

# Evaluating ecosystem impacts of gear regulations in a data-limited fishery—comparing approaches to estimate predator–prey interactions in Ecopath with Ecosim

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Ecosystem models, such as Ecopath with Ecosim (EwE), are useful tools for developing ecosystem-based management strategies. Model development, however, requires data for the estimation of input parameters including time series for calibration. Most small-scale fisheries lack such information, making it difficult to reliably use ecosystem models for management strategy exploration. This is the case for the Chwaka Bay fishery (Zanzibar), where an increase in dragnets has led to concerns for unsustainable development. While EwE could help to explore the impacts of gear regulations in the bay, this is hampered by the lack of time series to estimate the predator–prey interactions (vulnerabilities) in the model. Here, we explore available approaches for estimating the vulnerabilities to simulate the effects of a dragnet prohibition with and without reallocation of fishing effort. Simulations suggest that banning dragnets would be beneficial for the fishing community judged by the increase in biomass of functional groups and fishers' profits, but not if dragnet fishers were to continue fishing in the bay by reallocating to other gears, indicated by the reduced fish biomass and fishers' profits. The overall trend (decreasing or increasing) in the changes of functional groups, ecosystem indicators, and profits were relatively consistent across vulnerability settings, illustrating that an unfitted EwE model can be used for qualitative management strategy exploration.

**Keywords:** Chwaka Bay, dragnets, Ecosim vulnerabilities, Ecopath with Ecosim (EwE), fishing effort reallocation, local ecological knowledge, small-scale fisheries, sensitivity analysis, Western Indian Oceans

## Introduction

Ecosystem simulation models are important for the support of the internationally mandated goal to move fisheries management towards an ecosystem-based approach to achieve sustainability. A number of ecosystem models are now available that enable the simulation of energy flows within a system while simultaneously integrating environmental effects and multiple human stressors (Shin and Cury, 2001; Christensen *et al.*, 2008; Fulton *et al.*, 2011). The most widely used is the user-friendly and free software environment Ecopath with Ecosim (EwE) (Christensen *et al.*, 2008), which has been used to create over 500 ecosystem models worldwide (Colleter *et al.*, 2015).

EwE allows for the spatial-temporal simulation of use and conservation scenarios, helping in better prioritizing effective management plans. These aspects make it a powerful tool in tropical, small-scale fisheries contexts because managers often need to evaluate alternative trade-offs between a multitude of different gears and target species, weighing environmental concerns with the socio-economic needs of fisher communities. EwE has also been successfully applied as a tool in

stakeholder workshops to prioritize management strategies in a participatory way (Bentley *et al.*, 2019; Sánchez-Jiménez *et al.*, 2019). This is particularly due to its capabilities to analyze and visualize complex ecosystem dynamics and the consequences of fishing impacts.

However, the use of EwE for the exploration of use and conservation scenarios requires an understanding of the trophic interactions between prey and predators in the system. These predator–prey interactions are based on the foraging arena theory, which divides the biomass of prey into a vulnerable and a non-vulnerable pool or stage (Ahrens *et al.*, 2012). The concept behind the separation of prey biomass is that species tend to avoid predation through various behavioural traits such as hiding, ontogenetic shifts, or diurnal migration, strongly structuring trophic interactions in time and space (Christensen and Walters, 2005). The transfer rate, or vulnerability ( $v$ ), between the two pools, defines the predation mortality the prey experiences or, put differently, the feeding rate of its predator. The vulnerability parameter, thus, expresses how far a group is from its carrying capacity. Setting appro-

appropriate values for this parameter in EwE is crucial as it will determine how much the base predation mortality can change if the biomass of a predator is changed (e.g. through fishing) in the future. As the vulnerability parameter cannot be derived empirically, it is—as a rule—calculated by fitting the model to observed time series of biological or fisheries indicators of one or more functional groups of the model.

Time-series data for such tuning, however, are rarely available for small-scale, tropical fisheries (Batista *et al.*, 2014), which impedes the use of the temporal module of EwE. Different approaches have been suggested to estimate vulnerabilities without time-series data (Cheung, 2001; Christensen and Walters, 2004), but they remain approximations. Since simulation outcomes are highly sensitive to this parameter (Shannon *et al.*, 2000), even small deviations can affect scenario outcomes.

In this work, we explore available approaches for estimating vulnerabilities to simulate conservation scenarios in the multi-species and small-scale fishery of Chwaka Bay (Zanzibar) in the Western Indian Ocean (WIO) using a recently developed Ecopath model (Rehren *et al.*, 2018a). Chwaka Bay is a highly productive fishing ground on the east coast of Zanzibar with an annual fisheries catch of approximately 5 t km<sup>-2</sup> (Rehren *et al.*, 2018a). Fishers report decreases in their catch rates (de la Torre-Castro and Rönnbäck, 2004; Geere, 2014), and the use of illegal and destructive gears has led to concerns for overfishing in the bay. Management attempts have mainly focused on the prohibition of the so-called dragnets (RGZ, 1988), which are a type of destructive seine net, like beach seines, deployed in intertidal areas and hauled by boats (Jiddawi and Ohman, 2002). Beach seines and dragnets have received great attention in the WIO region and are the focus of management in a variety of different coastal zones (RGZ, 1988; McClanahan and Mangi, 2001; Cinner, 2009; Wallner-Hahn *et al.*, 2016). This type of fishing has shown to be destructive since the nets are pulled over the seafloor destroying important habitats such as corals and seagrasses (Mangi and Roberts, 2006). Furthermore, they are among the least selective gears (McClanahan and Mangi, 2004; Rehren *et al.*, 2018b), and fishers often use small-mesh sizes leading to high juvenile retention rates (Hicks and McClanahan, 2012; de la Torre-Castro *et al.*, 2014). The combat of destructive seine nets has been successful in different parts of East Africa through spatial-temporal closures (McClanahan *et al.*, 2008) and gear exchange programmes (Wells *et al.*, 2010). In Chwaka Bay, by contrast, neither the prohibition of dragnets since the implementation of the Zanzibar Fisheries Act in 1988 (RGZ, 1988) and the specific Chwaka Bay by-law (2001) nor the gear-exchange programme conducted in 2005 within the framework of the Marine and Coastal Environmental Management Project (MACEMP) has been successful. A central reason for the failure of the gear exchange programme was the insufficient number of gears that were provided for a large number of fishers using illegal gears (Gustavsson *et al.*, 2014). Given the effort to manage dragnets in the bay, it is important to understand the benefits and repercussions of such gear regulations.

Within this context, our study has three main objectives. First, we simulated the effects of a complete prohibition and a reallocation of dragnet fishers to other gears on the relative changes in the biomass of functional groups and fishers' profits using the EwE approach. Second, to take into account the challenge of properly estimating the vulnerability parameters, we evaluated the sensitivity of quantitative and qualitative sce-

nario outcomes using six different estimation approaches (see section "Vulnerabilities settings"). Finally, as a third objective, we evaluated the robustness of our management options to changes in this key parameter to identify those outcomes that were less impacted by model parameter uncertainty.

## Material and methods

### The Chwaka Bay ecosystem

Chwaka Bay is a tropical bay system on the east coast of Unguja Island, Zanzibar (Figure 1). The bay is shallow (ranging from 3 m in the bay proper to about 20 m around the reef at the offshore border) and comprised of a mosaic of seagrass beds, mangroves, and corals. It is strongly dominated by a large biomass of primary producers and invertebrate consumer groups. Due to its high productivity and diverse habitats, the bay gives rise to an intense multi-gear, multi-species nearshore fishery, and the density of fishers in the bay (7 fishers km<sup>-2</sup>) is relatively high compared with other fishing areas on Zanzibar. The local community highly depends on the fisheries resources for income and protein supply (Jiddawi, 2012). The main fishing gears are basket traps, dragnets, handlines, spears, and, to a minor extent, floatnets, longlines, fence, and gillnets.

