



Large projected reductions in marine fish biomass for Kenya and Tanzania in the absence of climate mitigation

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ABSTRACT

Climate change is projected to cause significant reductions in global fisheries catch during the 21st Century. Yet, little is understood of climate change impacts on tropical fisheries, which support many livelihoods, as is the case in the Western Indian Ocean region (WIO). Here, we focus on two central WIO countries – Kenya and Tanzania – and run a multi-species fish model (Size Spectrum Dynamic Bio-climate Envelope Model; SS-DBEM) for 43 species of commercial and artisanal importance, to investigate the effects of climate change. We include both national Exclusive Economic Zones (EEZs) as domains. The model was forced by data from a biogeochemical model (NEMO-MEDUSA), run under the high emissions scenario Representative Concentration Pathway (RCP) 8.5, until the end of the 21st century. Impacts of fisheries and climate change were investigated by running SS-DBEM under five scenarios of fishing pressures to predict a range of possible future scenarios. Fishing pressure was represented as the Maximum Sustainable Yield (MSY), expressed as MSY0, MSY1, MSY2, MSY3 and MSY4 representing fishing mortality of 0, 1, 2, 3 and 4 times MSY, respectively. Large reductions in average fish biomass were projected over the 21st Century, with median reductions of fish species biomass of 63–76% and 56–69% for the Kenyan and Tanzanian EEZs respectively across the fishing scenarios. Tunas were particularly impacted by future climate change, with the six modelled species exhibiting biomass reductions of at least 70% in both EEZs for all fishing scenarios during the 21st Century. Reductions in fish biomass were much more severe during the second half of the 21st Century, highlighting the benefits to tropical fisheries of global action on climate change.

1. Introduction

Climate change is impacting marine fisheries across the world's tropical seas (e.g., Lam et al., 2020). Rising temperatures, reductions in primary production, deoxygenation and ocean acidification (Bopp et al., 2013) are likely to result in significant changes to ecosystems and reductions in catch this century around the world (Barange et al., 2014;

Bindoff et al., 2019; Lotze et al., 2019; Lam et al., 2020; Bryndum-Buchholz et al., 2019). But it is the tropical oceans where many of the first anthropogenic signals in physical and biogeochemical variables will exceed natural variability (Lam et al., 2020).

Fisheries in tropical regions contribute greatly to the well-being of people and society where coastal communities strongly depend on fisheries for food security, culture, livelihoods and economic

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development (Dyck and Sumaila, 2010; Teh and Pauly, 2018). It is estimated that 1.3 billion people inhabit the tropical coastal areas, with many highly reliant on fisheries for food (Kawarazuka and Béné, 2010). Fish contribute 50–90% of the dietary animal protein in Pacific Island countries (Bell et al., 2009), 50% in West Africa (Hicks et al., 2019) and 37% in Southeast Asia (Teh et al., 2011). With this dependency, it is clear that climate-driven reductions in fisheries production and changes in fish-species composition will increase the vulnerability of tropical countries – especially those with limited adaptive capacity.

The tropical Western Indian Ocean (WIO) however, seems to present a special case for the impacts of climate change. Comparisons of published earth system models (ESMs) from the coupled model intercomparison project phase 5 (CMIP5, a global collaborative effort to improve knowledge of climate change with global coupled ocean-atmosphere general circulation models) show a clear consensus that the tropical WIO will see increases in temperature and reductions in net primary productivity in this century (Jacobs et al., 2021; Bopp et al., 2013). Certainly, several earlier studies (e.g. Rao et al., 2012) have indicated a warming of the Indian Ocean (IO) warm pool (central–eastern IO with sea surface temperatures (SSTs) of >28.1 °C) over the past 50 years. Recent results by Roxy et al. (2014) based on observations of global temperatures coupled with ocean–atmosphere model simulations, suggest the northern WIO has been warming for more than a century at a rate faster than any other region of the world's tropical oceans, and is the largest contributor to the overall trend in the global mean SST. Roxy et al. (2016) found a large decrease of up to 20% in phytoplankton in this region over the past six decades. These changes have consequences, particularly the warming of the generally 'cool' tropical WIO against the rest of the tropical warm pool region will alter zonal SST gradients, and therefore has the potential to change the Asian monsoon circulation and associated rainfall, as well as alter marine food webs in this biologically productive region.

The tropical WIO warming has already made its mark. Prolonged increases in SST in 2016 led to severe coral bleaching of 30% of reefs resulting in eventual severe mortality of 10% of these reefs (Obura et al., 2017a). Moreover, historical analysis has shown that fish biomass declined during periods of higher temperature (Jury et al., 2010) and is influenced by East African monsoon conditions. Painter (2020) noted that the East African Coastal Current (EACC) heavily influences fisheries in the tropical WIO. Indeed, key species catch such as herrings, shads and anchovies are strongly correlated to local Chl-a concentrations, which are related to changes in EACC strength (Jebri et al., 2020). Jacobs et al. (2021) project a weakening of the EACC in future, which could have consequences for the fisheries in this region.

The economic value of marine fisheries in the WIO is estimated to be around US\$1.9 billion annually (Obura et al., 2017b). Fisheries in the region are presently split between inshore waters, largely fished by small-scale artisanal vessels, and offshore waters largely fished by Distant Water Fishing Nations (DWFN). The DWFN vessels mainly target tunas such as skipjack, yellowfin and bigeye. For Kenya and Tanzania (which throughout this article refers to both mainland Tanzania and the semi-autonomous island of Zanzibar) – central WIO countries both trying to improve food security as well as develop their blue economies—the tuna fishery is considered underexploited (van Hoof and Kraan, 2017; van Hoof and Steins, 2017), and hence hold great potential for future expansion by national fishing fleets. Estimates of annual total landings suggest that pelagic fish account for approximately 30% in Kenya and about 40–50% in Tanzania (Bultel et al., 2015; Kimani et al., 2018), with about 50% of the total landings being reef-associated demersal fish species.

