

Combined effects of temperature and fishing mortality on the Barents Sea ecosystem stability

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Abstract

Temporal variability in abundance and composition of species in marine ecosystems results from a combination of internal processes, external drivers, and stochasticity. One way to explore the temporal variability in an ecosystem is through temporal stability, measured using the inverse of the coefficient of variation for biomass of single species. The effect of temperature and fisheries on the variability of the Barents Sea food web is still poorly understood. To address this question, we simulate the possible dynamics of Barents Sea food web under different temperature and fishery scenarios using a simple food-web model (Non-Deterministic Network Dynamic [NDND]). The NDND model, which is based on chance and necessity (CaN), defines the state space of the ecosystem using its structural constraints (necessity) and explores it stochastically (chance). The effects of temperature and fisheries on stability are explored both separately and combined. The simulation results suggest that increasing temperature has a negative effect on species biomass and increasing fisheries triggers compensatory dynamics of fish species. There is a major intra-scenario variability in temporal stability, while individual scenarios of temperature and fisheries display a weak negative impact and no effect on stability, respectively. However, combined scenarios indicate that fisheries amplify the effects of temperature on stability, while increasing temperature leads to a shift from synergistic to antagonistic effects between these two drivers.

KEYWORDS

chance and necessity, climate change, cumulative impacts, fishing mortality, non-deterministic modeling, simulation modeling, temporal variability

1 | INTRODUCTION

Stability is an essential ecosystem feature that has relevance for conservation and management of resources in terrestrial and aquatic ecosystems (Donohue et al., 2016). Early works have investigated how species diversity and complexity influence stability (Ives & Carpenter, 2007; May, 1972; Pimm, 1984; Rooney & McCann, 2012). Ecosystem stability is generally expected to increase with diversity

(Campbell et al., 2011; Tilman et al., 2006) and complexity (May, 1972; McCann, 2000; Mougi & Kondoh, 2016). In contrast, a more recent study showed that species richness explained a relative small fraction of the variability in population or community abundances (Houlahan et al., 2018). Also, Jacquet et al. (2016) found no association between indicators of food-web complexity and stability.

Ecological stability is a multidimensional concept and encompasses many definitions (Donohue et al., 2013; Grimm &

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Wissel, 1997; Kéfi et al., 2019). Some definitions of ecological stability (e.g., resilience, persistence, reliability, or resistance) quantify the response of ecosystems to perturbations (Donohue et al., 2013; Van Meerbeek et al., 2021). This approach often focuses on the asymptotical behavior of the ecosystem (i.e., the long-term dynamics of the ecosystem after the perturbation). However, the asymptotical state of ecosystems is rarely observed in nature (Morozov et al., 2020), leading to an emphasis on transient dynamics, that is, short-term dynamics different from the asymptotical behavior (Dunn et al., 2021; Frank et al., 2011; Hastings, 2004). Stochasticity may promote the occurrence of transient dynamics (Hastings et al., 2021).

Rather than focusing on response to perturbation, one can focus on temporal variability as an indicator of ecological stability (MacArthur, 1955). Tilman (1999) proposed a measure of temporal stability, referred to as constancy (Orians, 1975), that is, the inverse of the variability of a variable (e.g., species biomass), often with reference to a specific value, such as the mean biomass. The inverse of the coefficient of variation is such a measure. It can be applied in a nonequilibrium context, and it can be generalized at the whole ecosystem scale (Hillebrand et al., 2018; Lehman & Tilman, 2000). Temporal stability of a food web or species can be calculated from ecological time series, informing us about the past dynamics. Unfortunately, using ecological time series has its limitations. First, ecological time series are often relatively short, typically less than 50 years (Evans et al., 2015; Lotze & Worm, 2009), and, second, ecological time series are not available for all species of ecosystems. Consequently, the variability of ecological time series only represents a fraction of the possible variability of marine ecosystems (Sivel et al., 2021). An alternative is to use numerical models to simulate ecosystem dynamics over multiple decades.

In this study, we used the Non-Deterministic Network Dynamic (NDND) model to simulate possible food-web trajectories. The NDND model is a mass-balanced stochastic food-web model (i.e., it simulates species dynamics based on their trophic interactions) based on the principles of chance and necessity (Planque et al., 2014). In chance and necessity modeling, chance reflects the indeterminacy of ecosystem processes, and necessity corresponds to the physical and biological constraints of the system (Mullon et al., 2009; Planque et al., 2014; Planque & Mullon, 2020). In other terms, one considers that possible events are not predetermined, but occur randomly (chance) within a set of physical and biological constraints of the system (necessity). The NDND model was designed to reproduce the high variability of natural systems by exploring their 'state space.' Lindstrøm et al. (2017) used the model to explore the Barents Sea food-web dynamics and concluded that the model was able to reproduce multiple emergent food-web patterns, including the temporal stability, observed over the past 30 years.

The Barents Sea (Figure 1a) is a subarctic shelf sea that has experienced significant warming ($\sim 1^{\circ}\text{C}$ increase in surface temperature) the past four decades (Timmermans & Ladd, 2019). This has resulted in an increase in primary production and a stabilization of the mesozooplankton biomass (Dalpadado et al., 2020). While higher temperature is expected to increase the metabolic rate of organisms (Carozza et al., 2019; O'Connor et al., 2007), there is no clear consensus how higher metabolic rates will affect the temporal stability of ecosystems. Vasseur and McCann (2005) highlighted a destabilizing effect of temperature-induced increase of metabolic rates on biomass densities in simple consumer–resource systems, whereas Fussmann et al. (2014) suggested the opposite for ecosystems. Furthermore, although fisheries are strongly regulated in the Barents Sea, they still represent

