Estimating fishing exploitation rates to simulate global catches of pelagic and demersal fish

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Abstract

Robust projections of future trends in global fish biomass, production and catches under different fishing scenarios are needed to inform fisheries policy in a changing climate. Trust in future projections, however, relies on establishing that the models used can accurately simulate past relationships between exploitation rates, catches and ecosystem states. Here we use fisheries catch and catch-only assessment models in combination with effort data to estimate regional fishing exploitation levels (defined as the fishing mortality relative to fishing mortality at maximum sustainable yield, F/FMSY). These estimates are given for large pelagic, forage and demersal fish types across all large marine ecosystems and the high seas between 1961 and 2004; and with a 'ramp-up' between 1841-1960. We find that global exploitation rates for both large pelagic and demersal fish are consistently higher than for forage fish and reached their peaks in the late 1980s. We use the exploitation rates to globally simulate historical fishing patterns in a mechanistic fish community model. We find a good match between model and reconstructed fisheries catch, both for total catch as well as catch distribution by functional type. Simulations show a clear deviation from an unfished model state, with a 25% reduction in fish biomass in large pelagic and demersal fish in shelf regions in the most recent years and a 50% increase in forage fish, primarily due to the release of predation pressure. These results can set a baseline from which the effect of climate change relative to fishing could be estimated.

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Estimating fishing exploitation rates to simulate global catches of pelagic and demersal fish

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Key Points:

- estimated global gridded fishing exploitation patterns for large pelagic, forage and demersal fish types using catch and effort data
- food-web simulations broadly replicated catch trends of diverse ecosystems on a global scale
- found global biomass declines due to fishing in large pelagic and demersal fish and increases in forage fish due to a trophic cascade

Abstract

Robust projections of future trends in global fish biomass, production and catches under different fishing scenarios are needed to inform fisheries policy in a changing climate. Trust in future projections, however, relies on establishing that the models used can accurately simulate past relationships between exploitation rates, catches and ecosystem states. Here we use fisheries catch and catch-only assessment models in combination with effort data to estimate regional fishing exploitation levels (defined as the fishing mortality relative to fishing mortality at maximum sustainable yield, F/F_{MSY}). These estimates are given for large pelagic, forage and demersal fish types across all large marine ecosystems and the high seas between 1961 and 2004; and with a 'ramp-up' between 1841-1960. We find that global exploitation rates for both large pelagic and demersal fish are consistently higher than for forage fish and reached their peaks in the late 1980s. We use the exploitation rates to globally simulate historical fishing patterns in a mechanistic fish community model. We find a good match between model and reconstructed fisheries catch, both for total catch as well as catch distribution by functional type. Simulations show a clear deviation from an unfished model state, with a 25% reduction in fish biomass in large pelagic and demersal fish in shelf regions in the most recent years and a 50% increase in forage fish, primarily due to the release of predation pressure. These results can set a baseline from which the effect of climate change relative to fishing could be estimated.

Plain Language Summary

Fishing can heavily impact the number and types of fish in a region. Yet, simulating the historical impacts of fishing on fish communities is challenging, especially on a global scale. This is because for many places, we do not know how many fish are in the sea and what fraction of these fish die from fishing each year. In this study, we estimated the historical rate by which fisheries have caught fish globally. We used these data in a mathematical model to simulate the number of fish in the sea; both with and without fishing. The model shows that fishing has reduced the biomass of big predators (large pelagic and demersal fish) with 25% in shelf regions. This decline led to less predation on forage fish and a 50% increase in forage fish biomass, despite forage fish fisheries. These simulations provide a starting point for estimating the relative effects of climate change and fishing on future fish communities.

1 Introduction

Marine capture fisheries contribute to global food security with landings of 90 million metric tonnes annually in the last decades (FAO, 2022; Watson, 2017). Fisheries operations support employment and trade but have also caused global concerns about the impacts of fishing on individual populations of harvested species, fish communities and the structure and function of the ecosystem (Jennings & Kaiser, 1998; Myers & Worm, 2003). Historical simulations of fish biomass and fisheries production are important to describe how and why the oceans have changed due to fisheries. In addition, these simulations can provide a baseline of fish biomass under current exploitation rates to support assessments of climate change impacts on fisheries and marine ecosystems (Blanchard et al., this issue).

Marine ecosystem models of upper trophic level organisms, hereafter termed MEMs, have been used to simulate historical fish community biomass (Bianchi et al., 2023; Blanchard et al., 2012; Christensen et al., 2015; Galbraith et al., 2017; Petrik et al., 2019). MEMs typically require instantaneous fishing mortality rates to simulate fish catches and changes in fish biomass with fishing. MEMs have faced challenges in parameterizing the effects of fishing due to uncertainty in fishing exploitation levels for fish populations, functional types and communities in most national waters and the high seas. As a result, some MEMs have used a fishing mortality rate that approximates model estimated maximum sustainable yield (MSY) and compared these to observational estimates of peak catches in historically fished ecosystems (Blanchard et al., 2012; Petrik et al., 2019). Other MEMs, simulating historical fishing catches over time, have adopted approaches that translate fishing effort, often measured by engine power and days at sea, to fishing mortality and catch and use bootstrapping to find a set of model parameters that produce the best agreements with observed fish catches (Christensen et al., 2015; Galbraith et al., 2017). In such approaches, estimating model parameters that relate to fishing processes can be challenging and computationally expensive for complex MEMs, that may require multiple fishing mortality estimates per year and spatial domain. Furthermore, many regional-scale MEMs take fishing mortality rates as direct input rather than fishing effort (SI in Blanchard et al. this issue). However, existing fishing mortality estimates are often based on single-species stock assessments for particular regions, e.g. Jacobsen et al. (2017), and not available across regions and functional types. Thus standardized data on fishing mortality rates for different regions of the world, required for systematic model intercomparison projects (such as the Fisheries and Marine Ecosystem Model Intercomparison Project, FishMIP) of fishing impacts, are currently lacking.

Catch-only stock assessment models combine time series of catch with population dynamic models to estimate stock status in cases where data is limited and estimates of stock abundance are unavailable (Froese et al., 2017; Thorson et al., 2012). Despite that catch-only models can lead to biased estimates of stock status and poor management advice (Bouch et al., 2021; Free et al., 2020; Ovando et al., 2021), they are an effective means of assessing stock status for the majority of global fisheries that lack sufficient data for formal stock assessments. Catch-only models may thus, in the context of global and regional model intercomparison projects, offer a transparent way to externally estimate the rate at which fish biomass is caught, i.e. the fishing mortality rate, for a large range of ecosystems and fish types. Fishing mortality rate estimates could usefully serve as standardized inputs to MEMs to simulate fish catches and historical changes in biomass, where observational estimates of fisheries catches and biomass may be used for model validation (Blanchard et al., this issue).