We used a recently constructed Ecopath model of the Chwaka Bay ecosystem (Rehren *et al.*, 2018a; Figure 2a) to simulate different fishing effort scenarios (*cf.*, section "Fishing effort scenarios"). The Chwaka Bay model comprises 28 functional groups ranging from primary producers to pelagic fish. The model is mainly rooted in local data and has a pedigree of 0.53 (see Supplementary material S1 for the basic input parameters).

### Use of Ecopath with Ecosim as a modelling tool

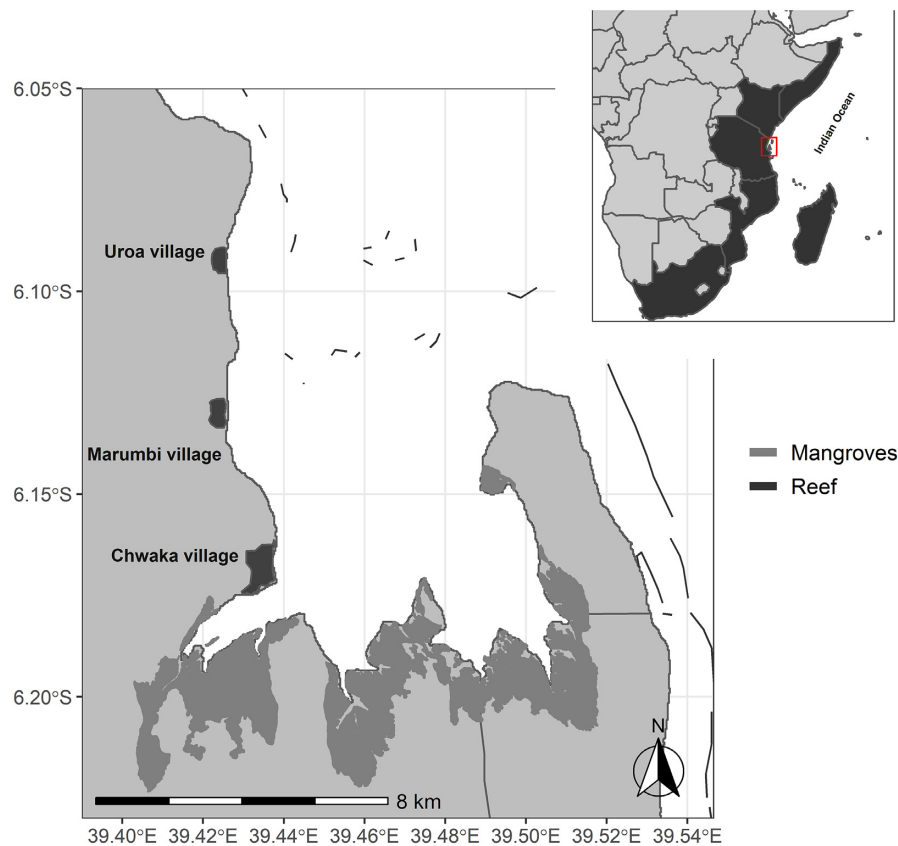
Ecosim is the time-dynamic model of EwE, which allows simulating the effects of changes in fishing and environmental conditions on the biomass dynamics of functional groups over time (Christensen *et al.*, 2008). The equations are based on the parameters from the Ecopath baseline mass-balance model, expressing the biomass growth rate as

$$\frac{dB_i}{dt} = g_i \sum_j^n Q_{ji} - \sum_j^n Q_{ij} + I_i - (M0_i + F_i + e_i) B_i, \quad (1)$$

where  $dB_i$  is the rate of change in biomass of group  $i$  over time interval  $dt$ ,  $g_i$  is the net growth efficiency (production/consumption ratio),  $I_i$  is the immigration,  $M0_i$  is the non-predation mortality rate,  $F_i$  is the fishing mortality rate, and  $e_i$  is the emigration rate. Total consumption rates are estimated by the summations:  $Q_{ji}$  is the total consumption by group  $i$  and  $Q_{ij}$  are the feeding rates of each predator  $j$  on that group  $i$ . The feeding rates are calculated based on the foraging arena theory (Ahrens *et al.*, 2012), separating  $B_i$  in vulnerable and non-vulnerable pools:

$$Q_{ij} = \frac{v_{ij} a_{ij} B_i B_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j / D_j}, \quad (2)$$

where  $a_{ij}$  is the effective search rate of predator  $j$  feeding on prey  $i$ ,  $T_i$  and  $T_j$  are the relative feeding times of prey  $i$  and predator  $j$ , respectively,  $S_{ij}$  are the seasonal or long-term forcing effects,  $M_{ij}$  are the mediation forcing effects, and  $D_j$  is the effect of handling time as a limit to consumption rate.  $v_{ij}$  are



**Figure 1.** Chwaka Bay, Zanzibar, Tanzania. The bay comprises large mangrove stands in the south, a fringing reef at the bay opening, and coral patches inside the bay. Seagrass meadows are found throughout the bay, with dense aggregations towards the central part.

the transfer rates of prey  $i$  shifting from a vulnerable state to a non-vulnerable state.

### Vulnerabilities settings

Equation 2 demonstrates the importance of the vulnerability parameter: it will determine how much the base predation mortality can change if the biomass of a predator is changed in the future, for instance through fishing.

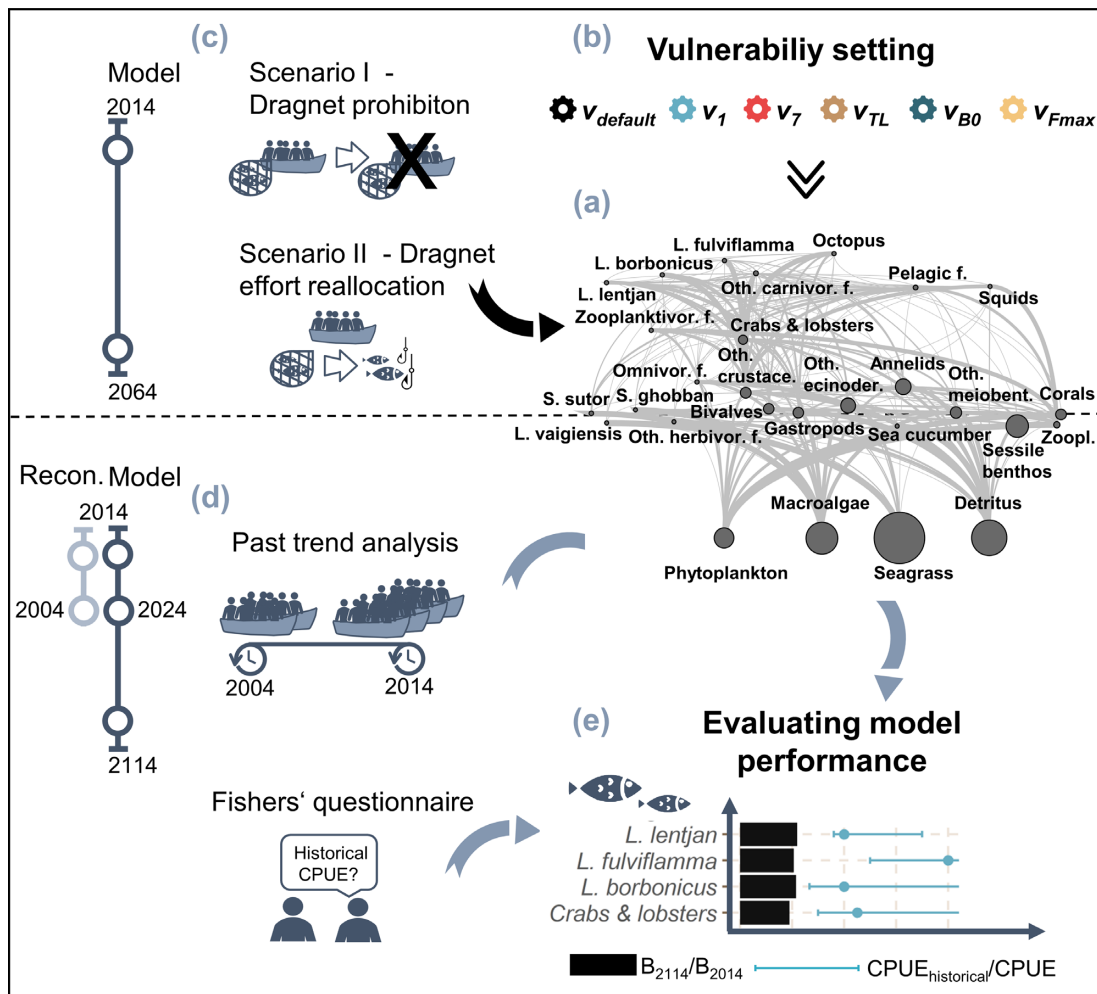
In the absence of time-series data to estimate the vulnerabilities, we used six different approaches to approximate these parameters (Figure 2b): (i) a default value of 2 for all predator–prey interactions ( $v_{default}$ ); (ii) a value of 1 for all predator–prey interactions to simulate an ecosystem with predators close to their carrying capacity ( $v_1$ ); (iii) a value of 7 for all predator–prey interactions to simulate an ecosystem with predators further from their carrying capacity ( $v_7$ ); (iv) the trophic level approach (Cheung, 2001; Cheung *et al.*, 2002) ( $v_{TL}$ ); (v) setting predator–prey interactions based on the ratio between the current and unfished biomass of the predator ( $v_{B0}$ ) (Christensen and Walters, 2004); and (vi) setting predator–prey interactions proportional to the relationship between the predators maximum fishing mortality and natural mortality ( $v_{Fmax}$ ) (Christensen and Walters, 2004).