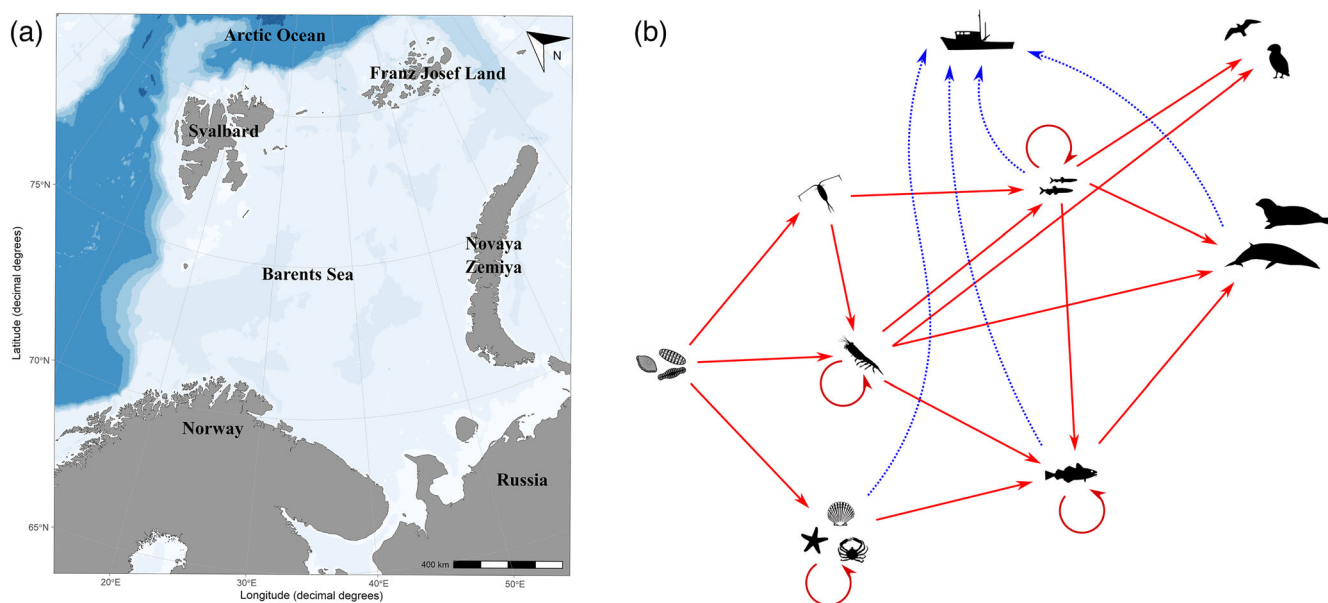


FIGURE 1 The study area of the Barents Sea (a) and its simplified food-web topology (b). Icons represent the eight species (phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, marine mammals, and birds). Red-full arrows represent the possible flows toward other species of the food-web. Red-circular arrows represent cannibalistic interactions. Blue-dashed arrows represent flows toward the fisheries.

an important disturbance of ecosystem dynamics (ICES, 2020a). Besides the decrease of population sizes of harvested species stocks, fishing may also lead to increased variability of harvested species (Hsieh et al., 2006).

Anthropogenic activities are expected to increase in the future (Hoegh-Guldberg & Bruno, 2010). Thus, their impact on ecosystems needs to be quantified properly to better inform management and to anticipate possible future changes in ecosystem structure and functioning. Past studies have assessed the effect of anthropogenic drivers on the ecosystem. They have pointed out that the effects of anthropogenic drivers should not be treated separately (e.g., Jarre et al., 2015; Shannon et al., 2010). Although the impact of anthropogenic drivers on marine ecosystems is well documented, their combined effects with climate change are still debated in the literature. Single-species modeling studies highlighted synergistic effects between climate change and fisheries on species biomass in different ecosystems (Fuller et al., 2015; Hidalgo et al., 2011; Koul et al., 2021). At the ecosystem scale, a recent multi-model study suggested additive effects of temperature and fisheries on species mean biomass as they found no major alteration of the effects of climate change when harvesting was accounted for in their models (Lotze et al., 2019). Another model study, using the end-to-end ecosystem model Atlantis, suggested that combined effects of temperature and fishing on biomass were variable for individual species of the Southern Benguela upwelling ecosystem (Ortega-Cisneros et al., 2018).

Several previous studies on combined effects of climate and fisheries (e.g., Perry et al., 2010; Planque et al., 2010) suggest that climate variability and fisheries have synergistic effects on ecosystem variability due to an increase in the sensitivity of marine ecosystems to climate variability. Barents Sea dynamics have displayed large fluctuations during the past five decades as the result of a combination of harvesting and ecological processes (Hjermann et al., 2004; Koen-Alonso et al., 2021). Relative high fishing pressure combined with poor recruitment, partly due to cannibalism as a result of poor feeding conditions, in the 1980s caused the cod stock to decline recovering only in the 2000s due to appropriate management policies (Lilly et al., 2013), while a combination of harvesting and predation triggered large fluctuations of the capelin stock on an interdecadal timescale since 1980 (Hjermann et al., 2004). As anthropogenic activities are expected to increase in intensity over the next decades, it is essential to understand how combined effects of climate change and fisheries affect the biomass variability of the Barents Sea ecosystem.

In this study, we explore the combined impacts of climate change and fisheries on the temporal stability of the Barents Sea food web. We performed simulations of food-web dynamics for scenarios of climate change (temperature) and fisheries (fishing mortality) using the NDND model for the Barents Sea. We estimated the temporal stability of the food web for each simulation to assess the impact of climate change and fisheries on the food web independently and to test for additive, synergistic, or antagonistic effects of both drivers on the temporal stability of the Barents Sea food web.

2 | MATERIAL AND METHODS

2.1 | The NDND model

The NDND model relies on modeling principles similar to those of Ecopath with Ecosim (EwE). It is a mass-balanced food-web model that simulates trophic flows (i.e., biomass transfer from a prey to a predator) to estimate species biomass at each time step (Planque et al., 2014). However, while EwE relies on the assumption that food-web processes can be fully described, the NDND explicitly accounts for unknowns and indeterminacy in ecological processes. Rather than providing a unique solution, NDND explore the set of possible trophic flow combinations given structural and physiological constraints. The values of trophic flows are randomly sampled (chance) given a set of simple physical and biological constraints (necessity). There are five constraints implemented in the NDND model: (1) Satiation constrains the food intake of a predator, (2) inertia constrains the maximum increase and (3) maximum decrease of species biomass at each time step, (4) the trophic flows must be positive, and (5) species biomass must be higher than a minimum value referred to as the refuge biomass.

The principles of the NDND model and the similarities and difference between the NDND and EwE are presented in Planque et al. (2014). The detailed application and parametrization for the Barents Sea ecosystem is derived from Lindstrøm et al. (2017) and Planque and Mullon (2020). The food-web topology comprises eight trophospecies (phytoplankton, herbivorous zooplankton, omnivorous zooplankton, benthos, pelagic fish, demersal fish, marine mammals, and birds), 18 trophic links, and four flows toward fisheries (Figure 1b).

We used the parametrization of the NDND model specified by Planque and Mullon (2020) as the reference scenario (Table 1). We updated the initial biomass of the herbivorous zooplankton, omnivorous zooplankton, pelagic fish, and demersal fish groups with the biomass data from the working group on integrated assessment of the Barents Sea (WGIBAR) for the year 2018 (ICES, 2020b). For phytoplankton, benthos, marine mammals, and birds, biomass data were not available. Thus, we kept initial biomass values estimated by Lindstrøm et al. (2017). We used the assimilation efficiency (γ) and digestibility parameter (κ) values from Blanchard et al. (2002). Satiation (σ) corresponds to the maximum ingestion rate of individual species, and we estimated theoretical values based on the work by Yodzis and Innes (1992). Inertia (ρ) corresponds to the maximum population growth and the maximum population decline over a year. It was estimated as the average between two theoretical values: (1) from Yodzis and Innes (1992) and (2) from Savage et al. (2004). Other losses (μ) correspond to all biomass losses that are not related to predation or fisheries (e.g., disease). It is equivalent to the field metabolic rate (FMR) that equals three times the basal metabolic rate of a species. We considered three distinct methods to derive species' basal metabolic rate: (1) the method by Yodzis and Innes (1992), (2) the method by Gillooly et al. (2001), and (3) the method by Makarieva et al. (2008). We estimated the FMR for all three methods and the average between all estimated values as parameter value for other losses. Import (I) was