While some commercial vessels operate in both countries, present-day national fisheries are largely comprised of small-scale artisanal boats (Okenwa et al., 2017; Samoilys et al., 2017; Musembi et al., 2019; Silas et al., 2020), with fishing restricted to simple gears such as hand-lines, gill nets and seines. Recent reconstructed estimates (2016–2018) of total marine fisheries production for Kenya ranges from 20 to 24,000

tonnes per year, with approximately 13,000 people employed as fishers (Government of Republic of Kenya, 2014; Government of Kenya, 2016; Kenya National Bureau of Statistics (KNBS), 2019; Government of Republic of Kenya, 2014). By comparison, the average total annual catch in the Tanzanian EEZ is approximately 100,500 tonnes per year (Bultel et al., 2015 using reconstructed catch data from 2000 to 2010). However, some uncertainty remains about the magnitude of catch, particularly for the small scale sector.

Given the amassing evidence of climate change in the tropical WIO, and the importance of (artisanal) fisheries for food security and building blue economies – we have specifically focused this study on the Kenyan and Tanzanian EEZs as illustrations representative of the tropical WIO region. To this end we are using a multi-species fish model (Size Spectrum Dynamic Bio-climate Envelope Model; SS-DBEM). Our first aim is to investigate the impact of climate change under a high-emissions Representative Concentration Pathway (RCP 8.5) climate change scenario, and to see how different fish species will respond to a changing ocean. The study looks at this impact with and without varying fishing pressures, on both reef-associated and pelagic fish species. Secondly, with ever-increasing pressure on inshore waters, we furthermore emphasize the tuna species as respective authorities have strong desires to expand these national fisheries (Tanzania National Report to the Scientific Committee of the Indian Ocean Tuna Commission, 2016; Ministry of Agriculture, Livestock and Fisheries Kenya, 2013).

2. Methods

2.1. Study region and target species

Future changes in fish biomass were projected for the EEZs of Kenya and Tanzania (Fig. 1). Forty-three fish species (Table 1) that are representative of exploited fish species were modelled, and the species choice aims to represent both commercial and sustenance types of species. These species were also chosen because they have sufficient biogeographic and biological data to be modelled with credibility in the region. Unfortunately, this meant that reef-associated species groups such as Siganidae, Lutjanidae, Scaridae, Pomacentridae and Acanthuridae could not be modelled due to a lack of biological and ecological data.

Using the classifications in Fishbase (Boettiger et al., 2012), there were seventeen reef-associated species and 26 pelagic species modelled, of which six were tunas.

2.2. Biogeochemical model summary

Changes in key physical and biogeochemical properties such as temperature, salinity, pH, chlorophyll and velocities were taken from version 2.0 of the NEMO-MEDUSA model (for details see Yool et al., 2013). Full details and model evaluation for the WIO are provided in Jacobs et al. (2021). NEMO-MEDUSA is an 'intermediate complexity' model of the global plankton ecosystem with a 0.25° spatial resolution. It incorporates the nitrogen, carbon, oxygen, silicon and iron cycles, representing large and small phytoplankton. This model was forced at the surface using air temperature projections from the HadGEM2-ES Earth System Model (Collins et al., 2011).

2.3. Fisheries model

The outputs from NEMO-MEDUSA were used to drive a dynamic bioclimate envelope model (DBEM), which projects changes in fish species distribution and biomass while explicitly considering known mechanisms of population dynamics and dispersal (both larval and adult), as well as eco-physiological changes caused by changing ocean conditions (Cheung et al., 2011). Specifically, we employed the SS-DBEM (SS = size spectrum) version of the DBEM that incorporates species interactions based on size-spectrum theory and habitat suitability (Fernandes et al., 2013, 2020). The SS-DBEM is a combined

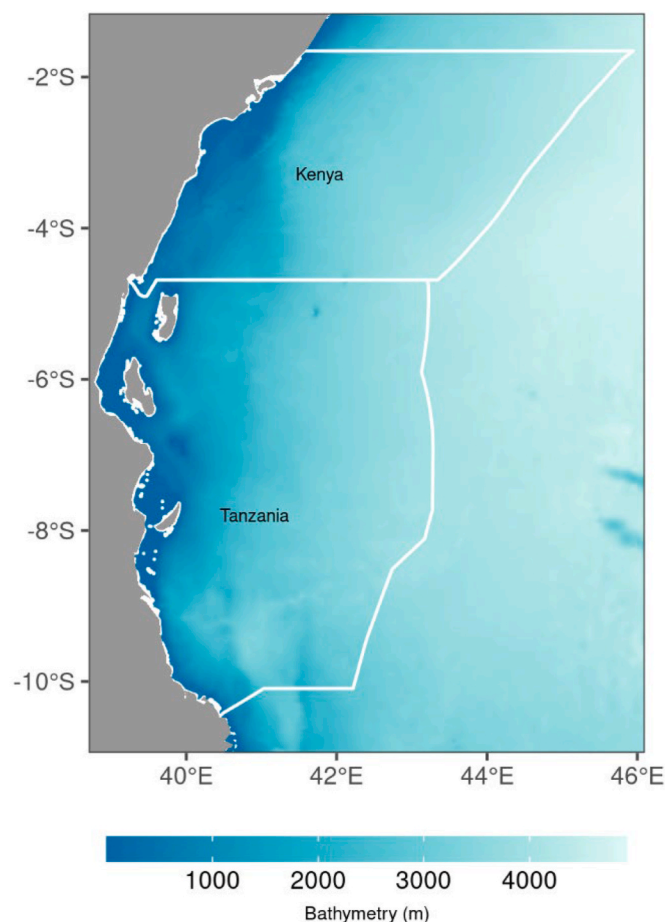


Fig. 1. Study region map showing the Kenyan and Tanzanian Exclusive Economic Zones (EEZs). Bathymetry shown is from the General Bathymetric Chart of the Ocean (GEBCO; Weatherall et al., 2015). Note: For Kenya the extended EEZ claim is used expanding the total EEZ by another 103,320 km².

mechanistic-statistical approach that has been applied to a large number of marine species globally and is one of the models participating in the *Fisheries model inter-comparison program* (FISHMIP; Tittensor et al., 2018; Lotze et al., 2019).