It is recommended to use the first three approaches to explore the model behaviour (Christensen *et al.*, 2008). In theory, the vulnerabilities can be set to infinity. However, high vulnerabilities can lead to the loss of functional groups and strong cyclic predator–prey interactions as the model will perform as a typical mass-action model with Lotka–Volterra dynam-

ics. For a system further from its carrying capacity ( $v_7$ ), we set the vulnerabilities to 7 because values above led to unrealistic behaviour in the Chwaka Bay EwE model.

The trophic level approach has been commonly used to approximate the vulnerabilities in the absence of time-series data (e.g. Chen *et al.*, 2008; Bacalso *et al.*, 2016; Kluger *et al.*, 2016). This approach assumes that the predator–prey interactions are proportional to the trophic level of the predator. The ecological rationale behind this approach is the assumption that the system already experienced fishing down the food web, where higher trophic levels are further removed from their carrying capacity than lower trophic levels (Christensen, 1996). EwE automatically scales the  $v$ -values according to the trophic level of the predator. The user can define the range of the scale, and we set it from 1.2 to 3.5 (the highest trophic level in our model).

The  $v_{B0}$  approach assumes that the unfished biomass of a predator is an approximation for its carrying capacity, which may hold for higher trophic levels, whereas there likely will be predator-release for lower trophic level species if fishing down the food web takes place. The vulnerabilities can then be set proportional to the ratio of the predator's current biomass and its unfished biomass ( $v_{B0}$ ). In the absence of quantitative information of historical biomass, we obtained an estimate of the current and historical ( $\geq 15$  years) catch per unit of effort (CPUE, catch per fisher and fishing duration) for the main species of selected functional groups through questionnaires with local fishers (Supplementary material S2). For this, a total of 53 full-time fishers with a minimum fishing experience of 15 years were interviewed.



**Figure 2.** Summary of the methodological approach. (a) Flow chart of the Chwaka Bay *Ecopath* model used. The circles are proportional to the biomasses of the different functional groups and the arrows represent the energy flows between them. (b) The six different vulnerability settings used for the parameterization of the predator–prey interactions in the EwE model. (c) The two different fishing scenarios simulated. (d) Reconstructed (Recon.) fishing effort scenarios (2004–2014) used to simulate past biomass values. (e) Comparison of the hindcasted biomass changes ( $B_{2114}/B_{2014}$ ) with perceived changes in CPUE levels ( $CPUE_{\text{historical}}/CPUE$ ).

From each interview, we first calculated the ratio between the reported historical and current CPUE of each species/group and then summarized the interviews by calculating the median, and the 25 and 75% quantiles. We only parameterized those functional groups for which we obtained enough information: (i) changes in CPUE were reported from at least five fishers and (ii) changes were reported for taxonomic groups (i.e. species or families) that together contributed at least 60% to the respective functional group. For functional groups comprising several species, we calculated a weighted median (see Supplementary material S3 for the results of the questionnaires).

The data of the questionnaires and an R-script of the analysis are available at <https://github.com/Jrehren/ICES-2021-Rehren-Evaluating-impacts-of-fishing-gear-regulations>. The median ratio was used as direct input for the ratio between the unfished and current biomass. EwE can use this ratio to internally estimate the vulnerabilities (without feeding time adjustment). In addition, we conducted a sensitivity analysis by parameterizing the functional groups using the 25% and 75% quantiles of the perceived changes in CPUE reported by the fishers (Supplementary material S4).

Finally, the last approach assumes that the maximum sustainable yield of a predator is approximately equal to its natural mortality under constant recruitment and sets the vulnerabilities proportional to the ratio between the maximum fishing mortality of a predator and its natural mortality ( $F_{\text{max}}/M$ ). We obtained  $M$  from the empirical equation of Pauly (1980). Values for  $F_{\text{max}}$  were obtained from relative yield per recruit analysis based on length–frequency data obtained in 2014 (Rehren *et al.*, 2018b) for most monospecific groups (i.e. *Siganus sutor*, *Leptoscarus vaigiensis*, *Lethrinus lentjan*, *Lethrinus borbonicus*, and *Lutjanus fulviflamma*). For *Scarus ghobban*, we used the  $F_{\text{max}}$ -value provided by EwE. Under this approach, we let EwE set the vulnerabilities of these groups proportional to  $F_{\text{max}}/M$  (without feeding time adjustment) and we set the vulnerabilities of the other functional groups to the default value of 2.

The  $v_{F_{\text{max}}}$  and  $v_{B0}$  approach initially led to very high vulnerability estimates of *L. lentjan* (>3000) and *Crabs and lobsters* (>300). The vulnerabilities can be constrained by defining how high the base predation mortality by a given predator ( $M_{2\text{base},ij}$ ) can increase relative to the prey's total natural mortality ( $M_i$ ) (i.e. vulnerability caps,  $v_{\text{cap},ij}$ , Chagaris *et al.*,

**Table 1.** Vulnerability settings and their corresponding values for each functional group (*cf.*, section "Vulnerabilities settings" for details)

Group	Vulnerability settings					
	$v_{default}$	$v_1$	$v_7$	$v_{TL}$	$v_{B0}$	$v_{Fmax}$
<i>S. sutor</i>	2	1	7	1.4	1.5	2.4
<i>L. vaigiensis</i>	2	1	7	1.2	1.5	2.2
<i>L. lentjan</i>	2	1	7	3.1	1.2	4–2535
<i>L. borbonicus</i>	2	1	7	3.2	1.4	1.8
<i>L. fulviflamma</i>	2	1	7	3.4	4.9	2.3
<i>S. ghobban</i>	2	1	7	1.4	1.8	22.8
Other carnivorous fish	2	1	7	3.2	2	2
Pelagic fish	2	1	7	3.0	2	2
Other herbivorous fish	2	1	7	1.3	1.7	2
Zooplanktivorous fish	2	1	7	2.5	2	2
Omnivorous fish	2	1	7	1.8	2	2
Octopus	2	1	7	3.5	3	2
Squids	2	1	7	3.1	1.9	2
Crabs and lobsters	2	1	7	2.4	1.5–136	2
Other crustaceans	2	1	7	1.6	2	2
Bivalves	2	1	7	1.4	2	2
Gastropods	2	1	7	1.4	2	2
Other echinoderms	2	1	7	1.5	2	2
Sea cucumber	2	1	7	1.2	2	2
Annelids	2	1	7	1.7	2	2
Other meiobenthos	2	1	7	1.4	2	2
Sessile benthos	2	1	7	1.2	2	2
Zooplankton	2	1	7	1.2	2	2
Corals	2	1	7	1.4	2	2

