

## Research



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# Assessing impacts of bycatch policies and fishers' heterogeneous information on food webs and fishery sustainability

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Ecosystem-based fisheries management (EBFM) has emerged as a promising framework for understanding and managing the long-term interactions between fisheries and the larger marine ecosystems in which they are nested. However, successful implementation of EBFM has been elusive because we still lack a comprehensive understanding of the network of interacting species in marine ecosystems (the food web) and the dynamic relationship between the food web and the humans who harvest those ecosystems. Here, we advance such understanding by developing a network framework that integrates the complexity of food webs with the economic dynamics of different management policies. Specifically, we generate hundreds of different food web models with 20–30 species, each harvested by five different fishers extracting the biomass of a target and a bycatch species, subject to two different management scenarios and exhibiting different information in terms of avoiding bycatch when harvesting the target species. We assess the different ecological and economic consequences of these policy alternatives as species extinctions and profit from sustaining the fishery. We present the results of different policies relative to a benchmark open access scenario where there are no management policies in place. The framework of our network model would allow policymakers to evaluate different management approaches without compromising on the ecological complexities of a fishery.

This article is part of the theme issue 'Connected interactions: enriching food web research by spatial and social interactions'.

## 1. Introduction

Fisheries across the world remain as vital as ever as they serve food, economy and livelihood to communities, locally and globally [1–3]. Fish and fish products are some of the most traded goods in the world [4–8]. Continual pursuit of profits that come from selling fishing products has led to fishing practices that threaten marine biodiversity, fishers' safety and food security [9–12]. Current fishery management practices have had partial successes in rebuilding fish stocks in collapsed fisheries and in maintaining the long-term sustainability of fisheries [13–16]. However, effective fishery management can be hindered by a host of factors, including failure to incorporate scientific knowledge [17], lack of compliance with fishery regulation [18], lack of ecological, catch or stock assessment data [19] and failure to account fully for ecosystem interactions [20,21]. In this paper, we focus on the last factor: that is, incorporating into management an understanding of the dynamic interaction of species throughout the marine food web, including impacts from human harvest.

Considering the food web to which the harvested species belong is a core element of ecosystem-based fisheries management (EBFM), which has

emerged over the past two decades as a promising complement to stock-centric, single-species management [9,15,22–24]. EBFM recognizes that effective management should not only focus on individual commercial species but also consider the broader ecosystem context, and seek a balance between ecological resilience and economic viability [9,25–27]. EBFM focuses, for example, on reducing excessive levels of bycatch associated with fishing [28–30], as these commercially unwanted species play a significant role in ecosystem functioning [9,27]. However, implementing EBFM is challenging because it not only requires knowledge of the dynamics of the commercial species but also that of the network of interactions between the commercial species and the other species in the ecosystem [22,31]. This ecological network determines how species affect each other and, therefore, how each species is affected directly or indirectly (e.g. via changes in the abundance of its prey or predators) by fisheries [32–38]. Likewise, the ecological network may determine that a fish stock declines despite a policy prohibiting its harvest if the fishery, for example, is extracting its prey. The challenge lies in understanding these complex dynamics and predicting how various changes, such as policy interventions, might impact ecological and economic outputs. While regulators in the United States and elsewhere are being pressed to incorporate EBFM, given the complexity of its implementation, development and application of this framework are still ‘evolutionary rather than revolutionary’ [23].

While traditional single-species models have moderate success in reducing overfishing of commercially important target species and incidental catch of endangered species, they fall short in capturing the complex dynamics that emerge from the ecological network [32,34,39]. To address this, we turn to ecological network theory (e.g. [33,35,36]). Ecological networks allow us to model species as nodes and their interactions as links, as well as, model the population dynamics of every species in the network using ordinary differential equations, which are affected by its interactions with other species in the network. Specifically, we use the well-known and widely used Allometric Trophic Network (ATN) framework [11,33,35,36,38,40–42] to model the dynamics of marine food webs, which is an extension of the bioenergetic model by Yodzis & Innes [43] to multi-species systems. Allometric scaling in this framework provides a biologically informed way to parameterize trophic interactions and ecological processes based on metabolic theory and life history traits (e.g. trophic level and vertebrate/invertebrate) [43]. Therefore, this framework is very useful for developing a general understanding of food web dynamics and how they generally respond to anthropogenic changes including disturbance caused by fisheries (e.g. [11,35,36,38]). This general understanding of food web dynamics differs from the more system-specific understanding produced by approaches like Ecopath with Ecosim, for which system-specific parameters need to be determined extensively (e.g. [44,45]).