TABLE 1 Initial parameters input for the NDND simulations

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Initial biomass (B_0 , tons·km ⁻²)	25	25.64	3.32	66	1.02	2.31	0.34	0.007
Import (I , tons·km ⁻²)	1000	8	2	0	0	0	0	0
Export (E , tons·km ⁻²)	0	0	0	0	0	0	0	0
Assimilation efficiency (γ)	1	1	1	0.94	0.9	0.93	1	0.84
Digestibility (κ)	0.65	0.9	0.9	0.6	0.9	0.85	-	-
Other losses (μ)	6.74	8.4	5.5	1.5	2.85	1.65	5.5	60
Inertia (ρ)	12.94	7.58	3.1	0.74	0.9	0.25	0.11	0.81
Satiation (σ)	-	128	42	25.2	13.5	5.5	10.9	123
Refuge biomass (β , tons·km ⁻²)	0.25	0.23	0.033	0.66	0.01	0.023	0.0034	0.0001

Notes: Units are given in brackets. Assimilation efficiency and digestibility are ratios and do not have units. Other losses, inertia, and satiation are ratios but integrated for a 1-year time period. Initial biomass, import, export, and refuge biomass correspond to total weights for a species but expressed per spatial unit. For demersal fish, initial biomass corresponds to $2.31 \times 1600 = 3696$ thousand tons for the entire Barents Sea area. Refuge biomass corresponds to $0.023 \times 1600 = 36.8$ thousand tons for the entire Barents Sea area.

taken from Lindstrøm et al. (2017) and corresponds to mean annual import of biomass from the Norwegian Sea into Barents Sea area for zooplankton species and to the annual net primary production for phytoplankton. Finally, refuge biomass (β) were set to the 1% of the initial biomass.

As in Sivel et al. (2021), we have expressed harvesting of fish species (i.e., pelagic and demersal fish) using harvest control rules (HCR), which resemble current fishing regulations in the Barents Sea (Gullestad et al., 2014). In this study, we added harvesting of benthos and marine mammals. Harvesting of benthos corresponds to harvesting of northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*). Harvesting of marine mammals represents harvesting of harp seal (*Pagophilus groenlandicus*) and minke whale (*Balaenoptera acutorostrata*). Given that catches of northern shrimp and snow crab represent only a small fraction of the total harvested benthos biomass and that no HCR was defined for minke whales (Howell & Bogstad, 2010), we implemented harvesting of benthos and marine mammals as a constant catch (C) at each time step, over the entire simulation. Total catches for snow crab were not available for the year 2018; thus, we implemented the total catches of benthos for the year 2017. The aggregated total catches of northern shrimp and snow crab in 2017 was 0.026 tons·km⁻² (Hjelset et al., 2018; NAFO/ICES, 2020). Annual catches of marine mammals are expressed in number of hunted individuals. To estimate the catch of marine mammals in biomass (i.e., in tons·km⁻²), we applied conversion factors of 0.15 and 5 tons·ind⁻¹ for harp seals and minke whales, respectively, which are within the range of reported values (Skern-Mauritzen et al., 2022). For harp seals, we excluded the pups (i.e., all individuals younger than 1 year) from the total count of hunted individuals. In 2019, 568 harp seals and 429 minke whales were caught, leading to a total catch of 0.0014 tons·km⁻²

(NAMMCO – North Atlantic Marine Mammal Commission, 2021). The initial harvesting parameters used for our simulations are presented in Table 2. For all harvested species, we assumed fisheries to be compensatory (i.e., losses due to harvesting are compensated by predation rates).

2.2 | Estimation of temporal stability

The NDND model simulates multiple biomass trajectories for the species of the Barents Sea food web. Temporal stability of individual species (S_i) corresponds to the inverse of the coefficient of variation (Lehman & Tilman, 2000):

$$S_i = \frac{\bar{B}_i}{sd(B_i)} \quad (1)$$

where \bar{B}_i is the mean biomass for species i and $sd(B_i)$ is the standard deviation of biomass of species i . Lehman and Tilman (2000) suggested a generalized formulation of temporal stability for the whole food web (S):

$$S = \frac{\sum_i \bar{B}_i}{\sqrt{\sum_i \text{var } B_i + \sum_{i,j} \text{cov } B_{i,j}}} \quad (2)$$

where the numerator is the sum of mean species biomasses (\bar{B}_i), $\text{var } B_i$ is the variance of biomass of species i , and $\text{cov } B_{i,j}$ is the covariance estimated from the biomass time series of species i and j (i.e., the sum of all terms of the species covariance matrix).

TABLE 2 Initial harvesting parameter input for the NDND simulations

	Phytoplankton	Herbivorous zooplankton	Omnivorous zooplankton	Benthos	Pelagics	Demersals	Mammals	Birds
Fishing mortality rate (Fmp)	-	-	-	-	0.05	0.4	-	-
Target biomass (bmp, tons·km ⁻²)	-	-	-	-	0.125	0.475	-	-
Trigger biomass (Blim, tons·km ⁻²)	-	-	-	-	0.125	0.25	-	-
Natural mortality (M)	-	-	-	-	0.85	0.2	-	-
Catches (C, tons·km ⁻²)	-	-	-	0.026	-	-	0.0014	-

Notes: Units are given in brackets. Fishing mortality (Fmp) and the natural mortality (M) do not have units because they are ratios integrated for a 1-year time period.

2.3 | Scenarios of temperature and fishing mortality

To assess the effect of climate change and fisheries on the stability of the Barents Sea food web, we used predefined scenarios of changes in temperature and fisheries catches.

The four temperature change scenarios were as follows: (1) decrease by one degree, (2) no temperature variation, (3) increase by one degree, and (4) increase by two degrees. The effects of temperature on physiological parameters were applied only for ectotherms (i.e., all species except marine mammals and birds). Conventionally, the impact of temperature variations on the values of metabolic rates is expressed as Q_{10} , which represent the temperature dependency of metabolic rates across a temperature range of 10°C (Gillooly et al., 2001). In the metabolic theory of ecology (MTE; Gillooly et al., 2001; Brown et al., 2004), the metabolic rates are expressed in terms of body size and temperature. According to the MTE, we estimated that a one-degree increase in temperature leads to a 10% increase in metabolic rates (Supporting Information). This applies to metabolic losses (μ), inertia (ρ), and satiation (σ), which are expected to be temperature dependent (Brown et al., 2004; Vasseur & McCann, 2005).

Fisheries scenarios explored variations in fishing mortality. We considered four fishing mortality scenarios: (1) a 50% decrease in fishing mortality, (2) no change (reference level), (3) a 25% increase in fishing mortality, and (4) a 50% increase in fishing mortality. We implemented the variation in fishing mortality by modifying the fishing mortality rate (*Fmp*) for pelagic and demersal fish and the annual catches (*C*) for benthos and marine mammals.

2.4 | Simulations

Simulations and statistical analysis were performed using R (v.4.1.0) (R Core Team, 2021). The sampling algorithm used in the NDND model is the Complex Polytope Gibbs Sampling algorithm (cpgs) from the RCaN package (Drouineau et al., 2021).

To explore exhaustively the possible trajectories of the Barents Sea food web, we generated 1000 biomass trajectories of 230 years for each scenario. We removed the 200 first years as a burn-in period to ensure that the simulated biomass used for estimating the temporal stability was independent from the initial conditions. The 200-year burn-in period was considered long enough as it covered several generations of the long-lived species in the Barents Sea. Temporal stabilities were thus estimated for time series of 30 years. This is comparable to the length of many existing observational time series for the Barents Sea ecosystem.

The simulated trajectories of phytoplankton correspond to the remaining biomass that has not been consumed at the previous time step and the import of phytoplankton into the Barents Sea. Thus, they do not reflect the dynamics of phytoplankton, and we removed phytoplankton from the analysis.