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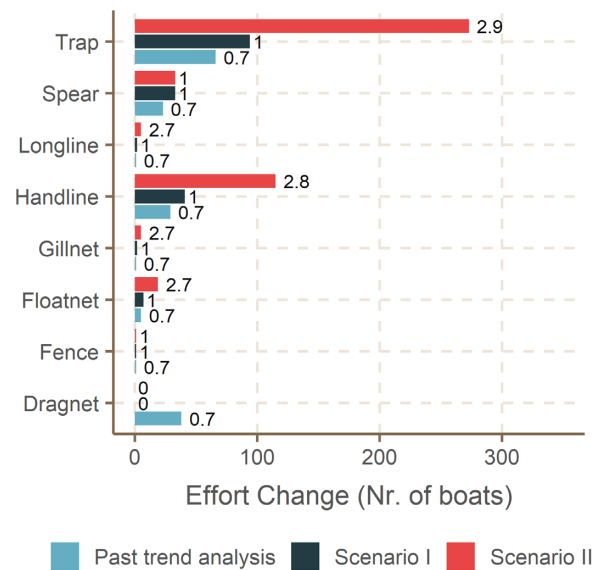
$$v_{cap,ij} = \frac{(M2_{cap}M_i)}{M2_{base,ij}}, \quad (3)$$

where  $M2_{cap}$  defines the percentage of the natural mortality of a prey that a predator can account for. We assumed that neither *L. lentjan* nor *Crabs and lobsters* could account for more than 75% of the mortality of any of their prey. A final list of the different vulnerabilities per group is shown in Table 1.

### Fishing effort scenarios

We simulated two different fishing effort scenarios (Figure 2c). In *Scenario I*, we simulated the enforcement of the dragnet prohibition in the bay through a stepwise reduction in the dragnet effort. The starting value of the simulation was the number of dragnet fishers operating in 2014, and this value was reduced each year by 20%. In *Scenario II*, we simulated the proposed reallocation of the dragnet fishery to other legal gears. For this, we reallocated all dragnet fishers that were active in 2014 to the other gears in proportion to the relative effort of those gears. We did not include the gear type fence in the reallocation because the use of this gear is restricted to the intertidal area, and considering the intense cultivation of seaweed in the bay's intertidal zone, it is not clear to what extent an increase in this fishery would be spatially limited. Furthermore, we did not reallocate dragnet fishers to spears because our fishery data did not allow for a differentiation between the legal wooden sticks and the illegal spear guns. The simulation time of the two different scenarios was set to 50 years. All scenarios started after the first simulation year. Figure 3 gives an overview of the relative change in the fishing effort of the different gears used for the different scenarios.

### Fishing effort changes



**Figure 3.** The final change in total fishing effort for the different gears and fishing effort scenarios (*cf.*, section "Fishing effort scenarios" for details on the scenarios). In *Scenario I*, the use of dragnets is successfully prohibited, and in *Scenario II*, dragnet fishers are reallocated to legal gears. The numbers in the figure depict the relative fishing effort compared to the baseline year 2014 (i.e. effort multipliers).

### Impacts of fishing effort scenarios

We evaluated the impacts of the two different fishing effort scenarios on the local community and the ecosystem using the relative changes in biomass ( $t\ km^{-2}$ ) of selected target functional groups. We, further, looked at fishers' profits (Tanzanian Shilling boat<sup>-1</sup> trip<sup>-1</sup>), which we calculate by multiplying the landings of each gear and functional group by its market price (i.e. the weighted market price of all species comprising the functional group) and subtracting the fuel and equipment costs (gear, boat, and engine costs). We did not account for equipment maintenance-related costs (refer to Rehren *et al.*, 2018a for more details on profit calculation). Further, we assessed five ecological indicators: (i) total biomass ( $t\ km^{-2}$ ), (ii) the ratio between fish and invertebrate biomass, (iii) total catch ( $t\ km^{-2}\ yr^{-1}$ ), (iv) the mean trophic level of the community, and (v) Kempton's Q as a measure of diversity. Ecological indicators were calculated with the ECOIND module in EwE (Coll and Steenbeek, 2017). Relative changes of profits, biomass, and ecological indicators were calculated as the ratio between the penultimate simulation year in which values had stabilized and the Ecopath model year 2014. We examined if biomass and profit declines exceeded a 30% threshold and considered changes of  $\pm 10\%$  as being relatively stable. We compared the changes in biomass, profits, and ecological indicators for the two fishing effort scenarios (*cf.*, section "Fishing effort scenarios") given the above-mentioned six different approaches to estimate the vulnerabilities (*cf.*, section "Vulnerabilities settings"). The relative biomass and catch of functional groups over time are shown in Supplementary material S5. In addition, we evaluated the association among the results from the vulnerability parameterization approaches by performing a hierarchical cluster analysis on the Euclidean distance between the relative biomass changes of the target functional groups (Supplementary material S6).

## Evaluation of vulnerability settings

We used reconstructed fishing effort of Chwaka Bay (2004–2014, Supplementary material S7) to drive the EwE model and simulate the “past” biomass levels of the functional groups under the six different vulnerability settings (Figure 2d). We then compared the simulated biomass changes with the perceived changes in the historical CPUE ( $\geq 15$  years) of interviewed fishers to evaluate the performance of the different vulnerability settings (Figure 2e). We recognize that without knowing the past state of the system rather than simulating the past biomass levels we are forecasting future biomass levels resulting from the current state of the system under a reduction of fishing effort. We also recognize that catch per unit of effort of individual fishers is not an unbiased proxy for abundance. Nevertheless, this analysis should be seen as an attempt to evaluate the performance of the different vulnerability settings in the absence of time-series data.

The period from 2004 to 2014 was chosen because for these years effort estimations of several months were available from the Department of Fisheries Development on Zanzibar. We simulated the change in effort starting in model year 2015 until 2024 (30% effort reduction, Figure 3) and then ran the effort of 2024 until 2114 to reach equilibrium (Figure 2d). We also compared this to running the model only until 2024 and not until equilibrium (Supplementary material S8).

The simulated biomass changes were then compared to the perceived changes in CPUE of those fishers, who had a minimum fishing experience of 15 years.

All figures were produced using the R version 4.0.3. (R Core Team 2020; [www.r-project.org](http://www.r-project.org)).

## Results

### Relative changes in biomass of target groups

The enforcement of a dragnet prohibition (i.e. *Scenario I*) in the bay generally increased the biomass of eight target functional groups (57%), of which *L. lentjan*, *L. vaigiensis*, *Other carnivorous fish*, *Pelagic fish*, and *Squids* increased in all vulnerability settings (Figure 4). A general decline was observed for *Crabs and lobsters*, *Octopus*, *Omnivorous fish*, *S. ghobban*, and *Zooplanktivorous fish*. Assuming an ecosystem that is further from its carrying capacity ( $v_7$ ) led to biomass reductions below 30% for 50% of the functional groups. Exceeding the 30% threshold was otherwise only observed once for *Zooplanktivorous fish* ( $v_{TL}$ , Figure 4).

A reallocation of dragnet fisher to the other gears (i.e. *Scenario II*) triggered the opposite pattern: eight target functional groups (57%) experienced a general biomass decline and for seven species this decline exceeded 30% in most vulnerability settings (Figure 4). The groups *L. lentjan*, *S. ghobban*, and *Squids* even fell below 10% of their initial biomass by the end of the simulation. Only *Crabs and lobsters*, *L. fulviflamma*, *Octopus*, *Omnivorous fish*, and *Zooplanktivorous fish* benefitted from a reallocation in most vulnerability settings and increased between 13 and 241%.

