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

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Key Points:

* We estimated global gridded fishing exploitation patterns for large pelagic, forage and demersal fish types using catch and effort data
* Food-web simulations with reconstructed fishing exploitation rates broadly replicated catch trends of diverse ecosystems on a global scale
* Global biomass declines due to fishing of large pelagic and demersal fish leads to increases in forage fish via a trophic cascade

Abstract

Robust projections of future trends in global fish biomass, production and catches are needed for informed fisheries policy in a changing climate. Trust in future projections, however, relies on establishing that models can accurately simulate past relationships between exploitation rates and ecosystem states. In addition, historical simulations are important to describe how the oceans have changed due to fishing. Here we use fisheries catch, catch-only assessment models and 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 1961-2004; and with a ‘ramp-up’ between 1841-1960. We find that global exploitation rates for large pelagic and demersal fish consistently exceed those for forage fish and peak in the late 1980s. We use the rates to globally simulate historical fishing patterns in a mechanistic fish community model. The modeled catch aligns with the reconstructed catch, both for total catch and catch distribution by functional type. Simulations show a clear deviation from an unfished model state, with a 25% reduction in biomass in large pelagic and demersal fish in shelf regions in recent years and a 50% increase in forage fish, primarily due to reduced predation. The simulations can set a baseline for assessing the effect of climate change relative to fishing. The results highlight the influential role of fishing as a primary driver of global fish community dynamics.

**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) by 25% in shelf regions. This decline led to less predation on forage fish and a 50% increase in forage fish biomass, despite fishing of forage fish. These simulations will allow estimating the relative effects of climate change and fishing on current and 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 with fishing (*e*.*g*., 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 MEM 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). Existing regional fishing mortality estimates are available for areas with formal stock assessments , e.g. Jacobsen et al. (2017) and Hilborn et al. (2020) but are missing for large parts of the world (Ovando et al., 2021). Thus global standardized data on fishing mortality rates for different regions of the world, required for simulating global historical fishing impacts and systematic model intercomparison projects (such as the Fisheries and Marine Ecosystem Model Intercomparison Project, FishMIP) 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 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, such that observational estimates of fisheries catches and biomass may be independently used for model validation (Blanchard et al., this issue).

The objectives of this study were threefold. First, we aimed to estimate regional fishing exploitation levels for three fish functional types: forage fish, large pelagic fish, and demersal fish. We did this by integrating fisheries catch data, catch-only assessment models, and fishing effort data. Second, we used the derived exploitation rates to simulate historical global fishing patterns for these functional types using the mechanistic fish community model FEISTY (Fisheries Size and Functional Type model, Petrik et al., 2019). We compared the simulated patterns with observational estimates of fisheries catch. Finally, we evaluated the changes in global fish biomass simulated by the model against a baseline representing an unfished ocean. This evaluation was done to elucidate the role of fishing as a global driver of fish community dynamics and to determine how historical fishing patterns have influenced the dynamics of the coupled ecosystem-fisheries system.

2 Methods and Data

2.1 Method summary

We utilized data from three distinct data sources to construct a time series of F/FMSY 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. We focused on obtaining an F/FMSY time series, rather than an F time series, as the F/FMSY time series provides a forcing usable in most MEMs, where FMSY depends on each MEM’s specifications and assumptions. Further, F/FMSY directly indicates the exploitation level, with values larger than 1 signalling an overexploited fish functional type, facilitating comparisons between regions and functional types. The data sources encompassed (section 2.2): 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) for 1841-2004, and 3) total nominal fishing effort data gridded at a 0.5-degree spatial resolution from 1961 to 2004. These data products (Novaglio et al., 2024) 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/FMSY time series 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/FMSY time series using conversion factors from the intermediate and high catch LMEs (see section 2.4). The F/FMSY 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 demonstrate how the gridded F/FMSY data set can be input into MEMs to generate historical time series of fish biomass and catch, they were input into the FEISTY model. FEISTY was 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 to estimate the fishing influence on fish biomass and compared the modeled fishing catch with reconstructed catch.