In this study, we used catch-only stock assessment models to estimate a time series of fishing mortality (F) relative to the fishing mortality that supports maximum sustainable yield (F_{MSY}) per Large Marine Ecosystem (LME) for three fish functional types: forage fish, large pelagic fish, and demersal fish. We focused on obtaining an F/F_{MSY} time series, rather than an F time series, as the F/F_{MSY} time series provides a forcing usable in most MEMs, where F_{MSY} depends on each MEM's specifications and assumptions. For all LMEs with intermediate and high catches, the F/F_{MSY} time series was estimated from time series of fisheries landings (Watson, 2017). For low catch LMEs and the high seas, the time series was estimated by combining global effort data with the F/F_{MSY} estimates from the intermediate and high catch LMEs. We allocated the estimated F/F_{MSY} per functional type, ecosystem, and year across a 0.5-degree spatial grid in proportion to total gridded effort in each ecosystem (Rousseau et al., 2022, 2024). We used the gridded estimates to simulate historical fishing intensity between 1961 and 2004 with the Fisheries Size and Functional Type model, FEISTY (Petrik et al. 2019). We compared the model simulations of FEISTY with observational estimates of fisheries landings in the same period. We then evaluated the simulated global changes in fish biomass as compared to an unfished ocean.

2 Methods and Data

2.1 Method summary

We utilized data from three distinct data sources to construct a time series of F/F_{MSY} per LME (including the high seas as one region), spatially allocated across a 0.5-degree spatial grid, for demersal, large pelagic, and forage fish. These data sources encompassed: 1) a global catch reconstruction aggregated by functional type and LME (including the high seas as one region) from 1961 to 2004, 2) nominal fishing effort data by functional type and LME (including the high seas as one region) between 1841 and 2004, and 3) total nominal fishing effort data gridded at a 0.5-degree spatial resolution from 1961 to 2004. These data products were prepared by FishMIP as part of the Intersectoral Model Intercomparison Project (ISIMIP) and are available at isimip.data.org, see Blanchard et al. this issue and Frieler et al. (2023) for further details.

We estimated an F/F_{MSY} timeseries using a data limited catch assessment model (see section 2.3) for all LME × functional type combinations with intermediate and high catches (see definitions below). For all remaining combinations and the high seas, we converted the nominal effort time series per functional type to an F/F_{MSY} timeseries using conversion factors from the intermediate and high catch LMEs (see section 2.4). The F/F_{MSY} values were then allocated per year across a 0.5-degree spatial grid in proportion to total gridded effort in each LME/high seas. To exemplify how the gridded F/F_{MSY} data set can be input into MEMs to generate historical time series of fish biomass and catch, they were input into the FEISTY model forced by outputs from GFDL's ocean model (MOM6-COBALTv2) (Adcroft et al., 2019; Stock et al., 2020) that provides monthly means of physics, biogeochemistry, and lower trophic level production (section 2.5). The ocean model simulations were run on a 0.25-degree spatial grid using boundary condition forcing from the Japanese 55-year Reanalysis (JRA-55) products (Tsujino et al., 2018) and temporally dynamic river freshwater and nitrogen fluxes (Liu et al., 2021). Ocean model outputs were interpolated to a regular 1-degree grid for the FishMIP contribution to the ISIMIP Phase 3a protocol (Blanchard et al. this issue) and interpolated to a daily time step for coupling with FEISTY. We ran scenarios both with and without fishing and compared the modeled fishing catch with reconstructed catch.

2.2 Catch and Effort Data

Fisheries catch, estimated as the sum of reported landings, illegal, unreported and unregulated catch and discards, were aggregated per functional type and LME for the period 1961-2004 from gridded catch data (Watson, 2017; Watson & Tidd, 2018). The demersal fish functional type included all species that were classified in Watson (2017) as demersal, bentho-pelagic, flatfish, reef-associated and bathydemersal. Forage fish included all fish classified in Watson (2017) as pelagic fish < 30 cm and large pelagic fish included all fish classified as pelagic fish > 30 cm. All other fisheries catch types, representing 17% of total catch, were not simulated in this study. Total industrial and artisanal fishing effort data by functional type and LME (including the high seas as one region) were aggregated from Rousseau et al. (2022, 2024) and then reconstructed for the period 1861-2004 using generalised additive models (SI of Blanchard et al. this issue). The data describe nominal effort of the active fleet based on the engine power of the active fleet multiplied with the average days at sea of one vessel. Gridded total industrial and artisanal fishing effort, on a 0.5-degree spatial resolution, for the period 1961-2004 were obtained from Rousseau et al. (2022, 2024).

2.3 Catch-only Assessment Model

We applied the Catch-MSY model (Martell & Froese, 2013) to estimate the relative historical fishing pressure in each of the LMEs. First, we modified the standard Schaefer formulation to the Pella-Tomlinson formulation of surplus production to be able to attribute different shape parameters to each of the functional types:

$$B_{i,t+1} = B_{i,t} + \frac{r_i}{(n_i-1)} B_{i,t} \left(1 - \frac{B_{i,t}}{K_i}\right)^{n_i-1} - F_{i,t} B_{i,t} ,$$

where B is the exploited biomass of functional type *i*, *n* is a shape parameter determining at which fraction of the unfished biomass MSY occurs, *r* is the population growth parameter, and *K* is the carrying capacity. We used the catch information as input data to infer the fishing mortality as $C_{i,t} = F_{i,t} B_{i,t}$. We *a priori* assigned *n* for each of the functional types before assessing the past F/F_{MSY} status using the *n* estimates from Thorson et al. (2012) (Table 1), who estimated the shape parameters based on an analysis of 147 data rich stocks in the RAM stock assessment database. The fit was conducted by testing a set of *r-K* combinations which gave a realistic historical biomass distribution. Here realistic is defined as the biomass always being above 0 and below the carrying capacity (which only works for fished stocks). We then used the median *r-K* combinations to recreate the historical biomass distribution and consequently calculate the estimated $B_{i,t}$. We used the estimates to calculate $MSY_i = \frac{rK}{n^{\frac{n}{n-1}}}$, and $F_{MSY} = \frac{MSY}{n^{\left(\frac{1}{1-n}\right)K}}$ and visually inspected fits to ensure that the MSY estimates were within reasonable boundaries considering the past catches.

Table 1. Shape parameters for the three fish functional types in the Catch-MSY model.