The similarity of the vulnerability settings in terms of biomass changes differed strongly with fishing effort scenario, leading to different clusters (Supplementary material S6). A system close to its carrying capacity ( $v_1$ ) triggered very little changes in the biomass of functional groups in both scenarios (within  $\pm 10\%$ ), while a system further from its carrying capacity ( $v_7$ ) experienced strong negative biomass changes

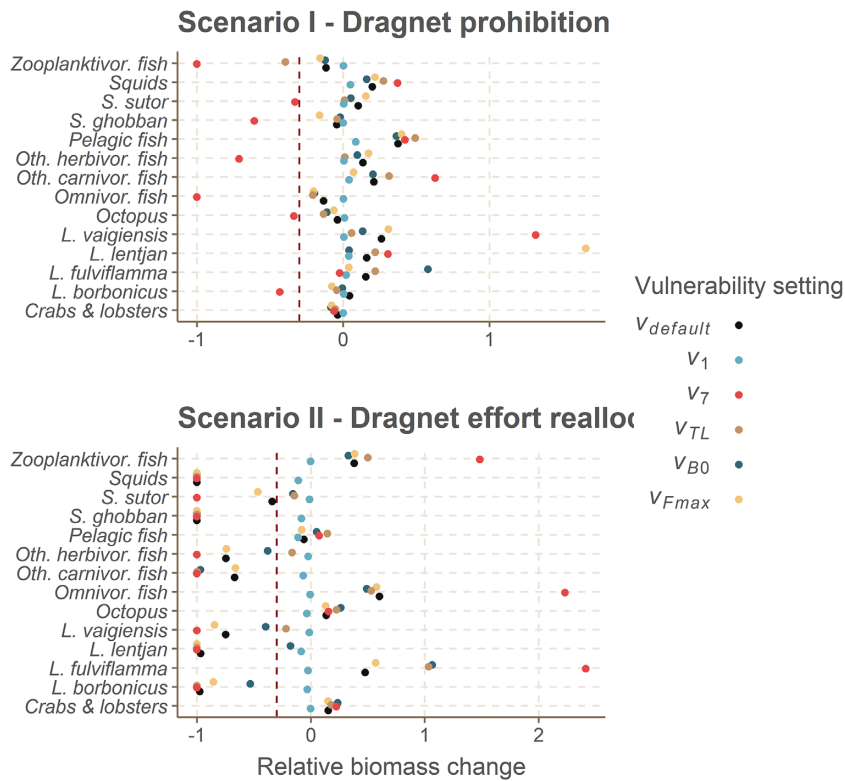
that generally exceeded the 30% threshold (Figure 4). While in *Scenario I*, a few functional groups showed similar directions and magnitudes in their biomass changes across the different vulnerability settings (i.e. *Pelagic fish* and *Squids*), in *Scenario II*, the biomass change was highly sensitive to the vulnerabilities (Figure 4). The most sensitive (largest biomass variation) in both scenarios to the vulnerability settings were *L. fulviflamma*, *Omnivorous fish*, *Zooplanktivorous fish*, *L. lentjan*, and *L. vaigiensis*.

### Relative changes in profit

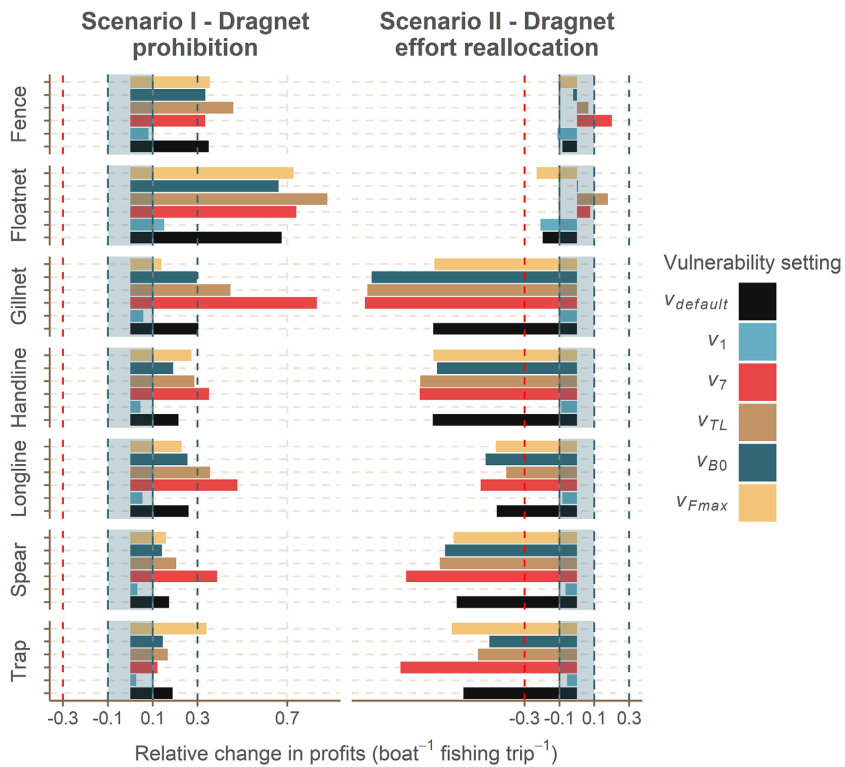
The enforcement of the dragnet prohibition (i.e. *Scenario I*) resulted in a relatively strong increase ( $>10\%$ ) in the profits of the other gears regardless of the vulnerability setting (except for  $v_1$ , Figure 5). This profit increase was highest for fence and floatnet fishers and varied from 33% ( $v_7$ ) to 88% ( $v_{TL}$ ). A reallocation of dragnet fishers (i.e. *Scenario II*) benefitted none of the other gears due to the resulting increase in respective effort. The only exceptions were fence and floatnet fishers when setting the vulnerabilities to 7 ( $v_7$ ) or proportional to  $TL$  ( $v_{TL}$ ). In these cases, the profits increased between 6.7 and 20%. For the other gears, the resulting loss in profits exceeded the threshold of 30%, except when setting the vulnerabilities to 1 ( $v_1$ ). In general, changes observed under  $v_1$  rarely exceeded 10%. Losses were particularly high for handline and gillnet fishers, with the latter experiencing negative profits ( $v_{B0}$ ,  $v_{TL}$ ,  $v_7$ ) as costs exceeded catch value. The sensitivity of profits to the vulnerability setting was highest for gillnet, spear, and trap fishers.