2.2 Catch and Effort Data

Fisheries catch, estimated as the sum of reported landings and 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, rays and bathydemersal. Forage fish included all fish classified in Watson (2017) as pelagic < 30 cm and bathypelagic < 30 cm and large pelagic fish included all fish classified as pelagic fish > 30 cm and bathypelagic > 30 cm. Shark catches were split evenly into 50% large pelagic and 50% demersal, following Petrik et al. (2019). All other fisheries catch types, representing 16% 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, Novaglio et al., 2024). 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:

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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 annual population growth parameter, *K* is the carrying capacity, *Fi,t* is the annual fishing mortality, and the time step, t, is one year. We used the catch information as input data to infer the fishing mortality as . We *a priori* assigned *n* for each of the functional types before assessing the past F/FMSY 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 Legacy Stock Assessment Database. The model was also tested with *n = 2* (Schaefer model) and *n = 1.4* (global estimate of *n)* for all functional types, but these shape parameters are less ecologically valid and resulted in an overestimation of forage fish catches (not shown). To initialize the catch-only assessment model, we randomly sampled 10000 *r-K* combinations per functional type from a uniform distribution (with *r* between 0.1 and 1.5 and *K* between 1 and 50 times the maximum catch). This broad parameter distribution was chosen to reflect the coarse functional type classification used in the FEISTY model. In addition, we made specific assumptions about the initial and final biomass to initialize the model. These biomass values were assumed to depend on the maximum catch *Cmax* and on the catch *C* in the first and last years, respectively:

We tested the sensitivity of the initial *r* conditions, and found that there was less than 15% difference in F/FMSY on average across LMEs and functional types unless forced until artificially low *r* values (*r < 0.3*).

For each functional type, 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 calculate the estimated . We used the estimates to calculate , and . The MSY estimate was compared to the historical catches, showing a median Catch/MSY ratio of 0.77 across LMEs and functional types (Supplementary Figure S1). This value indicates that MSY estimates are within reasonable boundaries. We used the 95% confidence interval around the estimated MSY and FMSY to obtain a measure of uncertainty (see section 2.4).

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 20 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/FMSY in 45 LMEs for demersal and large pelagic fish and 29 LMEs for forage fish. We compared the F/FMSY time series of several LMEs and functional types with stock assessment time series of F/FMSY 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 S2). The code used to produce the estimates are provided in the ‘Open Research’ section.

2.4 Time series of F/FMSY per grid cell

The F/FMSY time series from the catch assessment model only provides information for functional types in intermediate and high catch LMEs for 1961-2004. To extend the F/FMSY estimates back to 1841 for these LME × functional type combinations, we re-scaled a nominal effort time series specific to each functional type and LME for these years. This re-scaling was achieved by assuming a linear relationship between F/FMSY and nominal effort, using the average nominal effort and F/FMSY values from 1961 to 1965 as a reference for conversion.

For functional types in all low catch LMEs and the high seas, we also used factors to convert nominal effort time series to F/FMSY time series for the entire period, 1841-2004. To this end, we selected from each catch assessment model outcome the five years closest to FMSY. 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 FMSY in an LME. We standardized these nominal effort values to nominal effort at FMSY per km2 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. These standardized nominal effort at FMSY values served as the conversion factors to compute F/FMSY time series 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/FMSY time series using a conversion factor from an adjacent area or the global median of a functional type (Supplementary Table S2, see Supplementary Figure S3 for illustration of the conversion).

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 average effort in the years 1961-1965.

To estimate uncertainty in model simulations, we reconstructed two additional F/FMSY gridded products using the same approach as above, but now based on the lower and upper bound of the 95% confidence interval of F/FMSY as estimated from the set of r-K combinations from the catch-only assessment model. In addition, we estimated conversion factors and F/FMSY time series based on an assumption of technological creep, i.e. assuming a 2.6% increase in technological creep per year between 1841 and 2004 using 1950 as the reference year (following Rousseau et al., 2022). The differences in global catch and biomass simulations between these estimates and those derived using nominal effort are small (Supplementary Figure S4). This is likely because the majority of the F/FMSY time series are derived from the catch-only assessment model and the effort-based conversion factors are mainly used for lightly fished LMEs.