Present distributions, and thus seed populations, of selected species in the SS-DBEM are first estimated using the *Sea Around Us* method. Using data primarily derived from FishBase (www.fishbase.org) and SeaLifeBase (www.seaaroundus.org), it determines species distributions based on: a) presence; b) latitudinal range; c) range limiting polygons; d) depth range; e) habitat preference; and f) the effect of “equatorial submergence” (see Close et al., 2006 for more details on the method). This is combined with the NEMO-MEDUSA variables to determine the suitability of each species to different environmental conditions (e.g. temperature, salinity, oxygen concentration, bathymetry; see Cheung et al., 2008a, 2009 for more details), which create seed populations. The model is initialized with these seed populations using the estimated present distribution and then driven by ocean model outputs to evaluate the impact of recent (Queirós et al., 2018) or future (Fernandes et al., 2016) changes in environmental conditions on fish populations distribution. Combining ocean dynamics (e.g. advection) with mortality, growth, and dispersal processes, the model projects future patterns in distribution and biomass (see Cheung et al., 2008a; 2009, for more details) with the carrying capacity of each species being dependent on the environmental conditions and limited by primary production. The Size Spectra component of the SS-DBEM accounts for resource by comparing the biomass that can be supported in any given area (based on primary production and the derived size spectrum) to the energy demand of the

Table 1

List of pelagic and reef associated species modelled in study.

Family	Species	Common name	Environment
Belontiidae	<i>Ablennes hians</i>	Flat needlefish	Reef associated
Carangidae	<i>Atule mate</i>	Yellowtail scad	Reef associated
Carangidae	<i>Carangoides bajad</i>	Orangespotted trevally	Reef associated
Carangidae	<i>Carangoides malabaricus</i>	Malabar trevally	Reef associated
Carangidae	<i>Caranx ignobilis</i>	Giant trevally	Reef associated
Carangidae	<i>Caranx melampygus</i>	Bluefin trevally	Reef associated
Carangidae	<i>Caranx sexfasciatus</i>	Bigeye trevally	Reef associated
Carangidae	<i>Decapterus maruadsi</i>	Japanese scad	Reef associated
Carangidae	<i>Decapterus russelli</i>	Indian scad	Pelagic
Carangidae	<i>Elagatis bipinnulata</i>	Rainbow runner	Reef associated
Carangidae	<i>Gnathanodon speciosus</i>	Golden trevally	Reef associated
Carangidae	<i>Megalaspis cordyla</i>	Torpedo scad	Reef associated
Carangidae	<i>Selar crumenophthalmus</i>	Bigeye scad	Reef associated
Carangidae	<i>Seriola lalandi</i>	Yellowtail amberjack	Pelagic
Carangidae	<i>Trachurus capensis</i>	Cape horse mackerel	Pelagic
Clupeidae	<i>Herklotsichthys quadrimaculatus</i>	Bluestripe herring	Reef associated
Clupeidae	<i>Hilsa kelee</i>	Kelee shad	Pelagic
Clupeidae	<i>Sardinella gibbosa</i>	Goldstripe sardinella	Pelagic
Clupeidae	<i>Sardinella longiceps</i>	Indian oil sardine	Pelagic
Clupeidae	<i>Sardinops sagax</i>	South American pilchard	Pelagic
Clupeidae	<i>Spratelloides gracilis</i>	Silver-stripe round herring	Pelagic
Coryphaenidae	<i>Coryphaena hippurus</i>	Common dolphinfish	Pelagic
Dussumieriidae	<i>Dussumieria acuta</i>	Rainbow sardine	Pelagic
Dussumieriidae	<i>Etrumeus sadina</i>	Red-eye round herring	Pelagic
Engraulidae	<i>Engraulis encrasicolus</i>	European anchovy	Pelagic
Engraulidae	<i>Engraulis japonicus</i>	Japanese anchovy	Pelagic
Lethrinidae	<i>Lethrinus lentjan</i>	Pink ear emperor	Reef associated
Pristigasteridae	<i>Pellona ditchela</i>	Indian pellona	Pelagic
Rachycentridae	<i>Rachycentron canadum</i>	Cobia	Reef associated
Scombridae	<i>Acanthocybium solandri</i>	Wahoo	Pelagic
Scombridae	<i>Auxis thazard</i>	Frigate tuna	Pelagic
Scombridae	<i>Euthynnus affinis</i>	Kawakawa	Pelagic
Scombridae	<i>Katsuwonus pelamis</i>	Skipjack tuna	Pelagic
Scombridae	<i>Rastrelliger kanagurta</i>	Indian mackerel	Pelagic
Scombridae	<i>Sarda orientalis</i>	Striped bonito	Pelagic
Scombridae	<i>Scomber japonicus</i>	Chub mackerel	Pelagic
Scombridae	<i>Scomberomorus commerson</i>	Narrow-barred Spanish mackerel	Pelagic
Scombridae	<i>Thunnus alalunga</i>	Albacore	Pelagic
Scombridae	<i>Thunnus albacares</i>	Yellowfin tuna	Pelagic
Scombridae	<i>Thunnus obesus</i>	Bigeye tuna	Pelagic
Serranidae	<i>Epinephelus fuscoguttatus</i>	Brown-marbled grouper	Reef associated
Sphyrnidae	<i>Sphyrna barracuda</i>	Great barracuda	Reef associated
Xiphiidae	<i>Xiphias gladius</i>	Swordfish	Pelagic

species that are predicted to be present in the area. Energy is distributed to species in proportion to their energy demand and their growth rate (see Fernandes et al., 2013 for details). Because the model accounts for both environmental preference and population dynamics, any changes in environmental conditions will result in changes in life history (e.g. growth, migration), carrying capacity, and, consequently on the abundance and distribution of species.

The SS-DBEM fisheries model was initiated with seed populations produced using the above method for each species in 1990 and run until 2099. As mentioned, the model calculated biomass of fish each year after migration, reproduction and death (both natural and through fishing) were taken into account. Trial experiments in our study showed that the model reaches a stable state in under 10 years when run with constant conditions. We therefore treated the first 10 years of a model run as spin-up and only report changes between 2000 and 2099. The model was run on a global configuration, where all of the world's oceans are represented, to overcome any boundary condition issues. It is worth noting that the model is capable to run 100s of species globally (see [Cheung et al., 2019](#)) and as such does not need specific parameterization for this regional application.

The NEMO-MEDUSA outputs were re-gridded to match the SS-DBEM resolution of 0.5° but no further modifications were applied. We used temperature, salinity, pH, chlorophyll and currents as environmental drivers with which we forced the model. These drivers are necessary to account for habitat suitability (e.g. temperature, salinity and pH), defining the size spectrum and system carrying capacity (i.e. chlorophyll), dispersion (current), and impacts on metabolic rate (e.g. temperature). Of these multiple drivers, temperature and chlorophyll are the ones that explain most of the changes in fish biomass and are those we chose to share in this manuscript.