Functional type	***n***
Demersal	1.540
Small pelagics	0.599
Large pelagics	1.431

The catch-only assessment model performs best when the catch time series covers a period where fishing catches have a large degree of contrast, *i.e.*, both fishing above and below MSY. Consequently, we excluded certain LMEs with historically low fishing exploitation from the catch assessment analysis. Specifically, we excluded the Arctic and Antarctic systems, most Australian LMEs and the insular Pacific-Hawaiian LME, following Stock et al. (2017), and the high seas. Furthermore, in some LMEs with intermediate and high total catch, certain functional types exhibited low catches. We thus removed any functional type that contributed less than 5% to the total catch within a given LME. These exclusions resulted in an estimate of F/F_{MSY} in 45 LMEs for demersal and large pelagic fish and 34 LMEs for forage fish. We compared the F/F_{MSY} time series of several LMEs and functional types with stock assessment time series of F/F_{MSY} obtained from the Ram Legacy database v4 (RAM Legacy Stock Assessment Database, 2018) and the ICES Stock Assessment Graphs database (downloaded January 2023). The comparison was done for 135 stocks that were aggregated in 14 LME × functional type combinations (Supplementary Figure S1).

2.4 Time series of F/F_{MSY} per grid cell

The F/F_{MSY} time series from the catch assessment model only provides information for functional types in intermediate and high catch LMEs for 1961-2004. For each of these LME × functional type combinations, we estimated F/F_{MSY} time series for 1841-1960 using the nominal effort time series per functional type and LME and factors that convert nominal effort to F/F_{MSY}. To this end, we selected from each catch assessment model outcome the five years closest to F_{MSY} and MSY. We paired these selected years per functional type and LME with the nominal effort and averaged the nominal effort values. This average value approximates the total nominal effort per year that is needed to fish a functional type at F_{MSY} in an LME. We standardized these nominal effort values to nominal effort at F_{MSY} per km^2 by dividing by the areal extent of the fished part of each LME. The fished part was estimated using the total gridded effort information and by selecting all grid cells (sorted from high to low effort) that correspond to 95% of total effort in each LME. The standardized nominal effort at F_{MSY} served as the conversion factors to compute F/F_{MSY} time series for functional types in intermediate and high catch LMEs between 1841-1960 assuming a linear relationship between effort and mortality. In addition, we used the conversion factors to estimate F/F_{MSY} time series for 1841-2004 for functional types in all low catch LMEs and the high seas. This was done by converting the time series of nominal effort per functional type and LME to an F/F_{MSY} time series using a conversion factor from an adjacent area or the global median of a functional type (Supplementary Table S1).

The spatial allocation of fishing mortality for each functional type to each 0.5-degree grid cell was done in proportion to total gridded effort in each LME. For the period 1961-2004, the allocation was based on the existing annual information. For the period 1841-1960, we kept the spatial allocation the same as for the year 1961.

2.5 Mechanistic fish community model FEISTY

FEISTY is a temporally dynamic, spatially explicit, mechanistic model that simulates the biomasses of forage fish (small pelagics), large pelagic, and demersal fishes (Petrik et al. 2019). Fish functional types are defined by their maximum size, habitat, and prey preferences. Both large pelagic and forage fish feed on prey, fish and/or zooplankton, in the pelagic zone throughout their life. Demersal fish initially feed in the pelagic and then transition to the benthic zone as juveniles at 0.5 g. Demersal fish >250 g feed as generalists on both pelagic and benthic resources in shelf areas <200 m depth, whereas they feed solely in the benthic zone in deeper areas. FEISTY includes a multi-stage life cycle of these fishes and includes food-dependent growth and reproduction. All metabolic and feeding rates scale with individual body size. Maturation is modeled with a food-dependent function that translates individual-level assumptions about growth in body size to the population level (de Roos et al., 2008). Growth, reproduction, and mortality are the consequence of prey encounter and consumption, standard metabolism, predation, and fishing, which depend on (1) habitat temperatures that affect the speed of rates, (2) mesozooplankton biomass, mesozooplankton loss rates to higher predators, and detritus flux to the seafloor that set the food available to upper trophic levels, (3) explicit predator-prey interactions and competition. FEISTY has been reasonably successful in representing observed trends of peak fisheries catches (correlation between observed and modeled total catch per LME is 0.54) and reproduces the underlying mechanisms involved in structuring large pelagic vs. demersal fish (Petrik et al. 2019).

In past simulations when FEISTY was coupled to outputs from COBALT (Petrik et al. 2019, 2020), forcings included distinct medium and large zooplankton groups (small and large mesozooplankton). The simulations here were completed using the FishMIP protocol (Blanchard et al. this issue) that combines the COBALT medium and large zooplankton into one mesozooplankton group. Additionally, zooplankton loss rates to higher predators z_{HPloss} are not provided. Thus an empirical relationship between mesozooplankton biomass z_{bio} and upper water column temperature T_{pel} was developed to estimate these rates as successfully used in past FishMIP simulations (Heneghan et al., 2021; Tittensor et al., 2021): $z_{HPloss} = 10^{(-2.925+1.964\cdot\log_{10}(zoo_{bio}+eps))} + 1.958 \cdot 10^{-2} \cdot T_{pel}$, with *eps* being a value close to zero.

2.5 Model parameterization and simulations

All FEISTY model parameters were taken from Petrik et al. (2019). We implemented fishing in FEISTY from the F/F_{MSY} time series by identifying the fishing mortality that corresponds to F_{MSY} in FEISTY. F_{MSY} is a dynamic parameter that varies with the food web configuration, the amount of fishing on the other fish types, fishing selectivity, as well as the abiotic conditions. Finding F_{MSY} for each permutation of these factors was computationally prohibitive. Instead, we examined how F_{MSY} varied with prey production and temperature for large pelagic and demersal fish (Supplementary Figure S2; no such estimation could be made for forage fish as they are heavily depending on fish predation mortality). We found that changes in prey production had a limited effect on $F_{MSY,}$ but temperature had a large predictable effect resulting from a higher turnover rate of biomass in FEISTY in warmer waters, which makes fish more resilient to fishing. We thus approximated the temperature effect on F_{MSY} in FEISTY with

a temperature term that is linked to the thermal sensitivity of metabolism (0.063 ºC^{-1}). We set the daily fishing mortality F for each functional type *f*, including forage fish, as:

$$F_{i,f,t} = \frac{0.3}{365} \cdot \left(\frac{F}{F_{MSY}}\right)_{i,f,t} \cdot \exp\left(0.063 \cdot \left(T_{i,t} - 10\right)\right)$$

where T (°C) is the mean habitat temperature in grid cell *i* and day *t* (T = 0-100m mean for forage fish and large pelagics and T = bottom temperature for demersal fish), 0.3 is the obtained value of F_{MSY} in FEISTY at 10 ºC, and $(F/F_{MSY})_{i,f,t}$ is based on the time series derived as described in the prior section. Fishing gear selectivity was 100% for the largest size class of all functional types ($1 \times F_{i,f,t}$). In addition, large pelagic and demersal fish were fished with 10% selectivity at the juvenile stage ($0.1 \times F_{i,f,t}$). Model spin-up with the ocean-forcing variables and fishing mortality was done by repeating cycles of the ocean inputs between 1961-1980 (there are no ocean outputs prior to 1961) combined with the fishing mortality of 1841. We afterwards ran the model with daily time steps from 1841 up to 2004 using year-specific fishing mortalities from 1841 and year-specific ocean outputs from 1961. In addition, we ran FEISTY without fishing as an alternate scenario