2.5 Mechanistic fish community model FEISTY

FEISTY is a temporally dynamic, spatially explicit, mechanistic model that simulates the biomasses of forage (small pelagic), 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 fishes feed on prey, fishes 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, FEISTY was coupled to distinct medium and large zooplankton outputs of GFDL’s Carbon, Ocean Biogeochemistry and Lower Trophics COBALT planktonic ecosystem model (Petrik et al., 2019, 2020). COBALT has been shown to robustly capture the primary differences in chlorophyll, primary production, export fluxes, and medium and large zooplankton biomass across both ocean biomes and globally distributed LMEs (Stock et al., 2017, 2020). The simulations here were completed using the FishMIP protocol (Blanchard et al. this issue) that combines the COBALT medium and large zooplankton into a single mesozooplankton group. Additionally, zooplankton loss rates to higher predators are not provided. Thus an empirical relationship between mesozooplankton biomass *zbio* and upper water column temperature *Tpel* was developed to estimate these rates as successfully used in past FishMIP simulations (Heneghan et al., 2021; Tittensor et al., 2021): , with *eps* being a value close to zero.

2.6 Model parameterization and simulations

All FEISTY model parameters were taken from Petrik et al. (2019). We implemented fishing in FEISTY from the F/FMSY time series by identifying the fishing mortality that corresponds to FMSY in FEISTY. FMSY 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 FMSY for each permutation of these factors was computationally prohibitive. Instead, we examined how FMSY varied with prey production and temperature for large pelagic and demersal fishes (Supplementary Figure S5; no such estimation could be made for forage fish as they are heavily dependent on fish predation mortality). We found that changes in prey production had a limited effect on FMSY, 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 FMSY 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:

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 FMSY in FEISTY at 10 ºC, and (F/FMSY)i,f,t is based on the time series derived as described in the prior section. Fishing gear selectivity was 1 × *Fi,f,t* for the largest size class of all functional types. In addition, large pelagic and demersal fishes were fished with 0.1 × *Fi,f,t* at the juvenile stage. 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 inputs prior to 1961) combined with the fishing mortality of 1841. The pre-industrial time period from 1841-1960 was run using year-specific fishing mortalities from 1841-1960 and six repeating cycles of ocean inputs from 1961-1980. Finally, the historic time period between 1961 and 2004 was simulated with both year-specific fishing mortalities and ocean inputs. In addition, we ran FEISTY without fishing as an alternate scenario.

3 Results

3.1 Reconstructed fishing exploitation patterns

The reconstructed F/FMSY time series suggested that large pelagic and demersal fishes were, on average, fished with a higher intensity than forage fish (Figure 1). On a global scale, both large pelagic and demersal fishes peaked in exploitation rate in the late 1980s, but the exploitation patterns strongly varied between regions. The reconstruction indicates that the Arctic/Antarctic region had the lowest exploitation for all fish types and the Mediterranean and Black Sea region the highest. Large pelagic fishing intensity was estimated to peak 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 was found to be highest in the South Atlantic and Indian Ocean in the most recent years. Demersal fishing intensity was estimated to peak in the Mediterranean and Black Sea region before the 1970s. Demersal fishing intensity was found to be relatively constant, with F/FMSY around 0.6, in the North and South Atlantic between 1970s and 2000s. Demersal fishing intensity was highest in the Indian Ocean and Eastern Pacific in the most recent years. For forage fish, the reconstructed exploitation patterns were more variable, but most regions have a peak in forage fish fishing mortality in the 1980s and/or the 2000s.

Maps of the gridded exploitation patterns mirrored the above results (Figure 2). The maps indicate that most LMEs with a narrow shelf had a relatively high F/FMSY 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 were fished at higher intensity in the high seas than demersal and forage fishes.

A comparison between F/FMSY from data-rich stock assessments and the catch-derived F/FMSY shows that the catch-derived F/FMSY was comparable to but on average lower than the stock-derived F/FMSY (Figure 3 & S2). 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 were 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).