2.4. Fishing scenarios and climate change scenario

Five fishing scenarios were assessed to provide a means for comparing the relative importance of climate change and fisheries management in determining future fish biomass and fisheries yields. Fishing scenarios were all defined relative to each species' maximum sustainable yield (MSY). We define MSY as the highest average theoretical equilibrium catch that can be taken continuously from a stock under average environmental conditions ([Hilborn and Walters, 1992](#)). Assuming a simple logistic population growth function and under equilibrium conditions, MSY can be defined as:

$$MSY = \frac{B_{\infty} \cdot \text{int}R}{4}$$

where $\text{int}R$ is the intrinsic rate of population increase and B_{∞} is the biomass at a species' carrying capacity ([Schaefer, 1954](#); [Sparre and Venema, 1998](#)). In this model, the $\text{int}R$ for each species is calculated based on natural mortality ([Pauly, 1980](#); [Cheung et al., 2008b](#)). Note that the MSY is linked to the fishing mortality rather than the biomass at MSY.

Five fishing scenarios were defined: MSY0, MSY1, MSY2, MSY3 and MSY4 which represented no fishing mortality and fishing mortality at 1, 2, 3 and 4 times MSY, respectively. $MSY = 0$ allows the effect of climate change to be assessed alone. Scenarios where $1 < MSY < 4$ allows possible interactions between climate change and fishing. Fishing mortality was modelled using an MSY, which is calculated on a global basis and should therefore not be viewed as being representative of present fishing levels in either region here, but as indicative of the broader impacts of fishing. The choice of MSY does not reflect any specific or realistic reference points and this was done intentionally. Firstly, fishing level varies between years and countries. Secondly, since our intention is to look at the end of the century, making projections based on current fishing pressures would only provide so much information compared to using multiple scenarios. Consequently, while MSY0 (absence of fishing) or MSY4 may seem unrealistic they act as brackets for the impact of fishing, whether it be an increase or decrease in the activity. It is also important to note that overfishing of stock is not inexistent, for example [Froese et al. \(2018\)](#) found that for 397 European fish stock 69% are subject to ongoing over-fishing, with a global trend toward an increase in the number of stock being overexploited ([Froese et al., 2012](#)).

The impacts of climate change were assessed using RCP 8.5 ([Riahi](#)

[et al., 2011](#)). This is the high greenhouse gas emissions scenario where there is an additional 8.5 Wm^{-2} of radiative forcing, leading to atmospheric CO_2 levels exceeding 900 ppm by the end of the 21st Century. In our modelling run we use output from NEMO-MEDUSA which was run under RCP 8.5 from 1970 to 2099. The mean global surface air temperature increases by approximately 5 °C between 2000 and 2100 in the model used in our analysis under RCP 8.5 ([Yool et al., 2015](#)). We view this as a bracketing scenario, and not a "business-as-usual" one. RCP 8.5 is often referred to as a "business-as-usual" scenario within ecological assessments of climate change, but it instead should be viewed as a scenario with negligible action on climate mitigation and lower levels of economic decarbonisation than observed in secular trends ([Hausfather and Peters, 2020](#)).

2.5. Aggregation and summary statistics of fish communities

Fish biomass output at 0.5° resolution was aggregated to the level of each EEZ as follows. First, the biomass in each 0.5° by 0.5° cell was attributed to each EEZ by calculating the percentage of ocean area in each cell that lies within each EEZ. This was calculated using the high-resolution GEMCO bathymetry dataset ([Weatherall et al., 2015](#)). Total fish biomass within each cell was then allocated to the respective EEZ using this percentage. To compare changes in individual species, we calculated specific biomass indices. With a window of 10 years, we calculated the rolling mean biomass and then created a biomass index, which is the rolling mean divided by the mean biomass for the first 10-year period, i.e. 2000–09, so that the biomass index is 1 at the start of the time series. An index of 0.9 would indicate that biomass decreased by 10% since 2000–09. Similarly, we estimated species richness changes by calculating the mean annual species richness in the baseline 2000–09 and end-of century 2090–99 periods. EEZ regions were downloaded from the *Sea Around Us* project website ([Pauly, 2007](#)).

3. Results

3.1. Environmental drivers of change

Key regional environmental changes projected by NEMO-MEDUSA indicate that between the decades 2000–09 and 2090–99, there are increases in annual mean SST of 3.65 and 3.54 °C in the Kenyan and Tanzanian EEZ respectively, taking regional mean SSTs to above 31 °C in both by the end of the 21st Century ([Fig. 2, Table 2](#)). Similarly, seabed temperatures increase by 0.54 and 0.59 °C respectively, but note while trends are near-identical, the Kenya bottom temperatures are cooler on average by ~0.4 °C – possibly influenced by shelf edge upwelling on the North Kenya Banks ([Jacobs et al., 2020](#)).

Mean annual water column integrated net primary production (NPP) is also projected to decline between 2000–09 and 2090–99 by 21.5% and 11.8% respectively in each EEZ. These changes however are calculated from different baselines, as NPP in the Kenya EEZ during the first decade (2000–09) is almost double that of Tanzania. The rate of decline in the NPP over the remainder of the century is therefore faster for Kenya than it is for Tanzania. The rate of decrease appears prominent from ~2030 onwards. Surface dissolved oxygen concentrations ([Table 2](#)) decline by just under 6% in both EEZs, while bottom oxygen levels increase by 3.63 and 3.45% in the Kenyan and Tanzanian EEZs respectively. But note, much of the EEZs are below 1000 m.