3 Results

3.1 Fishing exploitation patterns

Large pelagic and demersal fish are, on average, fished with a higher intensity than forage fish (Figure 1). On a global scale, both large pelagic and demersal fish peak in exploitation rate in the late 1980s, but the exploitation patterns strongly vary between regions. The Arctic/Antarctic region has the lowest exploitation for all fish types and the Mediterranean and Black Sea region the highest. Large pelagic fishing intensity peaks in the North Atlantic before the 1970s and in the Eastern and Western Pacific and Mediterranean and Black Sea around the 1990s. Large pelagic fishing intensity is highest in the South Atlantic and Indian Ocean in the most recent years. Demersal fishing intensity peaks in the Mediterranean and Black Sea region before the 1970s. Demersal fishing intensity is relatively constant, with F/F_{MSY} around 0.6, in the North and South Atlantic and Western Pacific between 1970s and 2000s. Demersal fishing intensity is highest in the Indian Ocean and Eastern Pacific in the most recent years. For forage fish, the patterns are more variable, but most regions have a peak in forage fish fishing mortality in the 1980s and/or the 2000s.

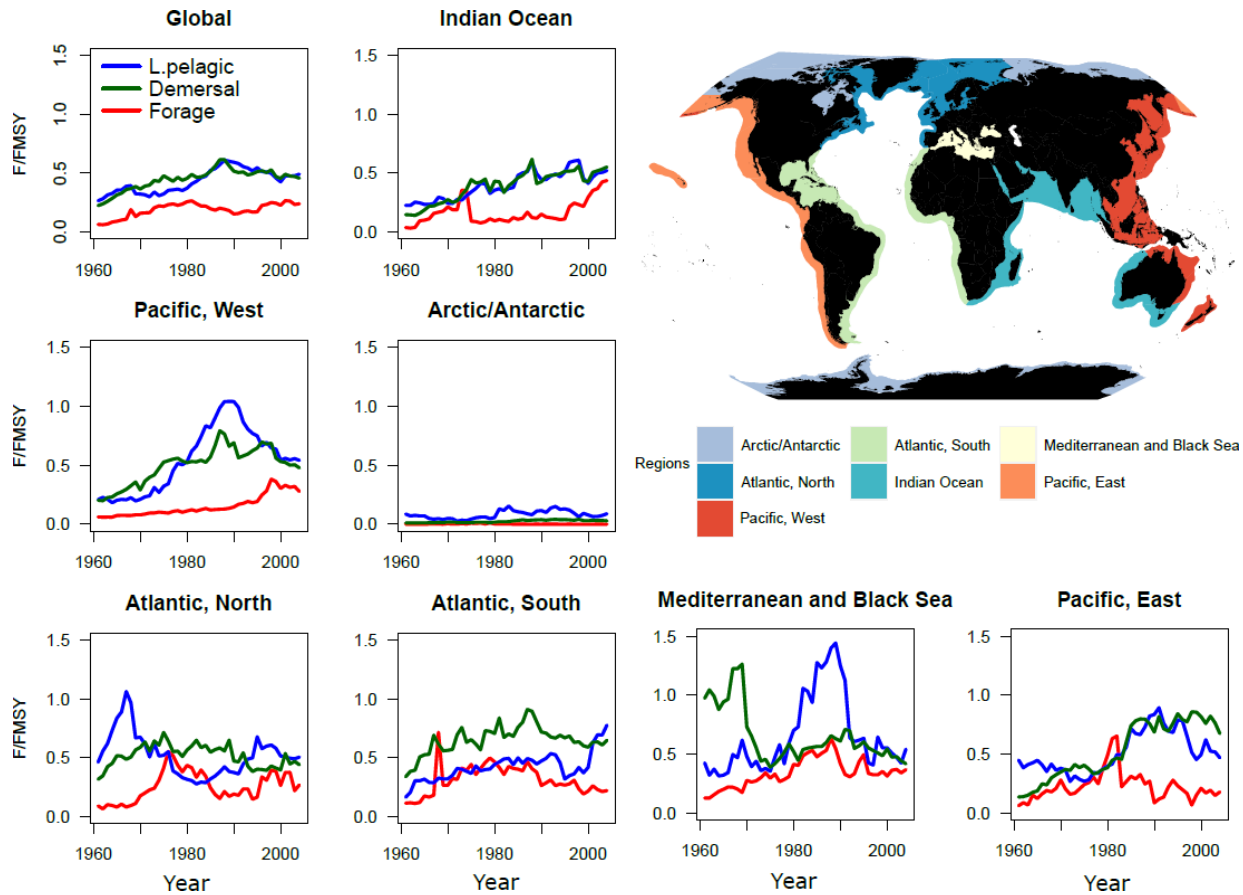

Figure 1. Time series of average annual exploitation rates (F/F_{MSY}) aggregated per region based on the average of all LMEs in each region (all LMEs are given equal weight).

Maps of the gridded exploitation patterns mirror the above results (Figure 2). The maps show that most LMEs with a narrow shelf have a relatively high F/F_{MSY} in the shallow areas and low values in the deeper regions. This distribution reflects the spatial allocation of fishing intensity in proportion to total gridded effort in each LME (see method). Large pelagic fish are fished at higher intensity in the high seas than demersal and forage fish.

