependence (*dd*) (see Supporting Information and Table S1, based on FishBase and the recruitment data). The model was formulated using a generalized additive model (GAM) using the *mgcv* library (Wood, 2017) in R 4.2.1 (R Core Team, 2022). We applied a shrinkage approach (using the flag `bs="ts"`) to remove insignificant variables by potentially modifying the smoother to effectively remove the variable. This process removes variables with limited impact on the persistence of the species. For the impacts of mass mortality events, we applied a three-way interaction term between the events' intensity, periodicity, and duration. We included a random species (*species*) effect to account

TABLE 1 Overview of the applied scenarios. All combinations of the mass mortality properties were investigated, for a total of 72 scenarios per species.

Mass mortality properties	Scenarios					
Intensity (early life mortality)	25%	50%	75%	99%		
Duration (years)	1	2	3			
Periodicity (years between events)	5	10	15	20	30	50

for the fact that multiple scenarios were performed on the same species. The model was formulated as:

$$\text{persist} \sim te_1(\text{fre}, \text{int}, \text{dur}) + s_2(M) + s_3(\sigma) + s_4(W_\infty) + s_5(a_R) + s_6(a_{\text{mat}}) + s_7(\text{dd}) + \text{species}, \quad (5)$$

where te_1 is a tensor product smooth, s_{2-7} are smooth terms and species is a random effect (coded with the $bs="re"$ command in *mgcv*) and using a binomial family. For simplicity and easier interpretation of biological significance, we limited the degrees of freedom by setting $k=3$ for te_1 .

The degree of density dependence (dd) was calculated from the fitted stock–recruitment functions by calculating the relative recruitment between a reduced spawner biomass of 50% relative to an unperturbed spawner biomass at the median reported value (sb_{med}):

$$dd = 0.5 \times e^{(0.5 \times \beta_1 \times sb_{\text{med}})}. \quad (6)$$

Following the output of the 72 scenarios, we defined three levels of risk of collapse (with a duration of 2 years): species with “High-risk” of collapsing are species collapsing due to relatively weak mortality events (intensity of 50% or less), seldom reoccurring (infrequent, 15 years or more in between). Species with “Medium-risk” of collapsing are species collapsing when confronted with relatively weak mortality events (intensity of 50% or less) that reoccurred often (frequent, less than 15 years in between) or to relatively strong mortality events (intensity of more than 50%) that seldom reoccurred (infrequent, 15 years or more in between). Finally, species with “Low-risk” of collapsing are species collapsing when confronted with strong mortality events (intensity of more than 50%) reoccurring frequently (high frequency of less than 15 years in between) or not collapsing in our scenarios.

3 | RESULTS

The output of the model applied to 39 fish species shows that the probability of persisting decreases with increasing natural mortality and recruitment variation, but increases with increasing degree of compensatory density dependence in early life survival (Figure 2). Moreover, the model effectively removed the effects for ages at recruitment and maturity and asymptotic size on the probability of persistence, while mortality, recruitment variations, and density dependence were not removed. In addition, the properties of the mass mortality events strongly affect the probability of persisting, with a generally higher probability of persisting in scenarios with lower frequency, lower intensity, and shorter duration of the events (Figure 2). The probability of persisting increases with the periodicity up to about 30 years. The intensity of the mass mortality event reduces the probability of persistence. For example, when a general fish population is confronted with a 2-year-long mortality event of 50% increased mortality with a 10-year frequency it has about 50% probability of persisting. A similar probability of persistence for a fish population would be found at a lower frequency, about every 30 years, with a higher intensity of mortality at 75%. At high frequency

(i.e., 5 years between events, Figure 2) of 2-year-long events, we found that fish populations have a relatively high probability of collapse, for both high and intermediate intensities (>25%). We found that more intense but rare events (e.g., 99% intensity every 20 years, Figure 2) lead to lower persistence compared with less intense events occurring more frequently (e.g., 25% intensity every 5 years). Increased duration of the mortality events generally reduces the probability of persisting. Fixing the intensity at 75% leads to about 50% probability of persisting with events occurring every 10 years with a duration of 1 year. If the duration is increased to 2 years, a 50% probability of persisting is expected with mass mortality reoccurring every 30 years. The probability of persisting varies between species. From the 39 species studied, six species are classified as “High-risk,” 22 species are classified as “Medium-risk,” and 11 species are classified as “Low-risk” (Figure 3). We found no indications of a clear trend between persistence and fish taxonomy. See Table S2 and Figure S1 for more information on the species-specific probability of collapse.