3.2. Climate change and fishing impacts on biomass and species richness

We present the impacts of climate change and fishing on species richness in [Fig. 3](#). In the present-day, modelled species richness is highest in the coastal regions with almost all species present in coastal cells in both EEZs (MSY0; [Fig. 3A](#)). But as clearly seen in [Fig. 3B](#), there is a considerable projected long-term impact of climate change (MSY0) on species richness in both EEZs with the mean number of species in each

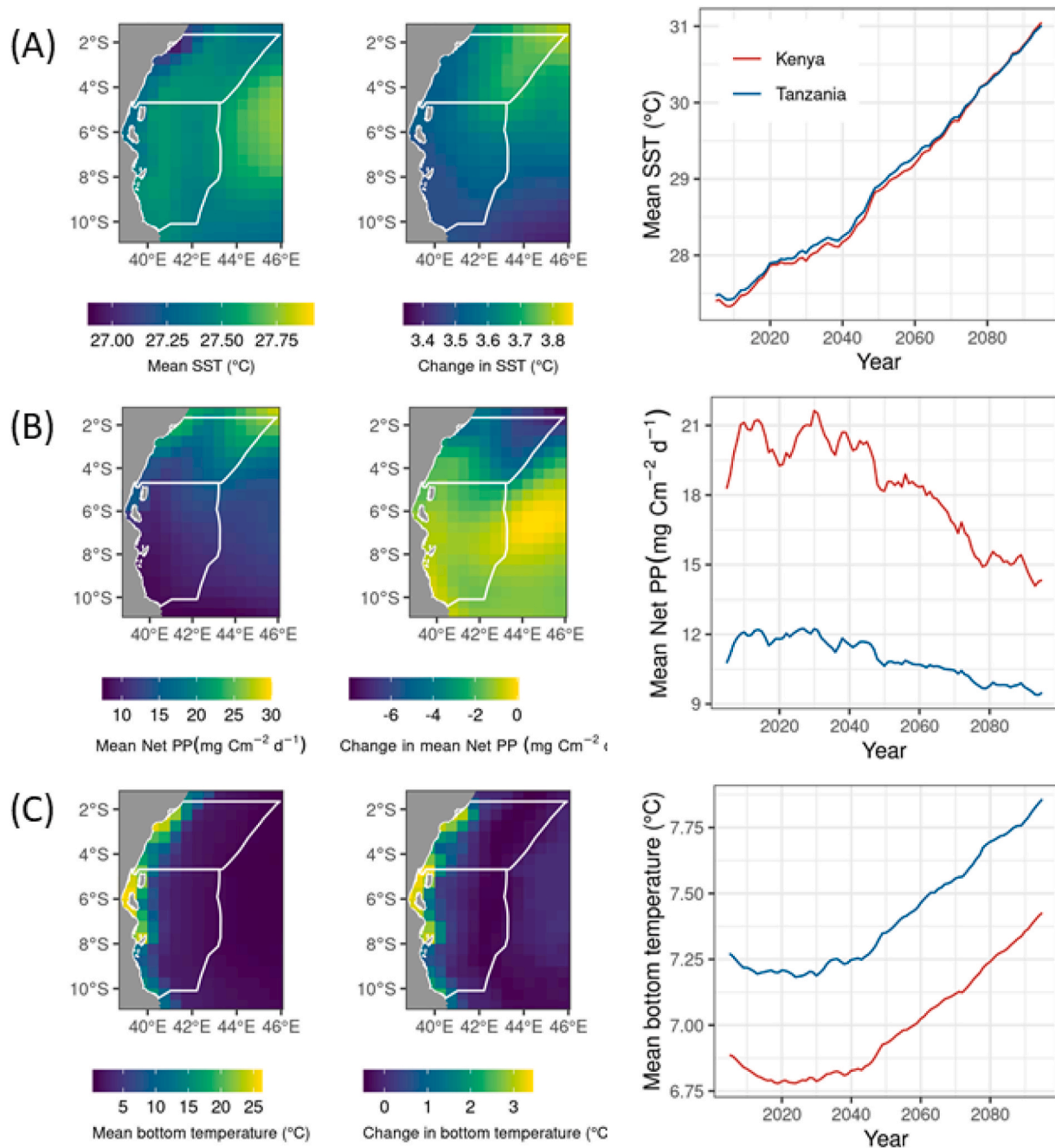


Fig. 2. Changes in spatially averaged values of key parameters from the NEMO-MEDUSA model under scenario RCP 8.5 for the Kenyan and Tanzanian EEZs: A) annual mean sea surface temperature (SST), B) water column integrated net primary productivity (Net NPP), and C) sea bottom temperature. Column 1 shows climatological mean values (2000–09), Column 2 change in the climatological mean between 2000–09 and 2090–99, and Column 3 a time series of the spatially averaged values using a rolling mean with a 10-year window.

grid cell in the Kenyan and Tanzania EEZs declining respectively by 8 and 5. This effect only appears in the second half of the 21st Century (Fig. 3B), with species richness increasing between the start and the middle of the century. This reflects the large changes in temperature and primary production that occur in the second half of the century (Fig. 2). These are a combination of the effect of temperature on the metabolic rates (higher temperature means faster metabolism), whether the temperature exceeds the thermal tolerance and availability of primary production to support the increased metabolism. Also notable in the Kenyan EEZ MSY0 (2090–99) plot is the band of very low (~10; blue) species richness in cells north of 3°S.

Increasing fishing pressure (MSY1-4) results in reductions in the

mean number of species per grid cell (Fig. 3A and B), we found a reduction by approximately 1/3rds in average species richness in the MSY4 scenario compared with the MSY0 scenario, which is a logical result to the increasing level of fishing. As shown in Table 3, across all scenarios and in both EEZs, at least 70% of the species have biomass declines during the 21st Century. However, in contrast to the species richness trends, changes in biomass in scenarios where MSY is set to 1, 2, or 3, appear to be less than in the case where MSY is set to either 0 or 4. This is due to an enhancement of individual species trends in response to the impacts of fishing. Species that were declining will do so faster while those that were increasing in biomass will increase faster. This is due to the fact that declining species free up resources for those that are doing

Table 2
Projected changes in key environmental drivers of fish populations from NEMO-MEDUSA. Changes shown are between 2000–09 and 2090–99.

EEZ	Variable	2000–09	2099–99	Absolute change	Percentage change
Kenya	Net primary production, water column total (mg C m ⁻² d ⁻¹)	18.27	14.34	-3.93	-21.51
	Mean oxygen for bottom 15m (mmol m ⁻³)	138.80	143.84	5.04	3.63
	Mean oxygen for top 15m (mmol m ⁻³)	205.40	193.49	-11.91	-5.80
	Mean temperature for bottom 15m (°C)	6.89	7.43	0.54	N/A
	Mean temperature for top 15m (°C)	27.40	31.05	3.65	N/A
	Net primary production, water column total (mg C m ⁻² d ⁻¹)	10.76	9.49	-1.27	-11.83
Tanzania	Mean oxygen for bottom 15m (mmol m ⁻³)	141.42	146.16	4.7	3.45
	Mean oxygen for top 15m (mmol m ⁻³)	204.46	193.05	-11.40	-5.58
	Mean temperature for bottom 15m (°C)	7.27	7.86	0.59	N/A
	Mean temperature for top 15m (°C)	27.47	31.01	3.54	N/A

well and as primary production increases so does the food available. Detailed changes for all species are given in the supplementary materials (Table S1).