### Ecological indicators

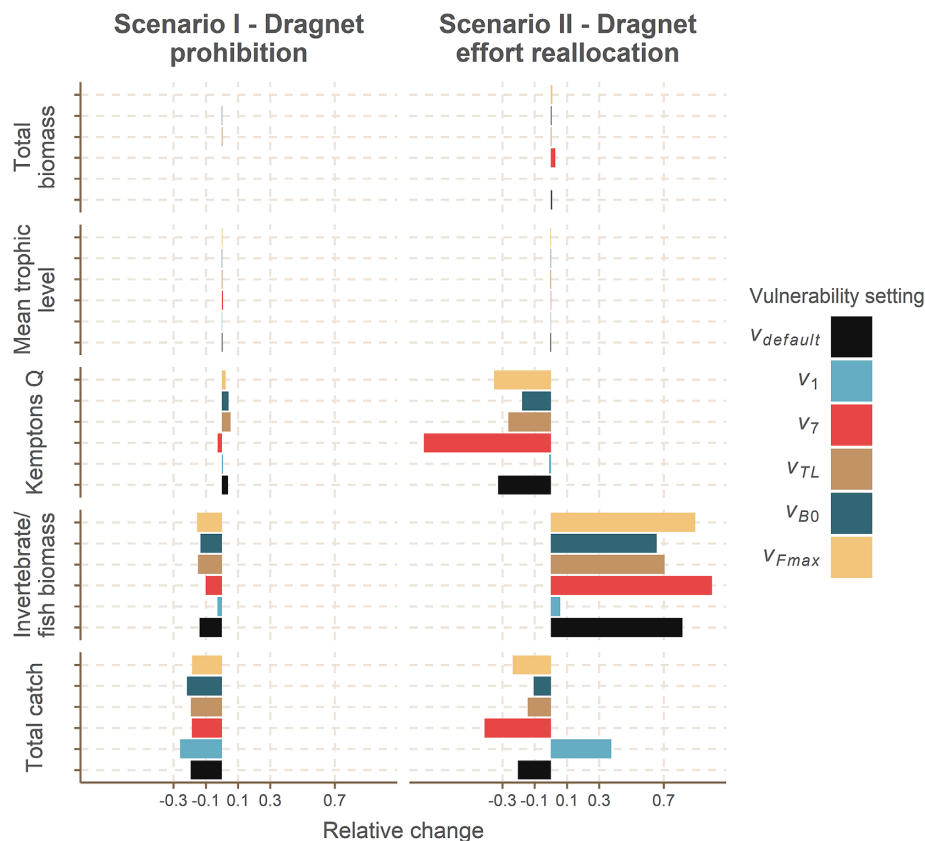
Enforcing the prohibition of dragnet fishing (i.e. *Scenario I*) in Chwaka Bay induced only slight changes to the total biomass, the mean trophic level, and Kempton's Q (within  $\pm 10\%$ ), independent of the vulnerability setting (Figure 6). So while the target fish and invertebrates are highly effected by the effort change (cf., section "Relative changes in biomass of target groups"), their contribution to the total biomass was very low (e.g. compared to primary producer biomass) with little effect on the total biomass of the system. The total catch and the ratio between invertebrates and fish, in contrast, decreased by more than 10%. The latter indicates a recovery of the fish biomass in the system. Similarly, a reallocation of dragnet fishers (i.e. *Scenario II*) had a low impact on the mean trophic level and the total biomass. In contrast, the ratio of invertebrates to fish increased and Kempton's Q decreased, indicating a less diverse system that loses relative fish biomass. The total catch decreased, particularly when assuming an ecosystem further from its carrying capacity ( $v_7$ ). While the small changes in *Scenario I* were consistent among the different vulnerability settings, in *Scenario II*,  $v_1$  and  $v_7$  differed from the others. Assuming a system close to its carrying capacity induced very little changes in the ecological indicators and was the only setting that predicted an increase in total catches. A system further from its carrying capacity, on the other hand, experienced strong reductions in the total catches and a strong decline in the system's diversity.



**Figure 4.** Relative biomass changes of selected fisheries target groups for each fishing effort scenario and vulnerability setting (50-year simulation period). The red dashed line indicates the threshold of a decrease of 30%.



**Figure 5.** Relative profit changes for the different fishing gears and vulnerability settings (50-year simulation period). Dashed lines mark increases above 30% (blue) and below 30% (red).



**Figure 6.** Changes in selected system indicators for the different vulnerability settings (50-year simulation period).

### Comparison of simulated biomass changes with fishers' perception

Generally, fishers (with a fishing experience  $\geq 15$  years) perceived that catches for all groups were higher (i.e.  $>10\%$ , Figure 7), when they had started fishing.

The only vulnerability setting that was able to reproduce this perception for most groups was  $v_{Fmax}$  (64%). The  $v_{B0}$ ,  $v_{default}$ , and  $v_{TL}$  settings predicted higher past biomasses only for 36–45% of the groups. The  $v_1$  setting predicted an increase above 10% in biomass for none of the groups and thus generally failed to reproduce the fishers experience (Figure 7). Simulations under  $v_7$  also predicted an increase only for 27% of the groups. For *Crabs and lobsters*, *L. fulviflamma*, *L. lentjan*, *Other herbivorous fish*, and *S. gobban*,  $v_7$  even predicted a biomass reduction below 30%.

The groups for which the trend was not well predicted were most of the monospecies groups and *Crabs and lobsters*.  $v_{Fmax}$  improved the biomass trends of *L. lentjan* and *S. gobban*, which had much higher vulnerabilities under this setting. But even a model with  $v_{Fmax}$  failed to predict the perceived higher biomasses in the past for *L. borbonicus*, *L. fulviflamma*, and *S. sutor*.  $v_{Fmax}$  and  $v_{TL}$  were the only vulnerability settings that simulated biomass ratios (for *S. gobban* and *Squids*) within the range of change reported by the fisher (between the 25 and 75% quantiles).

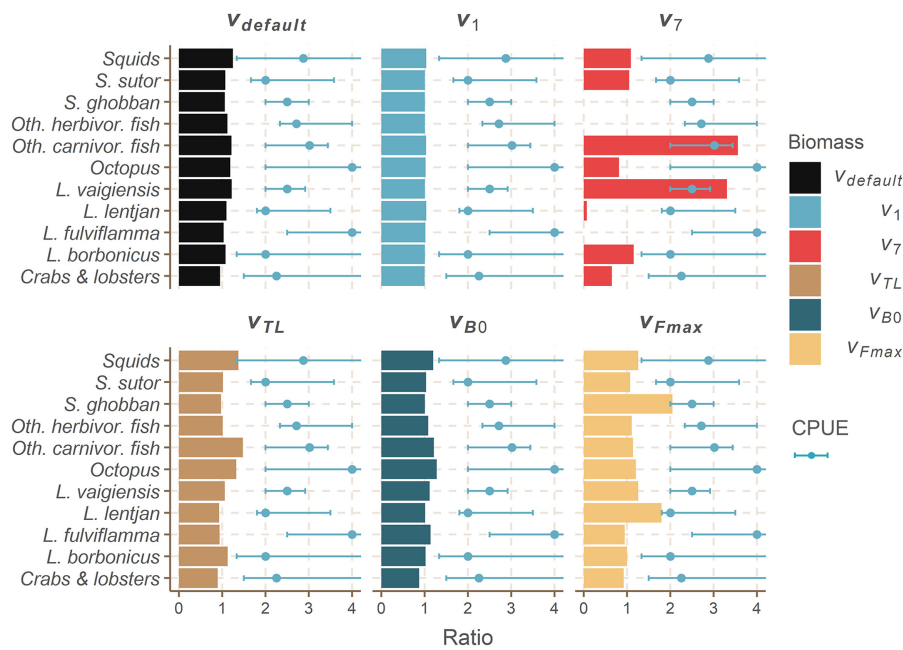
### Discussion

#### The prohibition of dragnets

Despite being prohibited in several coastal areas (Jiddawi and Ohman, 2002; Signa *et al.*, 2008; Tietze *et al.*, 2011; Samoilys *et al.*, 2019), destructive seine nets (e.g. beach seines, dragnets) are used throughout the western Indian Ocean. Current regulations and previous gear exchange programmes in Chwaka Bay have also been futile in banning illegal dragnets (de la Torre-Castro and Rönnbäck, 2004; Gustavsson *et al.*, 2014; Wallner-Hahn *et al.*, 2016). We investigated the consequences of a successful dragnet prohibition in Chwaka Bay using a trophic model and found a prohibition to benefit the ecosystem and the fishers' profits, but not if dragnet fishers continued fishing in the bay by reallocating to the other gears.

In our simulations, a successful prohibition of dragnets without reallocation (*Scenario I*) slightly increased the systems' diversity, and strongly increased the relative fish biomass and the biomass of most target functional groups. Some functional groups decreased in biomass, but only *Zooplanktivorous fish* decreased below 30% (not accounting for a system further from its carrying capacity,  $v_7$ ). These benefits are also reflected in the strong increase in fishers' profits. This is not surprising as dragnets and beach seines compete with other gears for the same species and often size classes (McClanahan and Mangi, 2001; Rehren *et al.*, 2018a). In certain





**Figure 7.** Relative change in biomass (2114/2014) of selected target groups in the Chwaka Bay EwE model for each vulnerability setting after simulating the reconstructed effort trend (bar charts). Points represent the median perception of interviewed fisher ( $\geq 15$  years' experience) of the relative change in CPUE (historical/current) and lines show the range of the 25 and 75% quantiles in their response.

areas of the south coast of Kenya, where beach seines have been successfully banned (McClanahan *et al.*, 2008), similar effects on the fisheries have been observed: CPUE (McClanahan and Mangi, 2001; McClanahan *et al.*, 2008; McClanahan and Abunge, 2014), total catch (McClanahan *et al.*, 2008), and fishers' profits (McClanahan, 2010; McClanahan and Abunge, 2014) were generally higher in areas with active enforcement. These areas also showed higher diversity, fish/invertebrate ratio, and mean trophic level of fisheries catches (McClanahan and Hicks, 2011). *Octopus*, in contrast, which was predicted to decrease by our model, has shown increases in catches after beach seine prohibitions (McClanahan, 2010).