4 | DISCUSSION

We provide a framework to quantify the tolerance level of fish populations to mass mortality events at the early stage. Applying this framework to a range of fish species, we pinpoint the species more sensitive to mass mortality events (Figure 3). With the general increase in the occurrence of mass mortality events (Fey et al., 2015) due to marine heatwaves (Smith et al., 2023), harmful algal blooms (Gobler, 2020), disease (Genin et al., 2020), oxygen stress (Köster et al., 2005), toxic spills (Jernelöv, 2010) among other events or combinations of stressors, such information is imminently needed to correctly manage populations, biodiversity, and human activities such as fishing (Pascual et al., 2023). A major finding is that fish populations seem to be more sensitive to intense extreme events than to frequent but less intense events. Furthermore, we show a large variation in persistence to reoccurring mass mortality events in the early life between species (Figure 3). This variation in persistence to mass mortality events is structured by the life-history traits of the species. We found that the probability of persistence decreased with increasing adult mortality and recruitment variation but increased with increasing degree of early-life compensatory density dependence in survival (Figure 2).

We found that the probability of persistence is linked non-linearly to the intensity and the duration of the mass mortality event (Figure 2), that is, the outcome of the events is not proportional to the product of the intensity and frequency (Commander & White, 2020; Fabina et al., 2015). In our study, a 1-year-long event with high intensity (i.e., 75%) is associated with a lower probability of persistence compared with a longer event (i.e., 3 years) with low intensity (i.e., 25%). Such effects can in part be explained by density dependence in early survival, which typically can compensate for a large proportion of juvenile mortality loss if intensities are moderate (25%–50%) over several years compared with strong intensities (75%–99%) over just 1 year