Fig. 4 shows the median change in biomass by species. High levels of consistency across the various fishing scenarios is observed. In the Kenyan EEZ, the median biomass reduction is between 63.2% and 76.4%, while for Tanzania, it is 55.7% and 69.0%. In contrast to species richness, the median biomass declines for most of the century, with an acceleration of the decline apparent in the second half of the century. This is consistent with the rise in temperature and reductions in primary productivity.

Across all fishing scenarios and in both EEZs the majority of species see biomass declines this century. For the Kenyan EEZ between 77.8% and 86.7% of species see declines across the fishing scenarios, while for the Tanzanian EEZ, 73.3%–82.2% of species have biomass declines.

Declines in biomass of tunas (Fig. 5) are notably larger and more consistent than for the other species studied (Fig. 4, Supplementary Table S1). Each species is seen to decline by more than 70% in biomass during the 21st Century in both EEZs and in all fishing scenarios. Most dramatically impacted are Albacore, Bigeye and Yellowfin, which all see declines of at least 90% in both EEZs. For five of the species, declines were projected to occur consistently throughout the 21st Century. However, Kawakawa tuna was projected to increase in abundance during the first half of the 21st Century before declining in the second half, this is likely due to the higher thermal tolerance of Kawakawa.

The addition of fishing in the model has a large impact on fishery species richness (Fig. 3). Under the extreme MYS4 scenario, species richness halves in both EEZs, while in the MSY1 scenario there is a reduction in species richness by 2–3 species, which is to be expected

considering that any fishing above MSY will result in stock decline. Climate change impacts across all fishing scenarios are broadly similar (Fig. 4), with comparisons between changes in decades 2000–09 and 2090–99 under each scenario showing high correlation. For example, for MSY0 and MSY1 the correlation coefficient between the percentages change in species biomass is 0.998 and 0.96 for the Kenyan and Tanzanian EEZs respectively.

4. Discussion

This analysis is the first regional study of the future impact of climate change on the marine fisheries of Kenya and Tanzania, and the first for the WIO region. The NEMO-MEDUSA global biogeochemical ocean model is consistent with other model projections (Jacobs et al., 2021), and indicates that temperatures are projected to increase while primary production will decrease this century. As a result, there is a median decline in species biomass of approximately 55–78% in both countries' fisheries by the end of the century under a high-emissions scenario (RCP8.5) and multiple fishing scenarios.

The results in this study are in agreement with previous work undertaken to assess the impact of unmitigated climate change on global fisheries. For instance, Cheung et al. (2019) found that the potential catch in the EEZ of Kenya and Tanzania would decrease by 48.4 and 52.4%, respectively, under RCP8.5 by the end of the century. Similarly, the FishMIP project (Lotze et al., 2019) found that across a range of models with different forcing, the loss of biomass in this region of the ocean would be over 30% under RCP8.5 by the end of the century. While the spread in projected change ranges from 30% in Lotze et al. (2019) to upward of 75% in our study the fact that three independent bodies of work show a decline in the fisheries in the region is not to be underestimated; while the magnitude might differ there is an obvious consensus toward a change that will not be without consequences.

Furthermore, a key result is that projected impacts of unmitigated climate change will be much more severe in the second half of the 21st Century, in part because of the rapid reduction in primary productivity. However, the end-of-century scenario shown here should be interpreted as an upper bound on future changes. This is because the emissions scenario RCP 8.5 is representative of a world where there is no action on climate change and reducing fossil fuel usage (Hausfather and Peters, 2020). Our results, therefore, indicate that the impacts of climate change on Kenyan and Tanzania fisheries will only become severe if little global action is taken to limit greenhouse gas emissions. This is further supported by the works of Cheung et al. (2019) as well as Lotze et al. (2019) who compared RCP2.6 (a low emissions with strong mitigation scenario) and RCP8.5, finding that changes in global mean potential catch or biomass of 5% or less under RCP2.6 but 17% under RCP8.5. Additionally, it is important to note that our projections highlight climate change as the main driver of change with the fishing pressure being an additional stressor that can amplify the response of the system to climate change, but in the long term does not drive the overall trend. This is made quite evident when in the projections under MSY 1 through 3, we projected an initial increase in biomass. As mentioned, this is likely due to a combination of increased primary production and redistribution of resources that favors the species that are less sensitive to other environmental changes and present an increase in their biomass. However, it does not change the overall direction toward a loss of biomass and species richness driven by climate change only the amplitude and speed of it. Lotze et al. (2019) looked at the impact of no fishing versus fishing within several models and across the two climate scenarios (RCP2.6 and RCP8.5) that they used and similarly to us found that the intensity of fishing (at current levels or less) did not substantially alter the effect of climate change.

We need to be mindful of a few more attributes of our modelling exercise. For one, NEMO-MEDUSA projects that net primary production (NPP) declines during the 21st Century, which is consistent with all CMIP5 ESMs (Jacobs et al., 2021). This certainly is well-aligned with