3.2 Simulations of fish catch

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

Comparisons of observed and modeled fish catches across LMEs over the years 1990-2000, resulted in high correlations for total catch (r = 0.90), demersal fish (r = 0.87) and forage fish (0.81) (Figure 5). Large pelagic fish had a correlation of 0.62 and lower modeled catches in several LMEs, among others, the Sulu-Celebes Sea and the Northeast Australian Shelf (Supplementary Figure S6). In absolute numbers, 38% of the LMEs have a total catch within ±50% of catch observations. No consistent mismatch in catch was apparent for specific latitudinal regions, except for forage fish that were underestimated in tropical regions and overestimated in temperate and polar areas (Supplementary Figure S6). The largest differences between observations and model were seen in the Humboldt Current (8.7 million MT y-1 higher in observations mainly due to forage fish catch), Gulf of Mexico (4.3 million MT y-1 higher in model), Mediterranean Sea (4.1 million MT y-1 higher in model), Benguela Current (4.1 million MT y-1 higher in model) and Arabian Sea (3.0 million MT y-1 higher in model).

3.3 Simulations of fish biomass

Global fish biomass in the unfished scenario varied between 1.72 and 1.85 gigaton per year in the period 1961-2004. Simulated unfished biomass was 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 S8 for each functional type). Relative to an unfished scenario, fishing resulted in a global biomass decline of 2% in large pelagics and 15% in demersal fish as of 2004 (Figure 6b). Both large pelagic and demersal fishes exhibited a 20-25% decline in shelf regions (Figure 6c). In contrast, forage fish biomass, simulated with the fishing scenario, increased 10% globally and 50% in shelf regions, primarily caused by the release of predation pressure from large demersal and pelagic fishes. Demersal fish reveal a clear decline in biomass with increasing fishing pressure across LMEs. Demersal fish biomass was around 60% of the unfished biomass in LMEs that were fished at FMSY (Figure 7b). The biomass response of large pelagics and forage fish across LMEs was 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.

4 Discussion

We estimated regional fishing exploitation levels (F/FMSY) for forage, large pelagic and demersal fish functional types utilizing fisheries catch and effort data. By applying the F/FMSY 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 triggered by the decline of fish predators due to fishing surpassed the anticipated increase of forage fish biomass due to climate change (± 4% fractional increase), which was 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 difficult to use within the model structure, or where a common set of mortality rates across MEMs is warranted.

4.1 Reconstructed fishing exploitation patterns

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. 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 handle these aggregated catch data as the method has solely been tested for individual stocks (Martell & Froese, 2013). We find global peaks in F/FMSY for demersal and large pelagic fishes in the late 1980s. These peaks occur approximately five years earlier than the estimated exploitation peak reported in Hilborn et al. (2020). Since these exploitation patterns are sensitive to the LMEs and functional types included, we consider the magnitude of this deviation to be acceptable. 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). The catch-only model also provided an estimate of unfished biomass, i.e. carrying capacity. For catch-only models, the relative values (e.g., F/FMSY and B/BMSY) are often considered more reliable that the absolute values 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.

A potential improvement to the exploitation patterns could involve utilizing stock assessment data from regions where a high proportion of the fish in the region are assessed. This approach could replace the current time-series of F/FMSY with a time-series based on the averages of assessed stocks. However, this method has several challenges, as the time series are often shorter and vary between species, and the spatial assessment areas differ between species. It is thus important to establish what constitutes a robust time series and to develop a method for extrapolating these series to periods with no available data. Implementing this updated method is likely to provide a more accurate representation of regions like Alaska, where our reconstructed historical exploitation levels are overestimated. The use of our reconstructed exploitation patterns should thus be applied cautiously, particularly for MEMs at a regional scale. Nonetheless, the reconstruction offers a transparent way to reflect the development of fisheries over time across regions and fish functional types. We expect that such a product may be useful beyond the modeling community as it can be used as a quantitative indicator of fishing activity in the sea in applications that examine human impacts, such as Halpern et al. (2022).

The spatial allocation of fishing mortality assumed it was in proportion to total gridded effort in each LME. This method might lead to a mismatch between fishing intensity and the accumulation of fish biomass. This mismatch is particularly an issue for pelagic species in productive open ocean areas, where fishing may not align with areas of high productivity. Allocating fishing mortality based on the biomass of each functional type could prevent such mismatches.