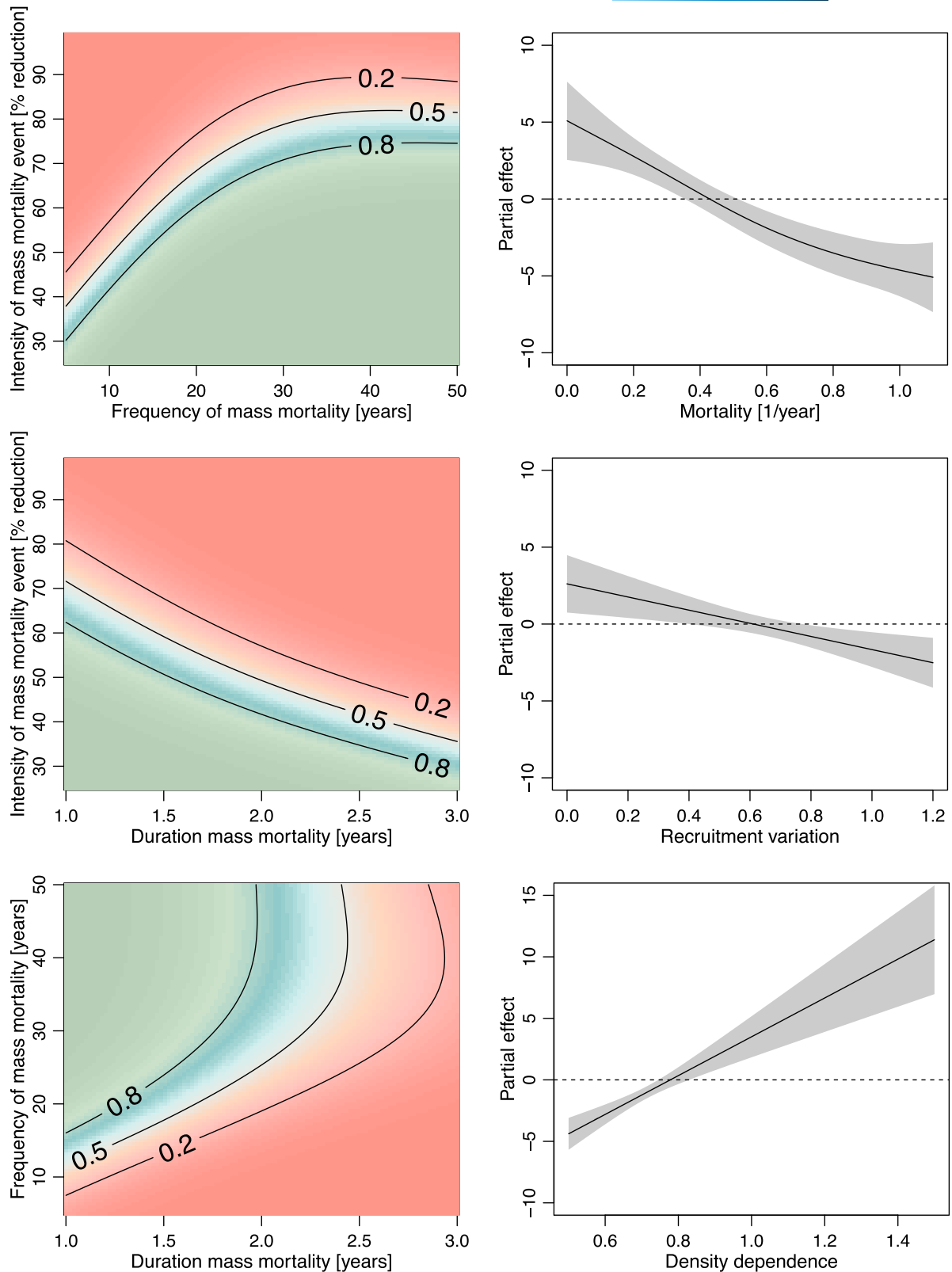


FIGURE 2 Probability of persistence for different mass mortality events in frequency, duration, and intensity. Here we considered the probability of persistence as the chance of not collapsing over 100 years across the three parameters period of reoccurring mass mortalities lasting 2 years and the intensity of extra mortality caused by the events (left upper panel), duration of the mass mortality reoccurring every 10 years and the intensity of extra mortality caused by the events (left central panel), and the duration of the mass mortality and the frequency of reoccurring mass mortalities (expressed in years between events) with an intensity of 75% (left lower panel). Solid lines show the contours at 20%, 50%, and 80% probability of persistence for the median models. The right panels show the partial effects of mortality, recruitment variations, and density dependence on the probability of persistence (on the logit scale).