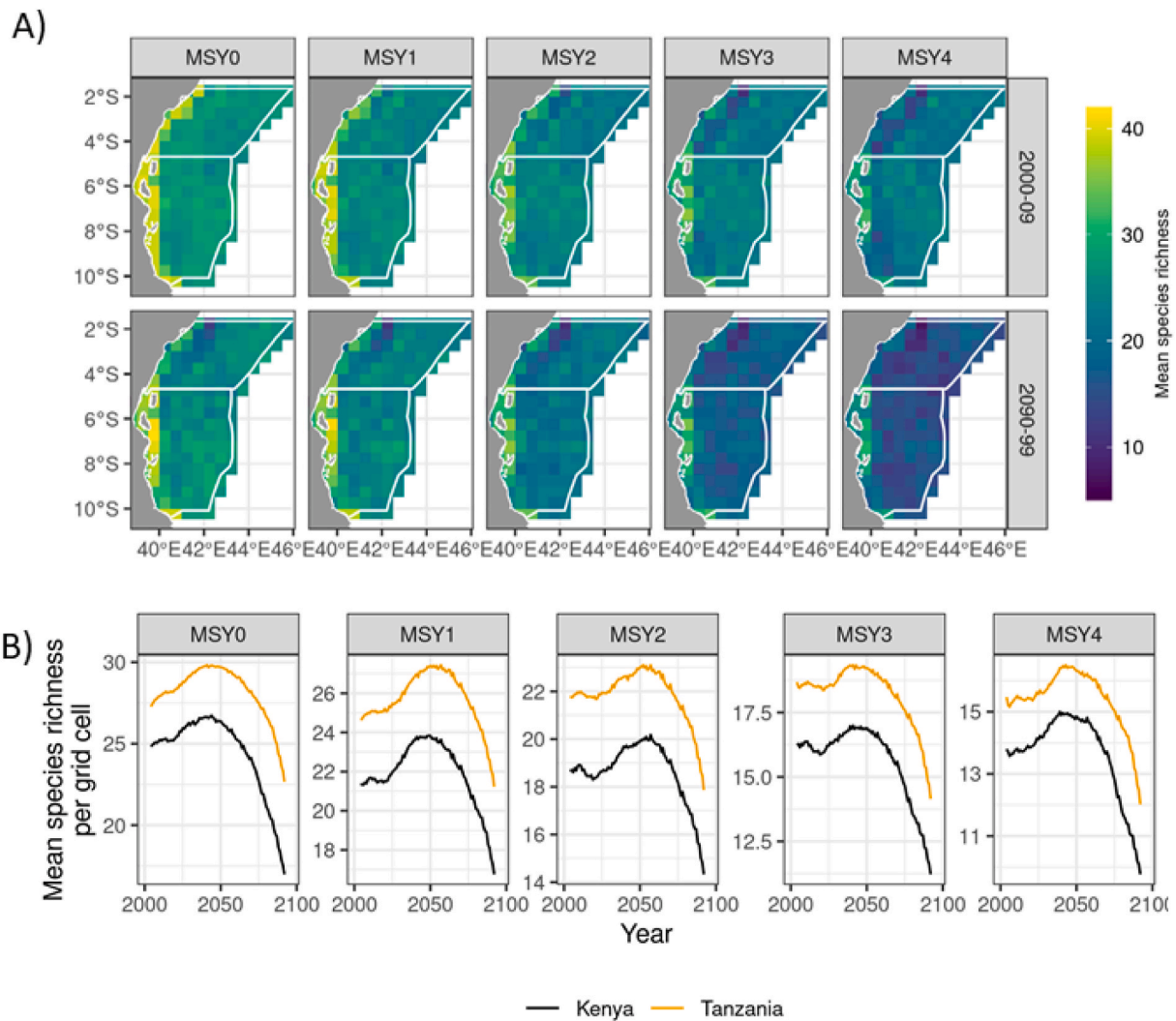


Fig. 3. Projected changes in species richness per grid cell during the 21st Century by the SS-DBEM fisheries model under RCP 8.5. A) Mean species richness for each MSY scenario (0–4) for decades 2000–09 (top panel) and 2090–99 (bottom panel). B) Spatially averaged species richness, measured as mean species richness per grid cell between 2000–09 and 2090–99 for each EEZ. Note the different scale for the Y-axis in Fig. 3b.

Table 3
Summary of projected changes in fish populations in each EEZ between 2000–09 and 2090–99.

EEZ	Metric	MSY0	MSY1	MSY2	MSY3	MSY4
Kenya	Percentage of species with declining biomass	86.7	80.0	77.8	77.8	77.8
	Median change in species biomass	-75.6	-71.3	-63.2	-73.6	-76.4
Tanzania	Percentage of species with declining biomass	82.2	77.8	73.3	75.6	75.6
	Median change in species biomass	-65.4	-58	-55.7	-56	-69

historical observations by Roxy et al. (2016). However, as with temperature, some caution needs to be exercised here in that NEMO-MEDUSA appears to under-estimate present-day NPP by about a factor of 4, which is consistent with the biases in all published CMIP5 ESMs. This potentially biases some of the fish species projections, as they will reach their NPP related limits much earlier than expected in reality. Another caveat to bear in mind is that we do not model all fish but rather those key species that have sufficient data to be included in the exercise.

Consequently, while we can draw broad conclusions from the behaviours of certain groups and make inferences for the other species, any management decision made based on this work should keep this in mind.

Notwithstanding the above, our projections show dramatic declines of at least 90% for bigeye, skipjack and yellowfin, and 70% for frigate tunas across both EEZs and all fishing scenarios – indicating tunas will be more impacted by climate change than the broader reef associated fish species (see Supplementary Table S1). The decline in the model is associated with a shift in population distribution (see Supplementary Fig. S3) which is consistent with previous work that has projected southern shifts in the geographic distribution of WIO tuna species (Dueri et al., 2014). It is also important to take into account the migratory nature of tuna meaning that factors outside of the area of interest for this study will impact them. Already, yellowfin tuna stock in the WIO is considered overfished (Indian Ocean Tuna Commission, 2016) and climate change pressures are likely to worsen the stock status. This is an important fact to be noted by fisheries managers and policy makers, as plans by Kenya and Tanzania to expand national fleets to catch more tuna may not be sustainable in the long-term. In this regard, the model projections indicate that inshore reef fisheries may be more resilient to future climate change than the offshore pelagics, even though they have been declining for the past decades (Samoilys et al., 2017). This is likely