2.5 | Analysis of temperature and fishing mortality effects

We estimated temporal stability for individual species and the whole food web using Equations (1) and (2), respectively. We analyzed the effect of variations in temperature and fishing mortality on temporal stability using violin plots to visualize changes in temporal stability across scenarios. Given that temporal stability is measured as the ratio between mean biomass and biomass variability, changes in stability can possibly arise from changes in mean biomass. We investigated the dependency of temporal stability to the mean biomass for the whole food web and the species. For this purpose, we plotted temporal stability against mean biomass. To eliminate the scale difference between biomass variations at different mean biomass levels (Fisher, 1937), we plotted mean biomass on the log₁₀ scale.

To identify the nature of combined effects of variations of temperature and fishing mortality on temporal stability, we compared the anomalies between the measured median temporal stability in all scenarios and the median temporal stability in the reference scenario to the expected anomalies for additive effects (see Figure S2). Piggott

et al. (2015) redefined the terms of antagonism and synergism as deviations from an additive effect prediction. The authors emphasized the importance of the direction of the effect of stressors and define five directional interaction classes: additive (the combined effect corresponds to the sum of both individual effects), +synergistic (the combined effect is positive, and it is larger than the sum of both individual effects), -synergistic (the combined effect is negative, and it is larger than the sum of both individual effects), +antagonistic (the combined effect is negative, and it is smaller than the sum of both individual effects), and -antagonism (the combined effect is negative, but it is larger than the sum of both individual effects). Here, we defined the combined effects of temperature and fisheries on stability as follows:

- No deviation from the additive expectation corresponds to additive effects of temperature and fishing.

- A deviation greater in absolute term than the additive effect indicates synergism, while a smaller deviation indicates antagonism between temperature and fisheries.

3 | RESULTS

3.1 | Impact of temperature and fishing mortality on biomass

Simulated biomass of each species covered a large range of values (Figure 2). While lower trophic levels biomass varied by one order of magnitude, marine mammal's biomass varied by two orders of magnitude. Additionally, fish and bird's biomass varied up to four orders of magnitude. Interestingly, the total biomass of the food web only

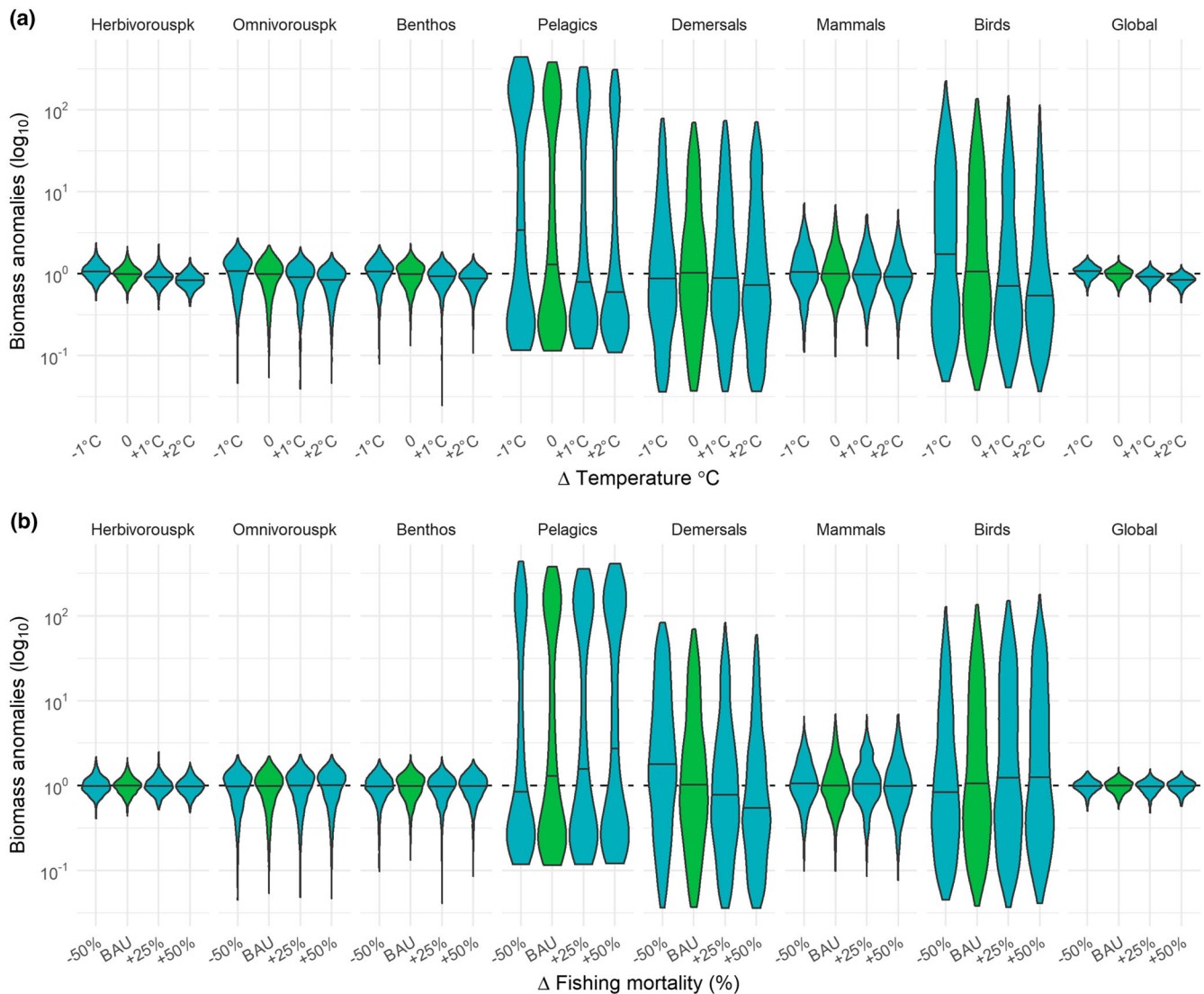


FIGURE 2 Effect of variations of temperature (a) and fishing mortality (b) on the simulated biomass of each species and the entire Barents Sea food web (global). The reference scenario (i.e., no variation in temperature and fishing mortality) is identified in green. The variations in biomass are expressed as anomalies on the log₁₀ scale regarding the median of the reference scenario. The black-dotted line indicates biomass values equal to the median biomass of the reference scenario.

varied by a factor of three. Simulated biomass of each species and of the whole food web revealed that changes in temperature and fishing mortality influenced biomass (Figure 2). Higher temperature had a negative effect on the biomass of all species (Figure 2a). Yet, demersal fish displayed lower biomass in the scenario with lower temperature (-1°C). Pelagic fish biomass decreased by a factor of 5 between the scenario with the lowest temperature (-1°C) and the one with the highest temperature ($+2^{\circ}\text{C}$), while birds' biomass displayed a decline in biomass by a factor of 3. For other species (zooplankton, benthos, and mammals) and for the food web as a whole, the decrease in biomass associated with increasing temperature did not exceed 20%.