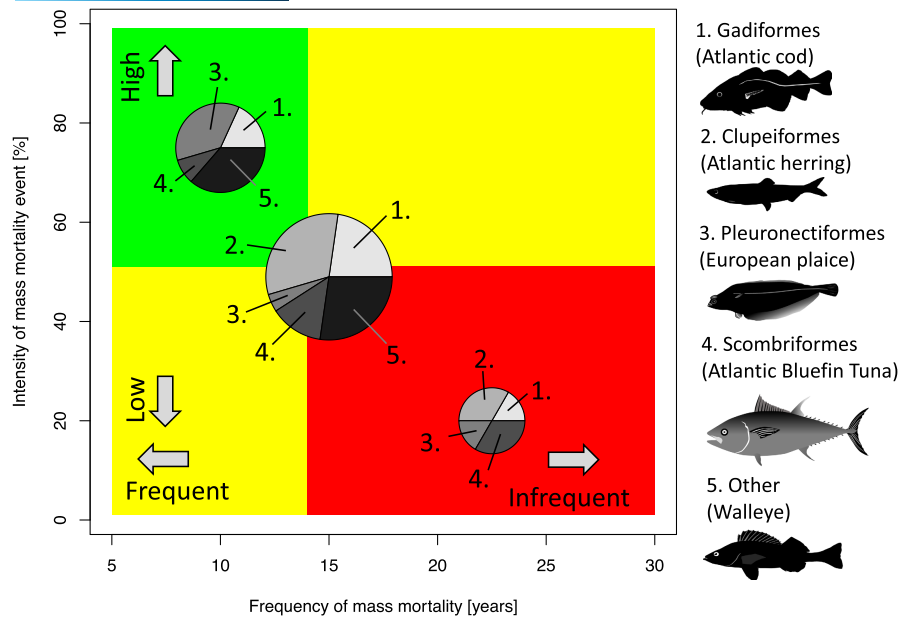


FIGURE 3 Assessment diagram of species sensitivity (risk of collapsing) to mass mortality events of different intensity and frequency. Here, we considered only 2-year duration mass mortality events. The red region indicates the species that are highly sensitive to mass mortalities that occur relatively seldom (every 15 years or longer) with relatively low intensity (50% or less mortality). The yellow indicates the region of medium sensitive species, that is, species that collapse with frequently reoccurring mass mortality events (10 years and shorter) with low intensity (50% or less mortality) or with less seldom (every 15 years or longer) with high intensity (75% and higher mortality). Finally, the green area indicates the more robust species, that only show a collapse when mass mortality occurs often (10 years or shorter) with high intensity (75% and higher mortality). The cake diagrams indicate the taxonomic order (right side, example species in parenthesis) of the species from our selection in each region, see [Table S2](#) for further details.

(Ohlberger & Langangen, 2015). Duration and frequency to some extent capture similar effects; that mass mortality events are happening more often. With a short duration (1 year), the frequency can be relatively high (occurring every 15 years) with fish retaining a high probability of persisting, while with a long duration (3 years), a collapse is likely also with a very low frequency (e.g., every 30 years, [Figure 2](#)). The main difference between the two is that with longer duration, there are no years in between the events for a potential recovery. This is an example of how a past event can affect the outcome of a present event, often referred to as ecological memory (Jackson et al., 2021).

The probability of persistence is associated with the recovery time (Stott et al., 2011), that is, the time to return to 95% of the original state. However, direct comparison with our results is challenging since most works on recovery time have been performed with density-independent models. Using a density-dependent fish model, White et al. (2022) showed that recovery time is typically shorter in short-lived species. Here, we found that persistence was more likely in long-lived species compared with more short-lived species that will likely recover faster than the longer-lived species. Moreover, species with strong density dependence in early life survival (i.e., a reduction in abundance in early life is less pronounced at later life stages) tend to be more persistent. Indeed, the time needed for the effects to translate into the population (at recruitment age) dampened the impact of mass mortality at the early life stages. Density dependence in survival typically reflects that individuals surviving a mass mortality event may be better off after the event as they typically have fewer competitors.

We also found that the variations in recruitment between years were an important structuring factor, that is, species with higher variations in recruitment have a lower probability of persistence. Species with relatively rare strong year classes will typically have a higher probability of collapsing and being sensitive to mass mortalities since single years strongly affect their biomass compared with species with more uniform year-class strength (cf. Haddon, 2011).

Among the causes of mass mortality events, marine heatwaves (MHWs) have recently attracted scientific attention (Smith et al., 2023). Fredston et al. (2023) suggested that MHWs have a limited impact on demersal fish populations. In this context, we here demonstrate that to have a significant impact, for example, beyond the natural variability generally observed in fish, multiple mass mortality events must occur over a relatively short period ([Figure 3](#)). This could be part of the explanation why so little effects associated with MHWs were observed (Fredston et al., 2023). By applying our framework, we can indicate how often MHWs must occur and in which species effects may be expected. In particular, based on our results we may not expect to observe a large reduction in population biomass unless mass mortality in early life occurs multiple times with less than 20 years intervals ([Figure 2](#)) and higher effects are expected in short-lived species, especially if they have a low degree of density dependence and large variations in recruitment.