Impacts of a dragnet prohibition on the ecosystem indicators and fishers' profits were relatively consistent among the vulnerability settings. Biomass changes of functional groups varied strongly due to the often extreme biomass decreases predicted under a system further from its carrying capacity ( $v_7$ ). Such trajectories, however, contrast with observations from actual beach seine prohibitions in Kenya where no such drastic changes of important target groups were reported (McClanahan and Abunge, 2014). Even so, a system further from its carrying capacity ( $v_7$ ) generally benefitted from the dragnet prohibition and all other vulnerability settings predicted relatively similar increases in biomass.

A dragnet prohibition without reallocation (*Scenario I*) reflects a strong effort reduction (Rehren *et al.*, 2018a). Enforcing such management action is challenging, given the lack of alternative employment opportunities. Seaweed farming and tourism have been proposed but seem to represent insufficient solutions (Eklöf *et al.*, 2012; Gustavsson *et al.*, 2014). Furthermore, many fishers are directly dependent on fish as a source of protein (Jiddawi and Lindström, 2012). Indeed, our simulated reduction in effort reduced the total fish catch by 20%. The management of the dragnet fishery in Chwaka Bay, thus, needs to assure that actions are not jeopardizing food security and employment of fishers.

Given these realities, gear exchange programmes can help to reduce the use of destructive fishing techniques, while ensuring the continuation of fishing as a livelihood. In East Africa, several gear diversification programmes have been conducted (Maina and Samoilys, 2011). On Zanzibar, including Chwaka Bay (Wallner-Hahn *et al.*, 2016), fishers generally support such programmes and managers, and scientists even perceive a need for them (Wallner-Hahn and de la Torre-Castro, 2018).

Our simulations, however, show that a complete reallocation of dragnet fishers (*Scenario II*) might severely impact the entire ecosystem, as it loses fish biomass, fish catches, and diversity. Accordingly, the biomass of most functional groups decreases, with several species falling below 70% of their original biomass. The effect is particularly strong for the key target species of trap and handline fishers because their effort is already high, and a reallocation intensifies the pressure they exert. It should be noted though that in our model dragnet fishing effects on seagrass or corals are not considered, though a major reason for its prohibition is the physical damage it causes on essential fish habitats due to the dragging technique (Mangi and Roberts, 2006; Mangi and Roberts, 2007; Wallner-Hahn and de la Torre-Castro, 2018).

The biomass changes of functional groups varied strongly between a system close to its carrying capacity ( $v_1$ ) and a system further from its carrying capacity ( $v_7$ ). While the latter predicted strong biomass changes below 30% for most of the selected functional groups, a system close to its carrying capacity ( $v_1$ ) predicted only little change. But even under  $v_1$ , a reallocation affected most functional groups negatively. The decline in biomass of the functional groups lowered the profits of most fishers by  $>30\%$  and this result was generally consistent among the vulnerability settings.

Our model results are based on rather simplistic assumptions and, thus, need to be viewed in the context of fisher's traditions and socio-economic realities. For example, Chwaka Bay dragnet fishers are less likely to switch to the more tra-

ditional traps but prefer other net fishing activities (Wallner-Hahn *et al.*, 2016). It must also be noted that the objective of the previous gear exchange programme in the bay was to re-allocate fishing effort further offshore to target pelagics such as tuna (Lindström and de la Torre-Castro, 2017).

It is difficult to evaluate our results with gear diversification efforts in the region because monitoring has been poor (Wells *et al.*, 2010; Maina and Samoilys, 2011). A gear exchange programme in 1999 conducted within the Tanga Coastal Zone Conservation and Development Programme (TCZCDP, Tanzania) led to a 1.7-fold increase in traps in 2001 compared to the year before implementation (Wells *et al.*, 2007). The strong effort increase was accompanied by a 50% decline in catch per unit of effort of traps, with a similar decline in the main target species *S. sutor* (Wells *et al.*, 2007). Just what our model predicted—albeit under a much lower effort reallocation. However, it is not clear to what extent beach seine fishing has stopped in Tanga after the implementation of the programme.

Nevertheless, our simulations indicate a high fishing pressure from the legal gears in Chwaka Bay; and further increases through gear diversification programmes without spatially expanding the fishery might have unforeseen consequences. To reallocate all dragnet fishers, we had to increase the effort of the other gears by 2–3-fold, highlighting the large number of jobs tied to the fishery and their role as a food provider for coastal fishing communities (Tietze *et al.*, 2011). Dragnet boats are usually owned by a captain who hires several fishers to pull the net over the seafloor and drive fish into it. The hired fishers do not need financial means or fishing experience, which is exactly what drives them into the fishery, particularly when livelihood opportunities are limited (Signa *et al.*, 2008; Wallner-Hahn *et al.*, 2016).

Given the job provision of beach seines fisheries to coastal communities, fisheries managers must balance the needs of the fishing community and the ecosystem health. In the case of Chwaka Bay, gear exchange programmes seem promising given the considerable support from all stakeholders (Wallner-Hahn *et al.*, 2016; Wallner-Hahn and de la Torre-Castro, 2018). But knowing that the fishing intensity on target species of many gears is already high, managers need to concentrate on the diversification of livelihoods and poverty alleviation strategies (Tietze *et al.*, 2011; Batista *et al.*, 2014). Finally, future gear exchange programmes in Chwaka Bay must entail comprehensive monitoring of fish biomass, catch, and effort to anticipate unforeseen consequences.

### Estimating predator–prey interactions

While EwE allows for an exploration of the consequences of different management strategies, its use for data-poor fisheries is often limited by the lack of time-series data to understand the predator–prey interactions (vulnerabilities) in the system. We investigated how much qualitative scenario outcomes depended on the vulnerability settings. In our model, the overall trend (decreasing or increasing) in the changes of functional groups, ecosystem indicators, and profits under two different fishing effort scenarios were relatively consistent across vulnerability settings.

The only exception was the response of *Pelagic fish* under a scenario of fishing effort reallocation. It increased using some vulnerability settings but decreased using others. These diverging trajectories affected the profits of floatnet and fence

fishers, whose main target functional group is *Pelagic fish*, adding uncertainty about potential consequences of a reallocation of dragnet fishers.

The magnitude of change in the biomass of several functional groups also differed strongly between the vulnerability settings. As previous studies reported, the changes predicted under a system close to its carrying capacity ( $v_1$ ) were extremely low (Ainsworth and Walters, 2015; Natugonza *et al.*, 2020), indicating that neither management intervention would lead to significant effects on the system. On the contrary, under a system further from its carrying capacity ( $v_7$ ), several groups decreased in biomass below 30% in both scenarios, resulting in strong decreases in profits under a reallocation of dragnet fishers. These strong declines, but also the absence of change are somehow contrary to reports on the effects of successful beach seine prohibitions at the south coast of Kenya (McClanahan, 2010; McClanahan and Abunge, 2014), which demonstrated positive effects on the catch and profits but did not report strong adverse effects. Moreover, both vulnerability settings generally failed to simulate higher past biomasses as perceived by Chwaka Bay fishers. Therefore, they seem to misrepresent the predator–prey interactions and might have led to unrealistic model behaviour.