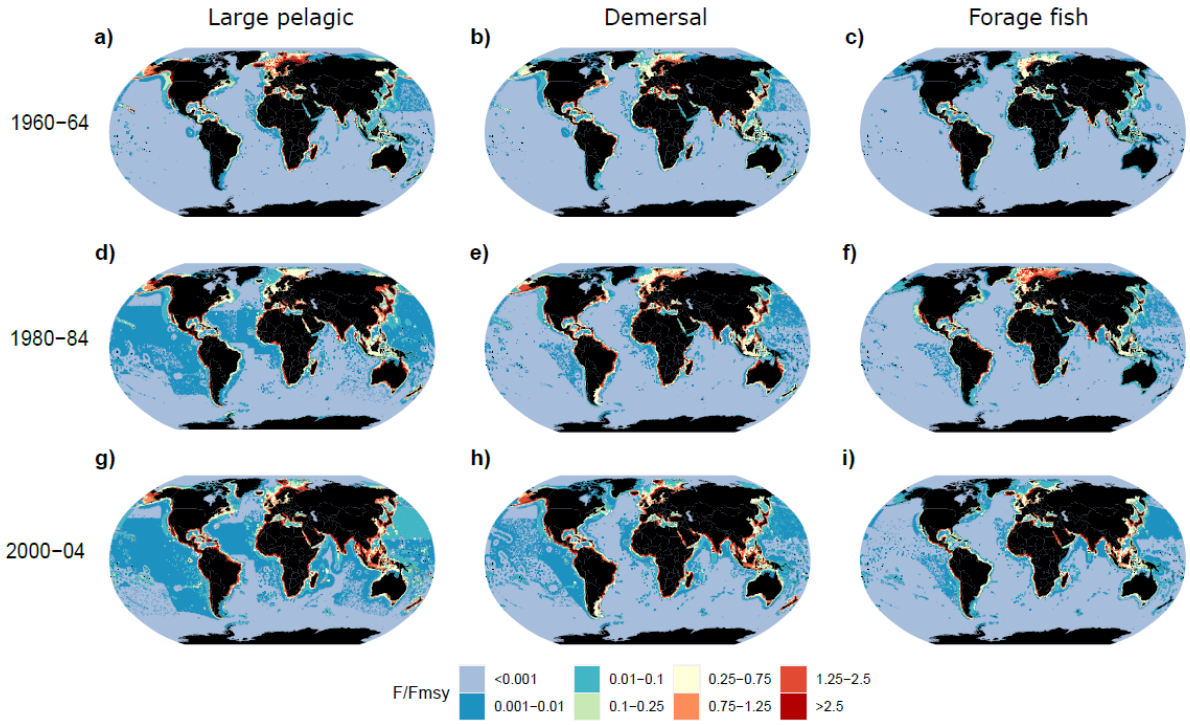

Figure 2. Maps of gridded average F/F_{MSY} for large pelagic (**a**, **d**, **g**), demersal (**b**, **e**, **h**) and forage fish (**c**, **f**, **i**) in the early 1960s, 1980s and 2000s.

A comparison between F/F_{MSY} from data-rich stock assessments and the catch-derived F/F_{MSY} shows that the catch-derived F/F_{MSY} is comparable to but on average lower than the stock-derived F/F_{MSY} (Figure 3 & S1). Part of this difference may be attributed to the selection of species; the stock assessment data consist of the most important fished species, whereas the catch-derived estimates are based on the whole community catch. Nevertheless, it is likely that the catch-derived assessment has underestimated fishing mortality in some regions. The reverse, an overestimation of fishing mortality, happened in the Eastern Bering Sea and the Gulf of Alaska (Figure 3).

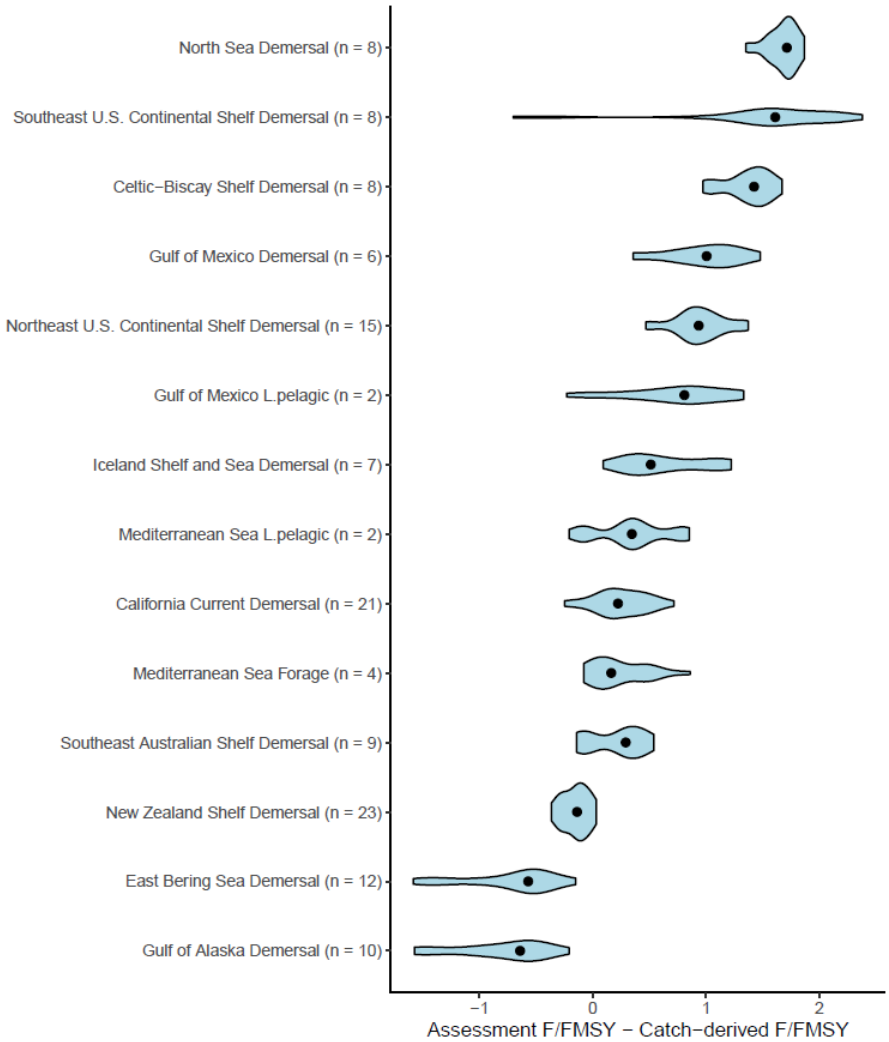

Figure 3. Violin plots with annual differences between stock assessment F/F_{MSY} and catch-only derived F/F_{MSY} for 14 LME × functional type combinations between 1980 and 2004. The stock assessment F/F_{MSY} are based on the geometric mean (equal weighting of each stock). The dot shows the median difference. A difference of 1 (-1) indicates that the assessment-derived F/F_{MSY} is one F_{MSY} higher (lower) than the catch-derived. See supplementary Figure S1 for individual time-series of each stock.

3.2 Simulations of fish catch

Simulated time series of global catches derived by applying the F/F_{MSY} estimates above to FEISTY show good agreement with reconstructed fisheries catches, especially for total fish and large pelagic fish catch (Figure 4). Model estimates of demersal fish are typically 5 to 10 million metric tonnes per year lower. Forage fish modeled catches are close to the fisheries catch data but show a steady increase over time which is not observed in the data.