Related to MHWs, the Pacific cod (*Gadus macrocephalus*) has been reported to experience elevated early life mortality occurring with the heatwaves in 2015, 2016, and 2019 and experienced a

strong reduction in population biomass (Almeida et al., 2024). With mortality events occurring with only 3 years in between, our model predicts a likely strong reduction in population biomass (Figure 2). However, we note that MHWs may often simultaneously affect multiple life stages, such as the increased early life and adult mortality in fish associated with the MHW in the North Pacific Ocean in 2015–2016 (Free et al., 2023). We did not include such considerations here, but the probability of collapse will typically increase with additional mortality in adult life stages (White et al., 2022).

Another example of mass mortality in early life of fish can be found in Atlantic cod in southern Norway in 1988. The toxic algae *Chrysochromulina polylepis* bloom caused high mortality (more than 60%) in juvenile cod, however with limited population-level effects (Gjøsæter et al., 2000). This is largely in line with our modeling results with limited effects at the population level for events with long periodicity (Figure 2), unless the mortality is very high.

In a recent work on wildlife population collapse (including fish), Cerini et al. (2023) suggest a more active and diverse monitoring for signs of stress. The recommendation includes for example combining monitoring of movement, behavior, resource abundance, body size, and reproductive rates (Cerini et al., 2023). Our works can be potentially very useful to develop a better predictive capacity of species collapse of fish. With our approach, it is possible to indicate which species are more sensitive to population collapse due to mass mortality and should be more closely monitored.

In our work, we have taken a baseline normalized approach to quantify the impact of mass mortality, which is useful for comparing an impact between systems (Ingrisch & Bahn, 2018). With this approach, we have been able to quantify the impact of the frequency and intensity of early life mass mortality events of a range of different fish species to understand and potentially predict where and in which species such events may be most severe. We suggest that our approach can be used as a first guide to pinpoint which species should be closely monitored to better predict and potentially mitigate adverse population-level effects of mass mortality events (Buttay et al., 2023). Buttay et al. (2023) suggested that mitigation efforts (i.e., a reduction of fishing mortality) will be more effective when applied shortly after a mass mortality event affecting the early life of cod.

Our approach accounts for the main factors affecting the population dynamics of fish and a comparison with more detailed models indicated that the models applied here were generally performing well (Langangen et al., 2023). However, we did not consider potential altered density dependence at low population size, such as Allee effects, which have been documented in, for example, cod (Keith & Hutchings, 2012; Winter et al., 2020). Nor did we consider the potential for alternative states or regime shifts (Möllmann et al., 2015; Sguotti et al., 2019). If present, both may potentially lead to worse outcomes than in our simulations, hence in this context, our results may be interpreted as a “best case” scenario. Here, we considered a perturbed to unperturbed biomass reduction of 50% an indication of collapse. We note that the species included in this analysis have been harvested for a long time (hence the data availability) and would be expected to be at a significantly reduced biomass compared with preharvest levels (e.g.,

harvesting at maximum sustainable yield typically leads to 50% reduction or more in the biomass). Our collapse criteria are compared with this already reduced biomass level. Using a higher percent perturbed to unperturbed biomass reduction as collapse criteria would typically lead to higher persistence but would not likely change which species are more sensitive to mass mortality events in early life. Moreover, we did not explicitly account for species interactions. Species interactions are known to affect the impact period and intensity of mass mortality events (Commander & White, 2020) and could also lead to indirect ecosystem effects (Durant et al., 2020; Langangen et al., 2017). However, accounting for such effects demands more complex models (e.g., Stige et al., 2018), which is a potentially fruitful avenue for future research.

Despite some limitations, our results underline the importance of investigating the frequency and intensity of a disturbance in early life in concert. Here, we present a first approximation to predicting which fish species would be more sensitive to the projected increase in mass mortality events across the globe, attributed in large part to human-induced climate change and other human activities. Such predictions are urgently needed for devising mitigation plans in regions with high frequency and intensity of mass mortality.

AUTHOR CONTRIBUTIONS

Øystein Langangen: Conceptualization; investigation; writing – original draft. **Joël M. Durant:** Conceptualization; investigation; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

We declare having no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Fishbase at fishbase.se and the original RAM database (Myers et al., 1995) and can be found at <http://wayback.archive-it.org/org-990/20170328023231/http://ram.biology.dal.ca/~myers/data.html>.

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SUPPORTING INFORMATION

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