Here, we seek to advance the theoretical framework of EBFM by introducing three bioeconomic factors that have not been considered in ecological networks before. These factors are (i) unintentional bycatch, defined as species caught incidentally during fishing operations, (ii) heterogeneity in fishing success (based on their access to information) among individual fishers, measured in their ability to catch commercially important target species and avoid unwanted bycatch species, and (iii) different fishery management policies to achieve long-term ecological and economic sustainability of the fishery. This approach allows us to investigate the complex interplay between the species in the ecological network, their interaction with heterogeneous fishers, and intervention by management policies to attain long-term sustainability. We achieve this by incorporating fishers with different levels of fishing success as additional nodes into the ecological network, connected exclusively to target and bycatch species and simulating different fishery policies that close the fishing season for the year when the target quota and/or the bycatch quota are met. Indeed, our model advances from previous ecological network models (e.g. [35]) by successfully replicating average active fishing seasons, which typically range from a few weeks to a few months of a year [46–48].

The three bioeconomic factors we introduced in our network model are well-studied in the bioeconomic literature but only for a handful of species in that ecosystem [49–52]. Thus, our work contributes to the bioeconomic literature by considering the entire ecological network to which the target and bycatch species belong. We focus on management policies that play a crucial role in shaping the dynamics of fisheries but whose consequences can be far-reaching and sometimes unexpected because of the complex dynamics caused by the ecological network [21,53,54]. Specifically, we evaluate the effects of various management policies on both ecological and economic aspects and investigate trade-offs between conserving species, sustaining yields and promoting economic stability. Finally, we present new insights into the potential for sustainable fishing practices without compromising substantial economic profits and the employment that fisheries provide.

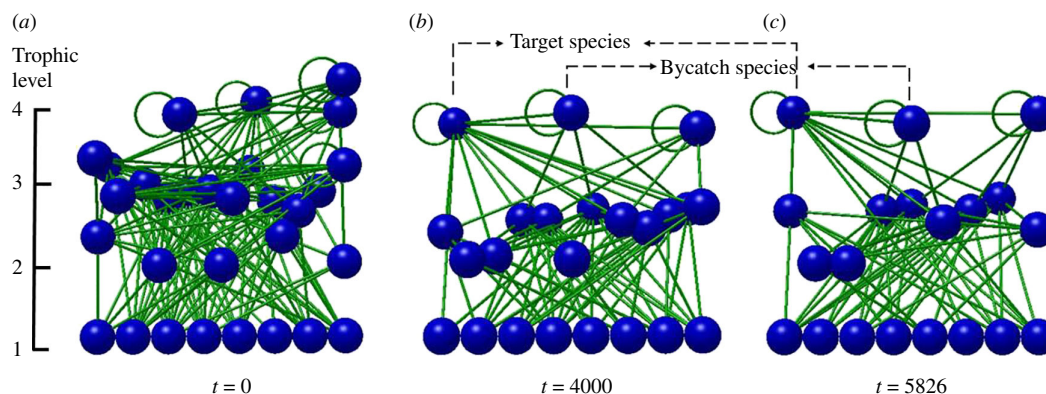
## 2. Methods

### (a) Experimental setup and policy implementation

We first generated trophic networks (food webs) using the niche model [55] (see §2b). Food webs generated using the niche model replicate observed empirical patterns (particularly in aquatic ecosystems) in features like the distribution of trophic species across different trophic levels and mean trophic chain length, among others [55]. Each species in the food web was then assigned an initial biomass using a uniform distribution,  $U\epsilon(0,1)$ . Subsequently, the ATN framework (detailed in §2c) characterized by equations (2.1) and (2.2) was applied to simulate each food web across a sequence of 4000 time steps without any fishing, as shown in figure 1. This preliminary period without fishing serves to dampen the potential impact of transient dynamics on the subsequent outcomes of fishery treatments.

Following this initial fishing-free interval, fishing is introduced only in those food webs that meet the following criteria: (i) they are connected (i.e. no isolated components), (ii) all consumers are linked to at least one basal species (primary producers) through trophic interactions, (iii) they have at least 20 species, and (iv) have at least one fish species. This treatment led to 400 distinct food webs, which were subjected to an additional 1825 time steps, equivalent to 5 years.