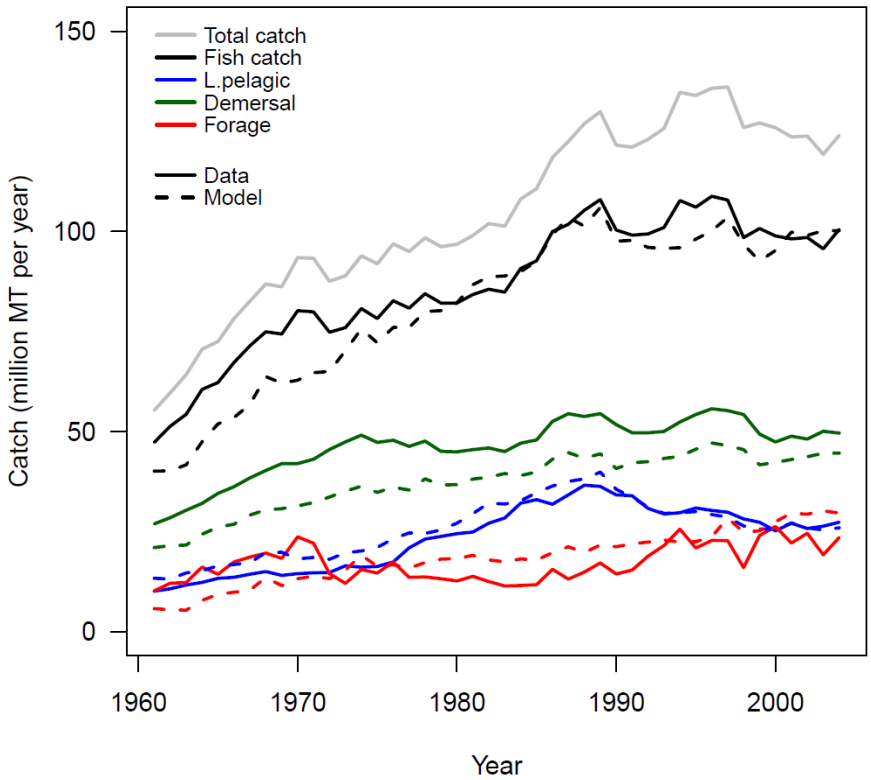

Figure 4. Time-series of observed (solid) versus model-based (dashed) catches. Fish catch includes all fish classified as large pelagic, forage fish and demersal in our study. Total catch includes all marine organisms and was not simulated in the study.

Comparisons of observed and modeled fish catches across LMEs show a high correlation for total landings (r = 0.85), demersal fish (r = 0.84) and forage fish (0.79) (Figure 5). Large pelagic fish have a correlation of 0.69 and lower modeled catches in several LMEs, among others, the Sulu-Celebes Sea and the Northeast Australian Shelf. In absolute numbers, the difference between model and data in total landings is less than 1 million MT y^{-1} in 78% of the LMEs. In addition, no consistent mismatch in catch is observed for specific latitudinal regions. The largest differences between data and model are observed in the Humboldt Current (9.4 million MT y^{-1} higher in data mainly due to forage fish catch), Mediterranean Sea (3.8 million MT y^{-1} higher in model), Arabian Sea (3.6 million MT y^{-1} higher in model) and Sea of Okhotsk (2.9 million MT y^{-1} higher in data).

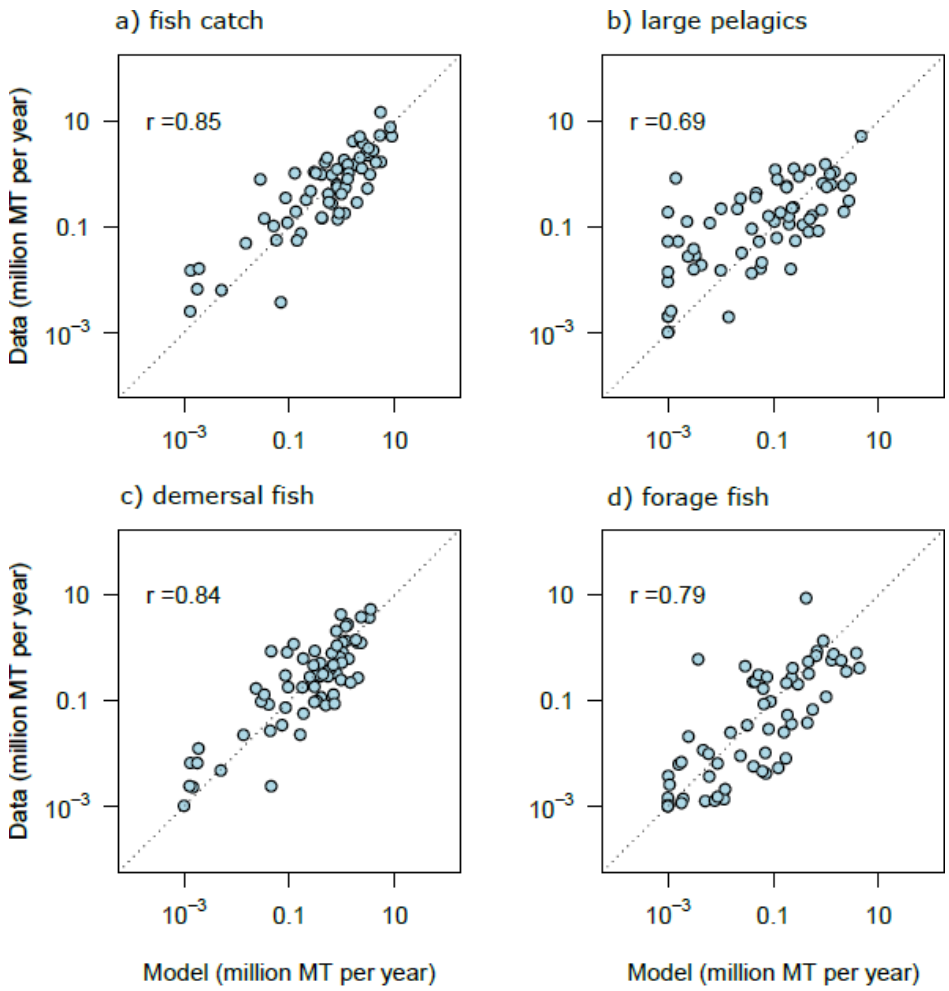

Figure 5. Comparison of observed and modeled fish catch per LME based on the mean catch between 1990-2000. Fish catch (**a**) includes all fish classified as large pelagic (**b**), demersal (**c**) and forage fish (**d**) in our study. A value of 0.001 million MT was added to both data and model outputs to limit focus on very low catches.