Increasing fishing mortality affected pelagic fish, demersal fish, and birds' biomasses (Figure 2b). Globally, fishing led to a redistribution of the biomass between these three species but did not significantly affect the total biomass of the food web. Pelagic and demersal fish biomass displayed opposite responses to higher fishing mortality. Between the scenarios with the lowest (-50%) and the highest fishing mortality ($+50\%$), pelagic fish biomass increased by a factor of 3, whereas demersal fish biomass decreased by the same factor. Birds displayed an increase in biomass of 50% between the three scenarios with the lowest fishing mortality (i.e., -50% , no variation, and $+25\%$). In the scenario with the highest fishing mortality ($+50\%$), birds' biomass was at the same level as in the scenario with an increase of 25% in fishing mortality. Zooplankton species, benthos, and marine mammals' biomasses did not display any response to variations in fishing mortality.

3.2 | Impact of temperature and fishing mortality on temporal stability

We estimated temporal stability from simulations for relatively short time periods (30 years) and observed a large range of temporal stability values for all species in all scenarios of temperature and fishing mortality (Figure 3). For example, the ranges of estimated stabilities for demersal fish covered one order of magnitude. This level of uncertainty remained similar across temperature and fishing scenarios. Median stability varied between temperature scenarios (Figure 3a) but displayed little variations between fishing scenarios (Figure 3b). Temporal stability declined in response to higher temperatures for benthos, pelagic fish, demersal fish species, and the whole Barents Sea food web. Yet, changes in median stability as a response to changes in temperature were small compared to the variability of stability estimates. We found the largest decrease in stability between the coldest and the warmest scenario for demersal fish (30%). For other species, the temporal stability between the coldest and the warmest scenario did not decrease by more than 10%.

3.3 | Effect of biomass variations on temporal stability

Given Equation 1, observed changes in stability can result from changes in the standard deviation of biomass and from the mean biomass. We

investigated the dependency of stability estimates to the values of mean biomass of individual species and the whole food web. For herbivorous zooplankton, omnivorous zooplankton, and benthos, stability increased with higher mean biomass (Figure 4). Pelagic fish stability decreased in response to increasing mean biomass when mean biomass was low ($<0.01 \text{ tons}\cdot\text{km}^{-2}$), while it remained constant for intermediate values of mean biomass (between 0.01 and $0.1 \text{ tons}\cdot\text{km}^{-2}$), and it increased when mean biomass was high ($>0.1 \text{ tons}\cdot\text{km}^{-2}$). For demersal fish, stability decreased gradually with increasing mean biomass. For marine mammals, birds, and the whole food web, we found no relationship between stability and mean biomass.

3.4 | Combined effect of fisheries and temperature on temporal stability

Variations in temperature were the largest driver of changes in temporal stability (Figure 5), and these changes were only observed for harvested species. The largest response was observed for demersal fish. For herbivorous zooplankton and birds there were no visible effect of temperature and fishing on stability. Increased fishing mortality had a positive impact on demersal fish and marine mammals' stabilities regardless of the temperature scenario. Omnivorous zooplankton displayed antagonistic effects of temperature and fishing, but we found no increase in stability anomalies in response to increased temperature and harvesting. Benthos and pelagic fish showed small differences in stability anomalies indicating mostly additive effects of temperature and fishing. In the higher temperature scenario ($+2^{\circ}\text{C}$), the response of stability to cumulated temperature and fishing pressures was lower than the addition of responses to individual pressures, indicative of antagonistic interactions. Demersal fish exhibited larger combined effects on stability than the additive ones in the scenarios with lower temperature indicating synergistic effects on stability. Contrarily, we found antagonistic effects of temperature and fishing on demersal fish stability in warmer temperature scenarios. Marine mammals displayed strong antagonistic effects of temperature and fishing mortality on stability, given that the expected anomalies were larger than the measured ones.

Stability of the whole food web displayed a similar pattern as the harvested species. Temperature and fishing had synergistic effects in scenarios of colder temperature and low harvesting. As for demersal fish, in scenarios of low fisheries and warmer temperatures, we found antagonistic effects. In scenarios of higher harvesting, the nature of combined effects was opposite to the scenario of low harvesting. In scenarios of colder temperature and higher fisheries, combined effects were antagonistic, while they were synergistic in scenarios of warmer temperature and higher fisheries.

4 | DISCUSSION

In this study, we explored the combined effects of temperature and fisheries on the temporal stability of the Barents Sea food web.

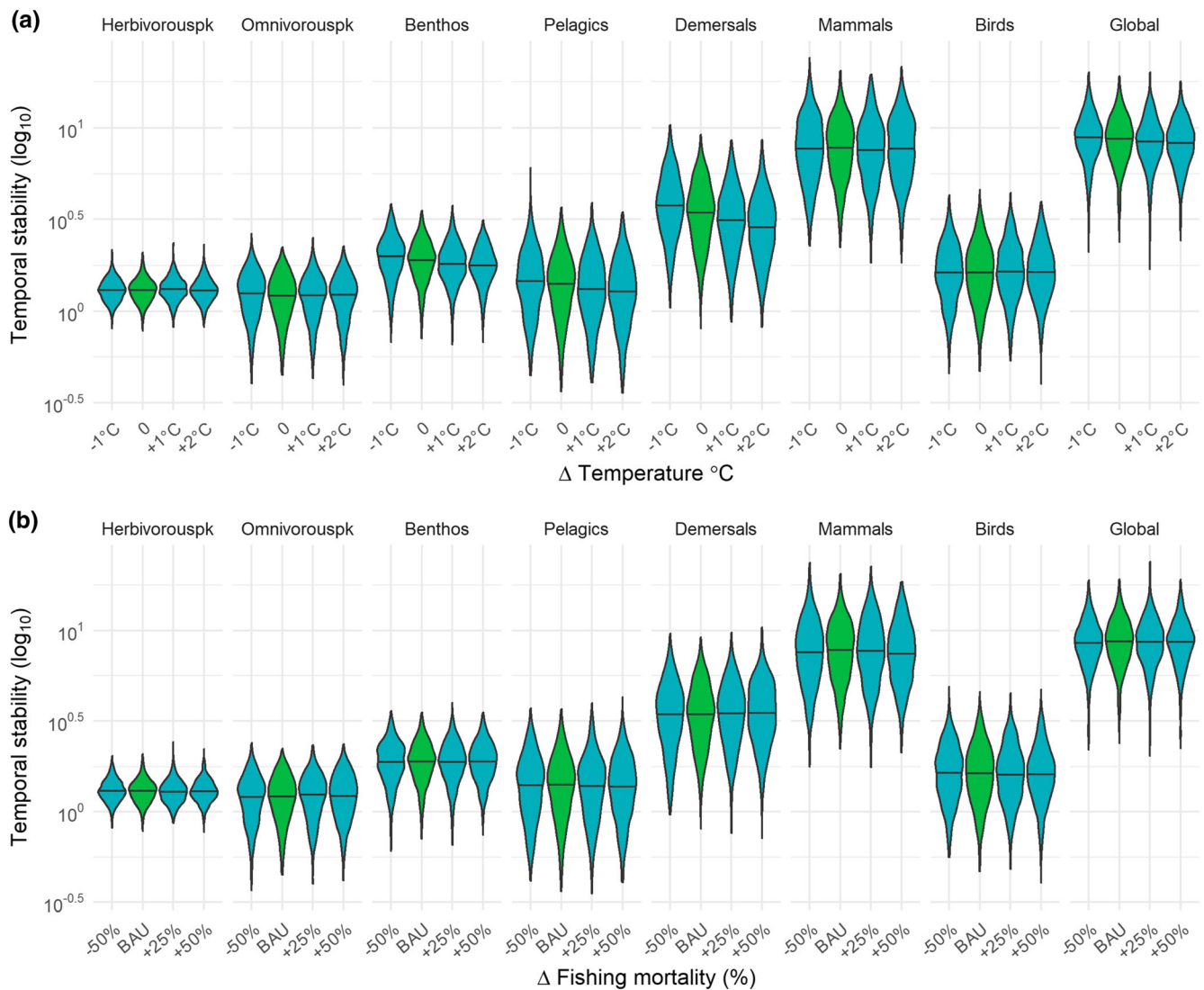


FIGURE 3 Effect of variations in temperature (a) and fishing mortality (b) on the temporal stability (on a log-10 scale) of each species and of the entire Barents Sea food web. Higher values indicate higher stability. The black lines in the violin plot correspond to the median of the stability of each species in each scenario. The reference scenario is identified in green.