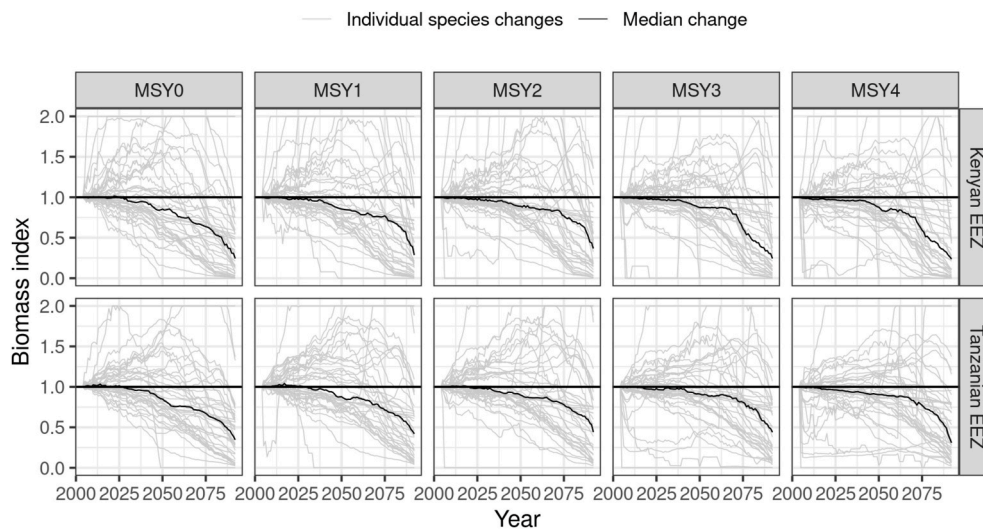


Fig. 4. Trends in biomass indices for all species and median changes. For each species the biomass index is calculated using a rolling mean of 10 years with the biomass relative to the starting period (2000–09). Each species is shown with a single grey line, with the increase limited to 2 for visual clarity. The solid black line shows the median change in biomass index.

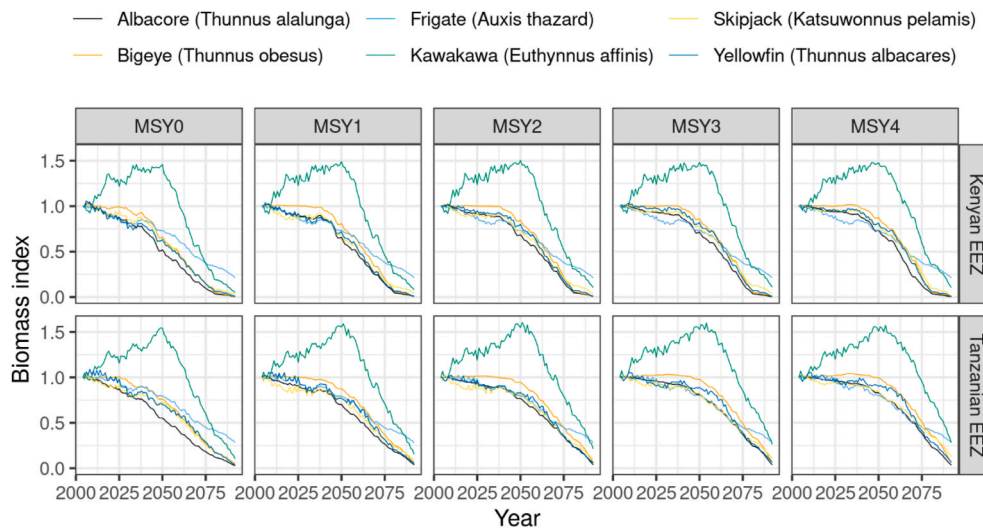


Fig. 5. Century-long trends in biomass indices for six tuna species (subset of 41 species) in the Kenyan and Tanzanian EEZs for varying catch scenarios. Biomass is calculated on a rolling 10-year basis relative to the mean biomass in 2000–09.

a model artefact due to the fact that we do not project changes in reefs due to climate change, meaning the reef habitat is not changing which might result in overly favorable conditions for the fish.

In summary, we have demonstrated large negative impacts of unmitigated climate change on the inshore (reef-associated) and offshore (pelagic) fisheries for both Kenya and Tanzania. The changes will not only impact the biomass of fish species but also their species richness, with some groups being more vulnerable than others. This will in turn have an impact on the sustainability of fisheries as fishers adapt to changes in species ranges by either changing their target species, increasing fishing effort (fishing time or travel time) or changing fishing practices to enhance efficiency (Ojea et al., 2020). Additionally, the development of new fisheries (North Kenya Bank, Kamau et al., 2021) will need to be mindful of the changing environment and identify which target species (and associated gear) will be both sustainable and flexible for use in a changing system. Furthermore, any areas where there is joint management (Pemba channel, Sekadende et al., 2020) will have to pay attention to shared stock to avoid unintentional exacerbation of the changing climate effect. Finally, offshore fishing (particularly by local

fishermen) is limited by initial capital investment, technical and cultural issues. In some instances fishing techniques are inherited hence fishers only become knowledgeable in using one gear over the other. This can be a challenge when it comes to shifting gears. Studies on fishing gears have documented deployment of gillnets of medium (10.2–17.8 cm) and large mesh sizes (20.3–30.5 cm) in offshore sand banks (Osuka et al., 2021). However, medium mesh sizes compared to large mesh size, were found to capture pelagic fishes such as tuna species and other scombrids and were associated with low capture of threatened sharks and ray species. From this study, a shift to fishing offshore would require promoting the use of the least-damaging medium gillnet mesh sizes. Some of the points mentioned above are reflected in recent policy documents of both Kenya (Kenya Tuna Fisheries Development And Management Strategy, 2013–2018, <https://aquadocs.org/handle/1834/9088>) and Tanzania (The Deep-Sea Fisheries and Management Act, 2021; <https://www.mifugouvuvu.go.tz/publications/58>). The Kenya strategy aims to transform the country’s tuna fisheries into modern commercial coastal and oceanic fisheries, while developing an effective tuna fisheries governance system and contributing toward an envisioned 10%

annual economic growth by 2030. The Tanzania Act focuses on regulation of the fisheries including conservation and management alongside development as well as regulations against illegal unreported unregulated (IUU) fishing with the tuna fisheries figuring prominently within it.

Our analysis is based on present-day, state-of-the-art ocean biogeochemical and fisheries models – all well accepted by the modelling communities. However, we must note that reality is much more complicated than the models which have their own limitations (e.g. NPP being underestimated in NEMO-MEDUSA or the lack of change in reef habitat in the SS-DBEM), and therefore, our results must be seen as illustrative of the future and not necessarily accurate. We recommend that further research such as a Climate Risk Assessment (CRA, Payne et al., 2020) be done to assess resilience and risk to fisheries associated with climate change.

Author contributions

RJW and SS wrote the manuscript. SS developed the fishing scenarios and ran the SS-DBEM model. RJW and SS analyzed the SS-DBEM model output. RJW produced the manuscript's Figures. All authors contributed to selection of fishery species, review of model outputs, and the revision of the paper. ZJ provided data from future projection biogeochemical model NEMO-MEDUSA.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ocecoaman.2021.105921>.

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