3.3 Simulations of fish biomass

Global fish biomass in the unfished scenario is varying between 1.72 and 1.85 gigaton in the period 1961-2004. Simulated unfished biomass is typically lower than the estimated unfished biomass (parameter *K*) derived from the catch-only model for LMEs with intermediate and high catches, though positively correlated (Figure 6a, and supplementary Figure S3 for each functional type). Relative to an unfished scenario, fishing has resulted in a global biomass decline of 10-15% in large pelagic and demersal fish and 25% decline in shelf regions as of 2004 (Figure 6b-c). In contrast, the simulations show a global increase of 25% in forage fish biomass in the fishing scenario and a 50% increase in shelf regions, primarily caused by the release of predation pressure from large demersal and pelagic fish. Demersal fish show a clear decline in biomass with increasing fishing pressure across LMEs. Demersal fish biomass is around 60% of the unfished biomass in LMEs that are fished at F_{MSY} (Figure 7b). The biomass response of large pelagics and forage fish across LMEs is largely unrelated to fishing pressure on each of these

types (Figure 7a and c), suggesting that the biomass changes in these groups are strongly impacted by trophic interactions beyond fishing.

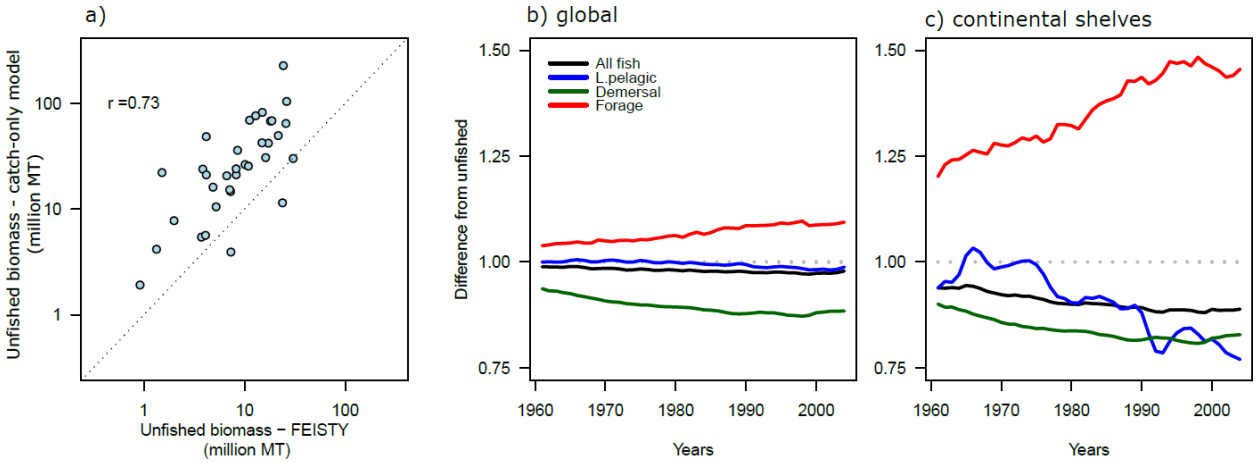

Figure 6. Comparison of simulated fish biomass in the unfished scenario averaged across years 1961-2004 and the estimated unfished biomass (parameter *K*) derived from the catch-only model average across years (**a**). Changes in fish biomass relative to an unfished scenario between 1961 and 2004 for the entire ocean (**b**) and all continental shelves <500 m in depth (**c**). Panel (**a**) is based on 34 LMEs for which we obtained an estimate of *K* for all three functional types using the catch-only model.

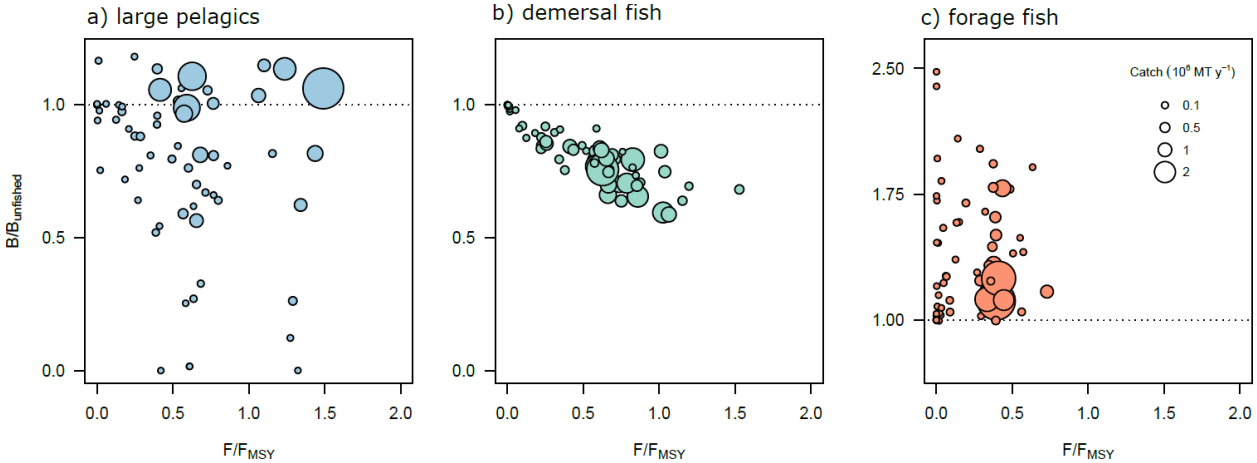

Figure 7. Relation between $B/B_{unfished}$ and F/F_{MSY} for all LMEs based on average values between 1990 and 2000. $B_{unfished}$ is the biomass in an unfished scenario. The size of the dot reflects the size of the observed fishing catch.

4 Discussion

We estimated regional fishing exploitation levels (F/F_{MSY}) for forage, large pelagic and demersal fish functional types utilizing fisheries catch and effort data. By applying the F/F_{MSY} estimates in a mechanistic MEM, we successfully conducted simulations of global catches and catch per functional type over time. In the FEISTY model, fishing at the estimated historical exploitation rates caused a 25% decline in the biomass of large pelagic and demersal fish predators and a 50% increase in forage fish biomass in shelf ecosystems over the simulated time period as compared to an unfished situation. The simulated increase in forage fish biomass is the result of a trophic cascade triggered by the decline of fish predators due to fishing (Frank et al., 2005). The observed increase in forage fish biomass due to fishing surpasses the anticipated increase of forage fish biomass due to climate change (± 4% fractional increase), which is triggered by a decline of fish predators that suffer from higher metabolic costs in a warming ocean and from declines in prey productivity (Petrik et al., 2020; Tittensor et al., 2021). These findings underscore the influential role of fishing as a primary driver of fish community dynamics, emphasizing the need to evaluate the impact of climate change within the context of an historically altered fish community (Brander, 2007). The exploitation levels provide potential standardized data forcing for simulation experiments, including model intercomparison projects, where fishing effort are problematic to run, or where a common set of mortality rates across MEMs is warranted.