Temperature negatively affected the species and food-web biomass, while fisheries redistributed biomass among individual species without affecting the total biomass of the food web. Individual drivers had weak effects on stability. However, we found amplified effects of temperature for harvested species. Also, we observed synergistic effects of temperature and fisheries in response to colder temperature scenarios and antagonistic effects in warmer temperature scenarios.

4.1 | Effects of temperature and fishing mortality on biomass

Globally, increasing temperature had a negative median effect on the biomass and stability of the Barents Sea food web. Decreasing zooplankton biomass observed in our simulations goes against historical observations, suggesting that zooplankton biomass would

increase in the Barents Sea in response to warmer temperature (Dalpadado et al., 2020). Furthermore, recent modeling studies suggested that increasing temperatures in polar marine ecosystems should lead to a significant biomass decline at the Horizon 2100 (Bryndum-Buchholz et al., 2019; Lotze et al., 2019). Recent studies suggest that biomass response to warmer temperature in the future is uncertain (i.e., biomass could display a positive or a negative response to warmer temperature), notably in polar regions (Heneghan et al., 2021; Tittensor et al., 2021). Our results are in line with the latter findings. Though median biomass response was negative, multiple simulated states of the Barents Sea food web indicates that negative and positive responses of biomass to warmer temperatures are possible. Lotze et al. (2019) suggested that biomass decreases were more important in higher trophic levels due to trophic amplification. Our results do not fully support this statement because the median biomass of demersal fish and marine mammals did not decline in response to higher temperatures as much as the

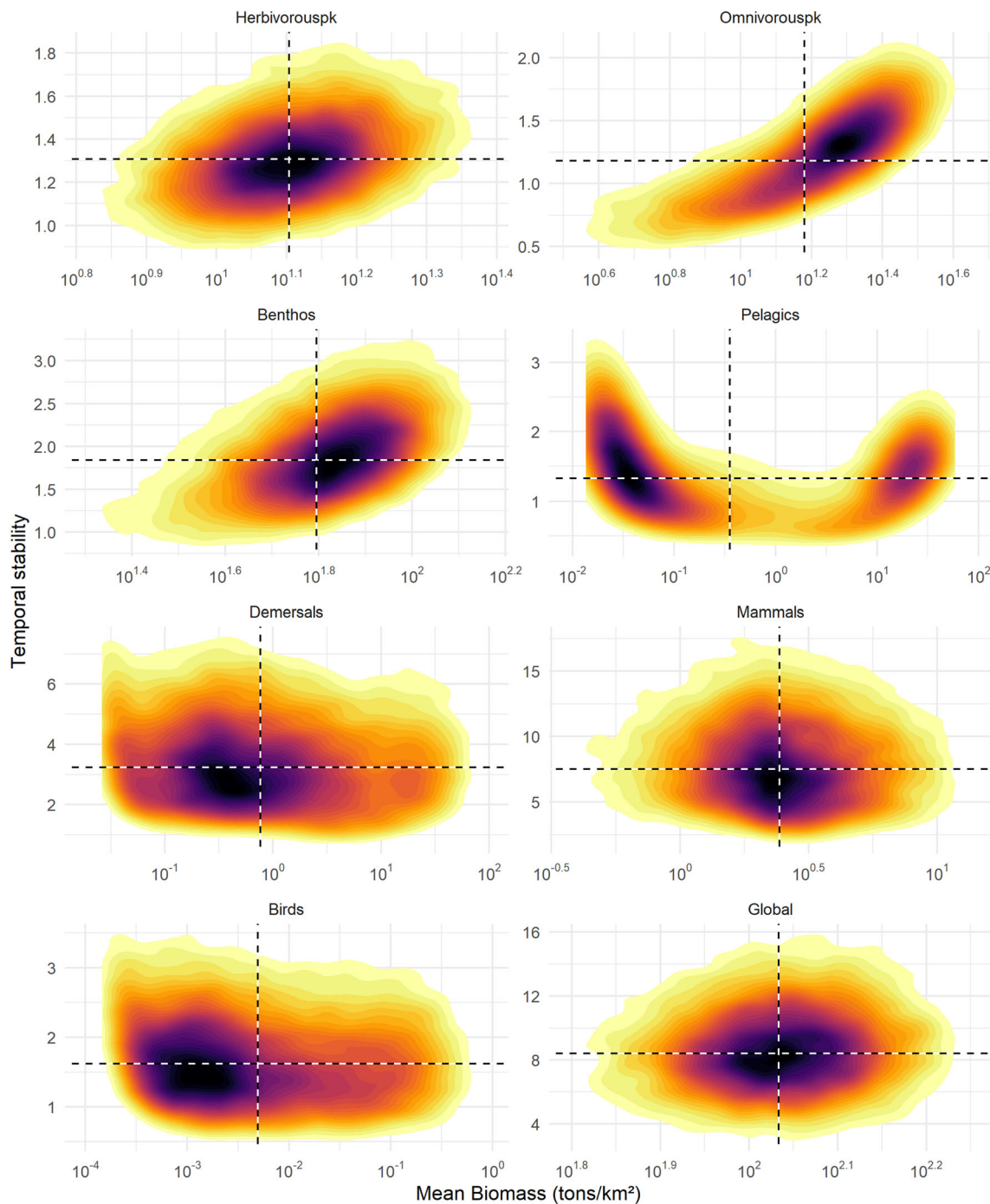


FIGURE 4 Density plots between mean biomass (on the log-10 scale) and temporal stability for all species and the whole food web (the darker, the denser). The black/white-dashed lines represent the geometric mean of the mean biomass by species and the mean temporal stability by species.

zooplankton species. In our simulations, demersal fish biomass decreased for the coldest temperature scenario. The analysis of the trophic flows showed that, for this scenario, the food intake by demersal fish was reduced, while it was not the case for other species in the model (Figure S4). This was caused by reduced feeding capacity at lower temperature, which was not compensated by changes in other temperature dependent processes (i.e., inertia and metabolic losses).