4.2 Simulations of fish catch and biomass

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, to focus on bottom-up processes (Petrik et al., 2019, 2020; van Denderen et al., 2021). 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 Petrik et al. (2019). Without these LMEs, our correlation for forage fish (and total catch) remain higher than the prior study (Supplementrary Table S2), whereas large pelagics have a lower correlation regardless of a good match at the global scale. Despite the improvements, especially for total catch and forage fish, a significant uncertainty persisted, namely the parameterization of FMSY which varies with temperature in the FEISTY model, whereas, both in the FEISTY model and in nature, FMSY varies in a more dynamic way due to biotic interactions within and between functional types. This dynamic nature of FMSY 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 FMSY ahead of using the F/FMSY 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). In FEISTY, the primary underlying factor for the complex responses is trophic interactions. In addition, some of these dynamics can be attributed to the structural characteristics of the FEISTY model. Fishes 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 (see fig. 5.11 on trawl selectivity in Andersen, 2019).

Part of the observed resilience to fishing is also linked to the food web dynamics in FEISTY. As anticipated, forage fish biomass increased in most LMEs in the fishing scenario in response to the decline of demersal and large pelagic fish due to fishing. Such trophic cascades initiated by pertubations of upper trophic levels from overfishing are commonly observed in regional food webs: on the Scotian Shelf by the loss of groundfish (Frank et al., 2005), in the Black Sea due to the loss of large pelagic fish (Daskalov et al., 2007), in the Baltic Sea due to the collapse of cod (Casini et al., 2008), and in the East China Sea due to the loss of large-sized fishes (Szuwalski et al., 2017). The mechanism is simply that the loss of larger piscivorous fishes releases the predation pressure on smaller fishes, which makes smaller fishes more abundant and increasingly resilient to fishing (Andersen & Pedersen, 2010). Here we show this trophic cascade universally across ecosystems. 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 driven 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). However, 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. Thus, the model may overestimate the large pelagic fisheries resilience and productive capacity in systems with high large pelagic fish diversity.

4.3 Conclusion

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. Overall, our results, especially the development of a novel, spatially-explicit time series of F/FMSY, provide capacity for 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, FEISTY model outputs and scripts for the catch-only assessment model are available on ZENODO (van Denderen et al., 2024). 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 data on fishing activity is available via Novaglio et al. (2024). Details for FishMIP-ISIMIP 3a Protocol are provided here: https://github.com/Fish-MIP/FishMIP\_2022\_3a\_Protocol

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**Tables**

**Table 1**. Shape parameters for the three fish functional types in the Catch-MSY model. The value for small pelagics was extracted from Thorson et al. (2012) as ‘Clupeiformes’, for Demersal as the average of Gadiformes and Pleuronectiforms, and for Large pelagics as ‘Others’

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

**Figures**

**A close-up of a graph

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**Figure 1**. Reconstructed time series of average annual exploitation rates (F/FMSY) aggregated per region based on the average of all LMEs in each region (all LMEs are given equal weight). The shaded areas are based on the 95% confidence intervals of the catch-only model.

**A group of images of the world

Description automatically generated**

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

**A diagram of a ship

Description automatically generated with medium confidence**

**Figure 3**. Violin plots with annual differences between stock assessment F/FMSY and catch-only derived F/FMSY for 14 LME × functional type combinations between 1980 and 2004. The stock assessment F/FMSY 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/FMSY is one FMSY higher (lower) than the catch-derived. See supplementary Figure S2 for individual time-series of each stock.

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**Figure 4**. Time-series of observed (solid) versus model-based (dashed) catches. Fish catch includes all fishes classified as large pelagic, forage fish and demersal in our study. Total catch includes all marine organisms, including some that were not simulated in the study. The shaded areas are based on the 95% confidence intervals of the catch-only model.

**A group of graphs showing different types of fish

Description automatically generated**

**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. Several LMEs have very low (observed and/or modeled) catches for large pelagics and forage fish. These LMEs are plotted as ‘×’ and were given a minimum value of 1 metric ton. They were not included in the estimate of the correlation. Note that a comparison of observed and modeled fish catch normalized by the size of each LME gives similar correlations (Supplementary Figure S7).

**A graph with different colored lines

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**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 (**a**). Changes in fish biomass relative to the 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 29 LMEs for which we obtained an estimate of *K* for all three functional types using the catch-only model. The shaded areas in (**b**) and (**c**) were based on the 95% confidence intervals of the catch-only model.

**Figure 7**. Relation between B/Bunfished and F/FMSY for all LMEs based on average values between 1990 and 2000. Bunfished is the biomass in the unfished scenario. The size of the dot reflects the size of the observed fishing catch.