The other four vulnerability settings predicted similar changes in profits and ecosystem indicators but also in the biomass of many functional groups. Few exceptions were observed, which added to the uncertainty about qualitative results. For example, the biomass of *L. fulviflamma* exploded (>100% increase), when reallocating dragnet fishers (*Scenario II*) and setting the vulnerabilities proportional to trophic level ( $v_{TL}$ ), or the ratio of the predator's current biomass and its unfished biomass ( $v_{B0}$ ). Likewise, the biomass changes of the emperor species *L. lentjan* varied from little change (<10%) to a strong increase (>70%), when banning dragnets without reallocation (*Scenario I*). This is due to its very high vulnerability values set under  $v_{Fmax}$ . In a participatory workshop in 2016, Chwaka Bay fishers generally agreed with the results of the stock assessment that fishing mortalities of *L. lentjan* are exceeding reference points (Rehren, 2017; Rehren *et al.*, 2018a). Using the ratio of the predator's maximum fishing mortality and natural mortality ( $v_{Fmax}$ ) also improved the predictions of the perceived past biomass values, suggesting that *L. lentjan* is indeed relatively further from its carrying capacity and may increase strongly after potential enforcement of the dragnet prohibition.

Our relatively low uncertainty in qualitative model results is an important finding because previous studies found qualitative results to be very sensitive to vulnerability estimates causing conflicting management recommendations (Mackinson, 2014; Natugonza *et al.*, 2020). It should be noted, though, that the range in vulnerability estimates under the different parameterizations in our study was relatively narrow. Furthermore, information on the ratio of the predator's maximum fishing mortality and natural mortality ( $v_{Fmax}$ ) as well as the ratio of predator's current biomass and its unfished biomass ( $v_{B0}$ ) was only available for some functional groups, resulting in the use of the default value for many others. This contrasts with time-series fitting exercises, where vulnerabilities can vary by orders of magnitude.

A model with the default vulnerabilities did not predict the perceived past biomass trends (increase >10%) for six of the eleven groups analysed, this included all monospecies functional groups except *L. vaigiensis*. Using the trophic level

of the functional groups ( $v_{TL}$ ) performed worse in predicting perceived past biomass trends, because of the additional lack of predicted increase in *Other herbivorous fish*. Contrastingly, Ayers (2013) found that in their model of the Thukela Bank (South Africa), scaling the vulnerabilities to trophic level reproduced expected biomass trends and was considered an adequate approach.

From the two approaches that were informed by external data ( $v_{Fmax}$  and  $v_{B0}$ ), only setting the vulnerabilities proportional to the ratio of the predator's maximum fishing mortality and natural mortality ( $v_{Fmax}$ ) performed slightly better than the default vulnerabilities in predicting perceived past biomass trends. This was due to a better prediction of the biomass of *L. lentjan* and *S. ghobban*, but a model with  $v_{Fmax}$  vulnerabilities still got the trend of *S. sutor*, *L. fulviflamma*, and *L. borbonicus* wrong. The estimates of  $F_{max}$  used here were obtained from length-based assessments (Rehren *et al.*, 2018b), which are often biased due to underlying length compositions that do not fully reflect the entire stock (Chrysafi and Kuparinen, 2015). As a result, our  $v_{Fmax}$ -values may over- or underestimate the true predator–prey interactions in the system. Similarly, estimating the predator–prey interactions from fishers' perception in CPUE changes is biased due to several reasons (Maunder *et al.*, 2006). Most importantly, due to changes in the catchability, which may stem, for example, from increases in fishers' knowledge about the target resource and advanced fishing equipment. As a result, this approach likely underestimates the vulnerabilities. However, even if reference points and CPUE of fishers are biased, they are more informative than using the trophic-level approach or assuming that the entire system is far or close to its carrying capacity. The inability of a model with vulnerabilities set proportional to the ratio of predator's current biomass and its unfished biomass ( $v_{B0}$ ) to outperform the default vulnerabilities is somewhat surprising because we used the perception of the fishers to estimate the current and unfished biomass as well as to evaluate the model performance. A possible explanation might be that our reconstructed effort scenario underestimates the true effort change that has taken place in the bay, resulting in relatively low biomass changes. This may also explain the general discrepancy between the perceived strong CPUE changes and the relatively low simulated changes in biomass. It should also be noted that we are not able to accurately simulate past biomass values as we lack information about the past configuration of the system. Therefore, with the comparison of fisher's perception and our model results, we only aim to better understand the performance of the different vulnerability settings.

Interestingly, estimating vulnerabilities from the trophic level of functional groups has been the most commonly used approach when time-series data are lacking (e.g. Chen *et al.*, 2008; Ayers, 2013; Ainsworth and Walters, 2015; Bacalso *et al.*, 2016; Kluger *et al.*, 2016). We only found one study that used  $F_{max}/M$  information to set initial vulnerability estimates (Mackinson, 2014) and no study that used local ecological knowledge. Given the accessibility of local ecological knowledge and its slightly better past biomass estimations, it should ideally be used as complementary information, when informing the predator–prey interactions in data-poor case studies.

Overall, the relatively consistent general trends, especially in the profits and ecosystem indicators, across the different vulnerability settings, illustrates that an unfitted EwE model can be informative enough to explore qualitative scenario outcomes. However, given the narrow ranges of vulnerabilities

used in our study, it would be interesting to see how qualitative model results vary under vulnerabilities informed by stock assessment and local ecological knowledge in other case studies.

## Conclusion

The enforcement of the dragnet prohibition in Chwaka Bay generally led to higher diversity, higher fish biomass, and higher profits for fishers regardless of the vulnerability setting. Simulations of a dragnet effort reallocation suggest that the fishing pressure exerted from traditional gears (e.g. traps and handlines) on some of the functional groups is already so high that further increases (through effort reallocation) might lead to strong negative consequences for the ecosystem and fishers' profits. Thus, gear exchange programmes should carefully monitor target groups to avoid unforeseen adverse effects and the management of Chwaka Bay's fisheries should direct efforts towards the provision of alternative livelihoods and poverty alleviation strategies.

The change in ecosystem indicators and the profits of the different gears were relatively consistent under the different vulnerability settings representing more robust performance indicators.

Informing the vulnerability settings via stock assessment outputs, as we have done (i.e. length-based relative yield per recruit analysis,  $v_{Fmax}$ ), led to improved predator–prey interactions for some of the functional groups.

The consistent overall trends in indicators, the biomass of functional groups, and fisheries profits illustrate that the exploration of management strategies with EwE can be informative even if time-series information is lacking and predator–prey interactions are uncertain.

Under best practice, users should either apply different information sources (e.g. local ecological knowledge or stock assessment) for the parameterization of the vulnerabilities or use a system close to its carrying capacity and further from its carrying capacity as bracket scenarios to understand to what extent the qualitative scenario outcomes are sensitive to the predator–prey interactions.

## Author contributions

All authors conceived and designed the research. NJ, OO, and JR collected the data. JR performed the analysis. All authors contributed to the article and approved the submitted version.

## Supplementary data

**Supplementary material** is available at the *ICESJMS* online version of the manuscript.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Data availability statement

The questionnaire data are available at <https://github.com/Jrehren/ICES-2021-Rehren-Evaluating-impacts-of-fishing-gear-regulations>. The other data underlying this article will be shared on reasonable request to the corresponding author.

## Funding

This project was funded by the German Research Foundation (DFG) within a research fellowship programme (RE 4358/1–1). The data used in the analysis were collected in 2014 within a PhD programme (SUTAS) funded by the Leibniz Gemeinschaft. The questionnaires on fishers' perception of historical fisheries catches were conducted within the National Geographical Society Early Career Grant, #EC-67901C-20. MC acknowledges funding support by the European Union's Horizon 2020 research and innovation programme under grant agreement No 869300 (FutureMares). VC acknowledges support from the Natural Sciences and Engineering Research Council of Canada (NSERC), Discovery Grant RGPIN-2019–04901. This work acknowledges the “Severo Ochoa Centre of Excellence” accreditation (CEX2019-000928-S) to the Institute of Marine Science (ICM-CSIC).

## Acknowledgements

We acknowledge the support of Nuru Salum from Mwambao Coastal Community Network and Hamadi Khatib a retired Senior Statistics Fisheries Officer with the interviews related to fishers' perception. We further thank the beach village assistants and fishers from Chwaka Bay, Zanzibar, for their collaboration and support with this research.

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Handling Editor: Morgane Travers-Trolet