Fisheries affected the biomass of pelagic fish, demersal fish, and birds. The decline of demersal fish biomass in direct response to increased fishery mortality triggered an increase in pelagic fish and birds' biomass, suggesting that predatory effects outweigh harvesting effects on pelagic fish. This is to some extent in line with a previous study (Lindstrøm et al., 2009), which showed that reduced abundance of cod from harvesting led to increased abundance of capelin, whereas reduced harvesting on capelin had minor impact on its own

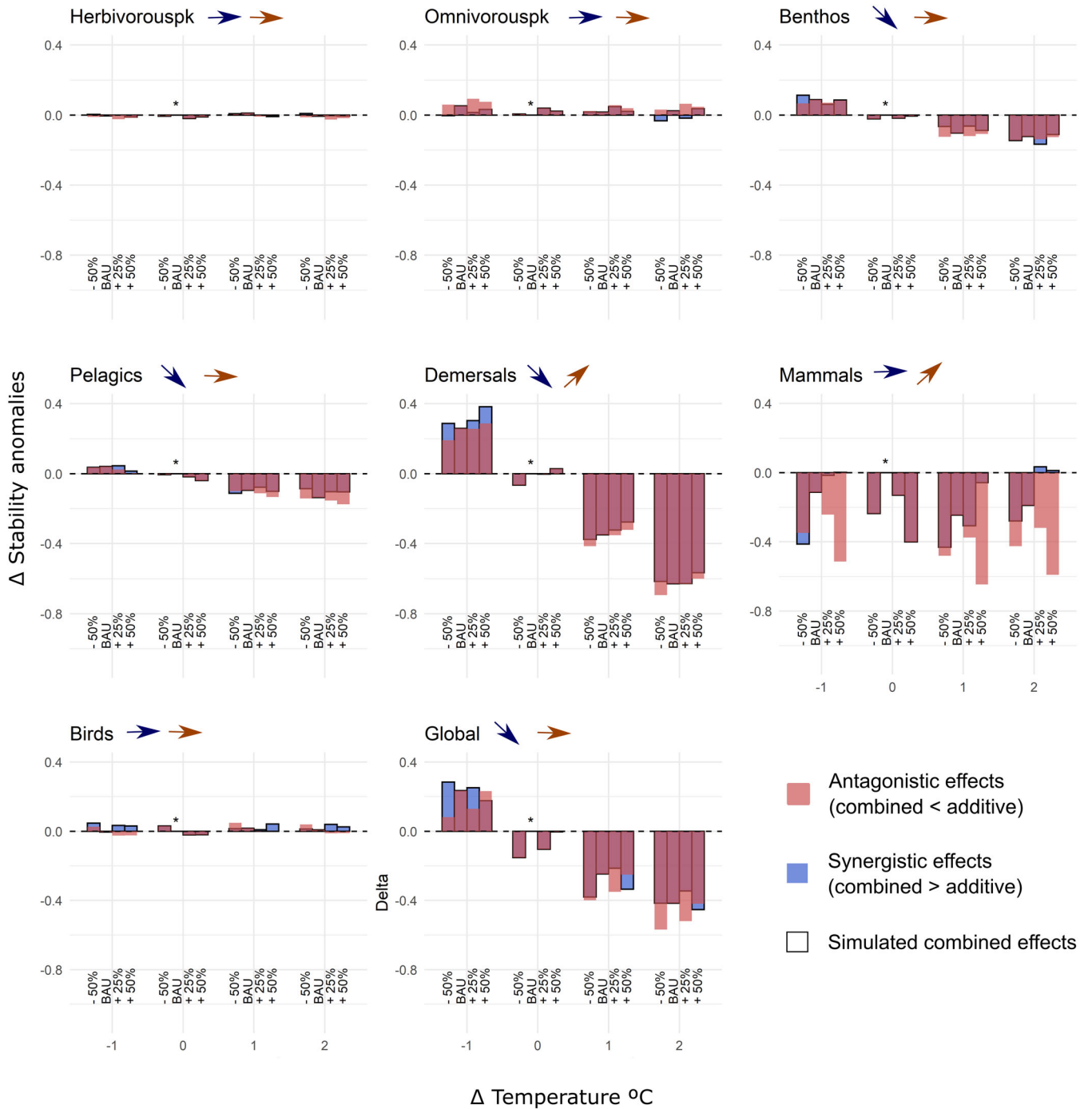


FIGURE 5 Combined effects of temperature and fisheries on the temporal stability of the Barents Sea food web and its species. Bars represent the anomalies in stability regarding the reference scenario (identified by “**”). Each bar represents a scenario of temperature and fishing mortality. Blue- and black-outlined bars represent the simulated combined effects of temperature and fisheries. Red bars represent the additive effects of temperature and fisheries. Complete overlap indicates additive effects. Larger combined effects than additive effects correspond to synergistic effects. Combined effects smaller than additive effects correspond to antagonistic effects. Dark blue arrows indicate the anomalies trend for scenarios of temperature. Orange arrows indicates the anomalies trend for scenarios of fishing mortality. The black-dashed line corresponds to anomalies of 0 (i.e., estimated stability equals stability of the reference scenario). The gray dashed lines represent the trends in stability anomalies for demersal fish.

dynamics and on the dynamics of cod and herring. This is further confirmed in the study by Myers and Worm (2003), which provides multiple examples of compensatory dynamics between pelagic and demersal fish in marine ecosystems due to released predation on

pelagic fish and competition. Using a simple end-to-end model, Heath et al. (2021) presented similar conclusions for the North Sea ecosystem, which are consistent with our results. The ensuing birds' biomass increase in our simulation can be explained by the increase of food

availability due to higher pelagic fish biomass. However, we see that the biomass of birds is also limited by satiation as their biomass do not increase for higher fisheries although pelagic fish biomass does.

Interestingly, the biomass of zooplankton species, benthos, and marine mammals was not affected by variations in the biomass of other species. The relative stability of marine mammals' biomass in response to decreasing demersal fish biomass reflects the shift in the diet of marine mammals from demersal fish to pelagic fish (Figures S3 and S4). We assume that the lack of response of zooplankton species to variations in upper trophic levels resulted from the decoupling of zooplankton and pelagic fish dynamics. This is thought to have occurred in the past when primary production was high (Dalpadado et al., 2020). When conducting model reconstructions of the past dynamics of the Barents Sea food web, with a parametrization similar to the current study, Planque and Mullan (2020) observed that assumed that zooplankton dynamics could be reconstructed with substantially lower primary production, which suggested that the assumed primary production in the model was likely too high. In this study, we can interpret the decoupling of zooplankton and pelagic fish dynamics as a result of too high import of phytoplankton biomass, which is a proxy for primary production in the NDND model. Another possible explanation is that we have underestimated some trophic flows in our simulations. For example, a recent study highlighted that feeding rates of baleen whales on krill (i.e., omnivorous zooplankton) estimated from metabolic rates were underestimated by at least a factor of 3 (Savoca et al., 2021). Allowing marine mammals to feed more on omnivorous zooplankton in the model could have significantly reduced the omnivorous zooplankton biomass and affect the trophic dynamics of other species feeding on omnivorous zooplankton.

In the NDND model, fishing mortality is implemented as a fully compensatory process, that is, the sum of the different sources of mortalities (predation, fisheries catch, and other losses) is bounded by inertia. An alternative formulation is to consider individual mortality sources as being additive and not jointly bounded. Full compensation of fishing mortality by other sources of mortality has not been observed in natural systems (Froese et al., 2016). It has been argued that the degree of fisheries compensation is expected to be on a continuum between compensatory and additive (Myers & Quinn, 2002; Péron, 2013). Further investigations are required to better assess the degree of fisheries compensation in the Barents Sea and to verify that the current conclusions are robust in the case of mortalities being partially additive and partially compensatory.