Previous global simulations of fishing within the FEISTY model were kept simple by implementing a constant fishing mortality rate across space and time, aiming to achieve MSY across the three functional types (Petrik et al., 2019). The dynamic fishing mortality rates introduced in this study improved correlations between simulated and observed catches during peak exploitation (Supplementrary Table S2). Part of these improvements can be attributed to comparing fishing catches in all LMEs, including the lightly fished LMEs that were omitted in the prior study. Without these LMEs, our correlation for forage fish (and total catch) remain higher than Petrik et al. (2019) (Supplementrary Table S2). This finding is in line with the re-constructed F/F_{MSY} estimates which indicated that forage fish has typically faced fishing mortality rates lower than F_{MSY} and are thus not fished at levels that would lead to peak exploitation. Despite these improvements, a significant uncertainty persists, namely the parameterization of F_{MSY} which is varying with temperature in the FEISTY model, whereas, both in the FEISTY model and in nature, F_{MSY} is varying in a more dynamic way due to biotic interactions within and between functional types. This dynamic nature of F_{MSY} poses a challenge in capturing fishing effects in food web models (Spence et al., 2021). We recommend that other MEMs approximate the temperature effect on F_{MSY} ahead of using the F/F_{MSY} estimates.

Among LMEs, we observe a 40% decrease in demersal fish biomass relative to unfished levels with fishing rates at MSY and no clear response in forage and large pelagic fish. These effects are different from what is assumed in some surplus production models where fishing at MSY is estimated to cause a 50% decline in total stock biomass relative to an unfished state (Mangel, 2006)(chapter 6). The primary underlying factor for the complex responses in FEISTY is trophic interactions. In addition, some of these dynamics can be attributed to the structural characteristics of the FEISTY model. Fish in FEISTY mature at relatively small sizes compared to their maximum potential size. This decision was made to encompass a spectrum of fish species with just 2-3 size classes within each functional type (Petrik et al., 2019). Additionally, the model includes gear selectivity parameters that target predominantly (in the case of large

pelagic and demersal fish) or exclusively (for forage fish) mature fishes, which allows fish to survive long enough to spawn in the model. Consequently, the resilience of fish biomass to fishing in FEISTY may be higher than for natural stocks and FEISTY may likely be underestimating the global changes in biomass of each functional type. However, these effects mainly influence biomass and less fisheries catches as gear selectivity is only expected to affect the maximum sustainable yield lightly (Andersen, 2019)(fig. 5.11, see trawl selectivity).

Part of the observed resilience to fishing is also linked to the food web dynamics. As anticipated, these dynamics increased forage fish biomass in most LMEs in the fishing scenario, which is a consequence of trophic cascades initiated by the decline of demersal and large pelagic fish with fishing in these systems (Andersen & Pedersen, 2010; Casini et al., 2008; Daskalov et al., 2007; Frank et al., 2005). However, the food web dynamics also led to a somewhat counterintuitive pattern, namely, an increase in large pelagic fish biomass with fishing in several LMEs, particularly those with high observed catches. Part of this counterintuitive outcome is likely a trophic cascade mediated through the larval and juvenile stages as competition with demersal fish is relieved. In addition, this counterintuitive outcome is underpinned by an ecological mechanism known as overcompensation (De Roos et al., 2007; Schröder et al., 2009). Overcompensation entails a positive population response to mortality, which results in an increased equilibrium level of the population. Overcompensation has been observed in theoretical models as well as in experiments in field and laboratory systems, but only in low-diversity systems (Schröder et al., 2014). Overcompensation is unlikely for large pelagic biomass dynamics in diverse marine ecosystems as less fished species of similar functional type could replace the more fished species.

Previous regional estimates of fishing exploitation used averages of assessed stocks (Hilborn et al., 2020). Here we estimated exploitation patterns from aggregated catch data to obtain estimates for each functional type and region. However, in natural ecosystems, a functional type is exploited with a mixture of stock-specific rates, rather than one single rate, and includes species without fisheries. The total catch in each functional type thus represents the cumulative of all catches, potentially representing the substitution of a newly exploited stock for an overexploited one. It is difficult to assess how well the catch-only model can deal with these aggregated catch data as the method has solely been tested for individual stocks (Martell & Froese, 2013). A comparison with regional averages of assessed stocks in our study indicated that the catch-only modeled exploitation rates tend to be lower. These lower values align with our expectations as stock assessment data primarily focuses on the most economically significant species within each functional type, often omitting information on less commercially important species that have a lower exploitation (Ovando et al., 2021). In addition, we found a large difference in unfished biomass estimates between the catch-only model and FEISTY. For catch-only models, the relative rates (e.g., F/F_{MSY} and B/B_{MSY}) are often considered more reliable that the absolute rates of biomass, such as the carrying capacity. The catch-only carrying capacity is also independently estimated for each functional type and this may cause the sum of these carrying capacities to overshoot the total fish productive capacity of each ecosystem. This potential overshoot of the catch-only estimates may explain why the unfished biomass estimates in FEISTY are consistently lower.

The methodology used for deriving fishing exploitation rates, the spatial allocation method, and the incorporation of mortality rates within the fish model FEISTY all introduce

uncertainties. These uncertainties are inherent when simulating global fish food webs and their fisheries. Nevertheless, the simulated ecosystem catches demonstrated an encouraging match to observed values, particularly in the case of total global catch. This alignment suggests that the model reasonably captures the productive capacities of diverse ecosystems on a global scale and can broadly replicate realistic long-term trends of fish catches. These results can support the quantification of future trends in global fish biomass and potential fisheries production and inform ongoing global assessments of climate change impacts on marine ecosystems.

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Open Research

The fishing exploitation pattern time series and the FEISTY model outputs are available on ZENODO (van Denderen et al., 2023). The files to run the FEISTY fish modeling simulations can be found at https://github.com/cpetrik/FEISTY/tree/master/CODE/FishMIP. Forcing data for GFDL-MOM6-COBALT is available in the ISIMIP Repository (Liu et al. 2022) and fishing effort is available via Rousseau et al. (2022). Details for FishMIP-ISIMIP 3a Protocol are provided here: https://github.com/Fish-MIP/FishMIP_2022_3a_Protocol

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