4.2 | Effects of temperature and fishing mortality on stability

In our simulations, increased temperature led to increased metabolic rates, which rendered the system more dissipative. Increased temperature also relaxed the inertia and satiation constraints, which in turn increased the range of possible biomass variations and the maximum food intake. Consequently, we expected higher temperature to

destabilize the Barents Sea food web and its species by increasing biomass variability. However, our results only partly support these expectations as only benthos and fish species temporal stability were affected by increased temperature. It indicates that the changes in biomass variability could be compensated by changes in mean biomass or by trophic feedbacks within the food web.

We expected increased fishing mortality to increase the variability of harvested species (Hsieh et al., 2006). Yet, we found minimal effects of fisheries on stability. The limited response of marine mammals' stability can result from low annual catch relative to the total marine mammals' biomass. The absence of effects of harvesting on pelagic and demersal fish stability indicates that mean biomass and biomass variance covary (Figures S6 and S7). In other words, biomass variations for both fish species are compensated by variations in biomass standard deviation.

Pelagic fish displayed three distinct relationships between stability and mean biomass. We interpret these relationships as being primarily a result of the model structure, which sets hard minimum and maximum limits to the biomass of small pelagics. The refuge biomass prevents biomass to decrease below a threshold value. When the biomass tends toward this value, predators continue feeding on this species, while its biomass cannot decrease further, which leads to decreasing variability. As temporal stability measures the biomass variability in relation to mean biomass, the lower variability corresponds to higher stability. A comparable effect is visible for extremely high values of biomass. In this case, a plausible explanation is that a combination of inertia and satiation that limits biomass increase, while higher biomass allows higher predation on pelagic fish. It results in an increase in stability with increasing biomass. Consequently, given the absence of relationship between stability and mean biomass at intermediate levels of mean biomass, we assume that if the structural constraints of the NDND model were modified, the relationship between mean biomass and temporal stability for pelagic fish could be similar to the one observed for demersal fish.

Individual effects of temperature and fisheries on the stability of the whole food-web were minimal. Our results suggest “mean-variance rescaling” (Cottingham et al., 2001), which implies that increasing mean biomass result in increased biomass variance. Mean-variance rescaling relationships are expected to increase stability (Grman et al., 2010). On the contrary, synchrony in species dynamics is expected to have a destabilizing effect on the food web and its species (Loreau & de Mazancourt, 2008). Thus, a possible explanation for the absence of temperature effects on stability is that mean-variance rescaling and synchrony compensate each other, which maintain stability at similar levels in all temperature scenarios. In our simulations, pelagic and demersal fish displayed opposite responses to increased fisheries, while the stability of the whole food-web remained constant for different levels of harvesting rates. Asynchrony leads to negative covariance, which result to increase the food web's stability (Loreau & de Mazancourt, 2008). Again, the combination of mean-variance rescaling effect with the stabilizing effect of species asynchrony is a possible explanation for the absence of response of food-web-level stability to increased harvesting rates.

Species that were not harvested in our simulations (i.e., herbivorous zooplankton, omnivorous zooplankton, and birds) displayed minimal combined effects of temperature and harvesting on estimated stabilities. Increasing temperature had a negative effect on benthos, pelagic fish, and demersal fish stabilities. We assume that increasing temperature did not affect marine mammals because temperature did not affect their metabolic rates in our study. Demersal fish displayed the strongest response to increasing temperature among all harvested species. It suggests that more intense harvesting amplifies the effects of increasing temperature on stability. This result is in line with the expectations that harvesting increases the variability of exploited species (Hsieh et al., 2006). Yet, it also shows that the harvesting rate also plays a role in the sensitivity of the food-web dynamics to temperature changes.

For benthos and fish species, we found that in colder scenarios, combined effects were synergistic, while they were antagonistic in warmer temperature scenarios. These findings are not in line with the existing literature. Nye et al. (2013) suggested that the combined effects of temperature and harvesting on the US continental shelf were mostly additive but that in some cases, strong synergistic effects were identifiable. Another study using the Atlantis model for the Benguela upwelling ecosystem highlights antagonistic, additive, and synergistic effects of temperature and fisheries (Ortega-Cisneros et al., 2018). However, their findings suggest that the nature of the combined effects of temperature and fishing was dependent on the species, while our results suggest that they depend on the temperature scenario.

The combined effects of temperature and fisheries on the whole food web displayed a similar pattern to the combined effects on harvested species (i.e., negative effect of temperature and positive effect of fisheries). However, the shifts in the nature of the combined effects in response to increased fishing mortality indicate that the effect of fisheries on stability is lower than expected if combined effects were additive. Furthermore, we consider that the negative effect of temperature on stability also reduces the effect of fisheries on stability. Indeed, individual effects of harvesting on stability is larger than the combined effects of temperature and harvesting in the crossed scenarios.

4.3 | Limitations

In this study, we have estimated the temporal stability over time periods of 30 years, a duration that is in line with many observational time series in the Barents Sea. Pimm and Redfearn (1988) suggested that variability increase with the length of time series. The NDND model can be used to simulate longer time series, and when this is done, temporal stability declines with increasing length of available time series (Figure S1). This is consistent with Pimm and Redfearn (1988) proposition. Our results are therefore valid for 30-year time series, but additional simulations would be required to verify that the conclusions hold for longer time periods.

We aimed at assessing the effect of climate change on the temporal stability of the Barents Sea food web using temperature variations as a proxy for climate change. We have implemented the effect of temperature on the metabolic rates of the concerned species. However, we have not considered other aspects of climate change in our analysis, such as climate-driven changes in primary production. We maintained a constant import of phytoplankton (i.e., proxy for primary production in the NDND model) in our simulations. Past observations displayed an increase in primary production in response to higher temperatures (Dalpadado et al., 2020). However, this increase is also closely related to the decrease of sea ice cover, which does not necessarily imply an increase of productivity per spatial unit. In addition, a modeling study suggested that increasing temperature would reduce primary production in the Barents Sea (Holt et al., 2016). In this context, as we did for temperature and fishing mortality, we assume that the effect of increased and decreased primary production on the Barents Sea food web needs to be further investigated to anticipate for both cases.

5 | CONCLUSION

In this study, we found that climate and fisheries affected the biomass of individual species in the Barents Sea, while the biomass of the entire food web was not significantly altered. Temperature increases generally led to reduced species biomass, while variations in harvesting rates led to compensatory dynamics between fish species. Counterintuitively, climate and fisheries did not strongly affect the stability of the food web. We also found that the effect of fisheries on stability was negligible compared with the effect of temperature. However, increased fishing amplified the effects of climate variations. Finally, we found that combined effects of climate and fisheries shifted from synergism to antagonism with increasing temperature.

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CONFLICT OF INTEREST

None.





AUTHOR CONTRIBUTIONS

ES wrote the manuscript along with BP, UF, and NY. All authors conceived the presented idea. ES analyzed model outputs. All authors discussed results and contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

The data and codes used to simulate output time series are available on the online repository <https://github.com/ElliotSivel/NDNDScenarios>. Output time series are available on request from the corresponding author. The data are not publicly available to the large size of data files.

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SUPPORTING INFORMATION

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

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