At the start of fishing, a target species and a bycatch species were selected among consumer species with trophic levels equal to or above 2 (to avoid choosing a producer species), as shown in figure 1. The target species was selected randomly at the end



**Figure 1.** An example of the temporal change of a food web network from (a) initialization, to (b) the start of fishing, to (c) after 5 years of fishing. Trophic species are represented by nodes, trophic interactions (who eats whom) as links, and the vertical axis represents the trophic level of species. The (a) initial network is generated using the niche model [55]. The ATN model is then run for 4000 daily time steps with the biomass of each species changing over time according to equations (2.1) and (2.2) (refer §2). Subsequently, a target species and bycatch species are selected, and fishing occurs for an additional 5 years (1826 time steps).

of the fishing-free interval (i.e.  $t = 4000$ ). Bycatch was either selected randomly or as the consumer species which had the lowest biomass at the end of the fishing-free interval (henceforth referred to as vulnerable bycatch species). Each day, the biomass of species changes based on equations (2.1) and (2.2), after which two conditions are evaluated: (i) Is the fishery (given current target species biomass levels) profitable for at least one fisher? (ii) Do the biomasses of species trigger constraints given by the policy (detailed in §2d), if any, in place? Once either of the two conditions fails, the fishery is shut down (all fishers' efforts are set to 0) for the remainder of the year. In the following year, if the biomasses of the species meet the two conditions, the fishery is open and the cycle continues. The annual dynamics mimic annual fishery closures that are features of real-world fisheries for the biomass of target species to recover [56,57]. An example of a time series from our model is shown in figure 2.

The dynamics of the food webs were run for each policy scenario, for all target–bycatch combinations possible in each food web. We calculated ecological (see figure 3) and economic (see figure 4) metrics as averages over all possible target–bycatch combinations and over all networks. All simulations were run in MATLAB 2021a [58] using the solver ode45 for numerical integration, with relative and absolute error tolerances both equal to  $10^{-8}$ .

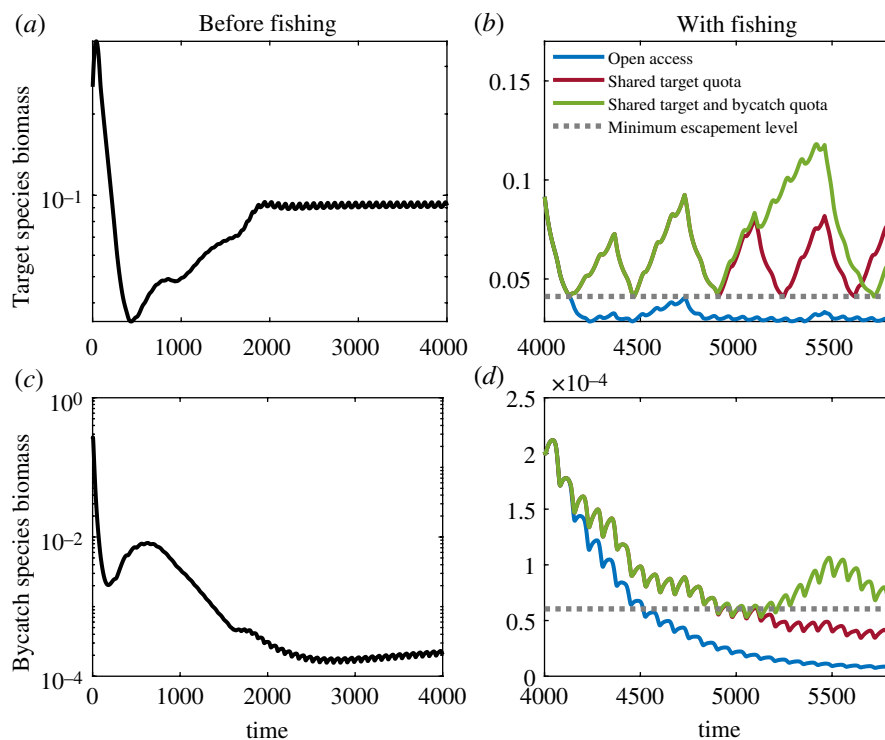
## (b) Network/food web structure

The network structure outlines the connections between fishers, prey and predators. Initially, each niche-model-generated food web consisted of 30 trophic species, where trophic species ( $S$ ) represent groups of individuals sharing the same resources (i.e. prey species or primary producers such as algae or phytoplankton) and consumers (i.e. predator or herbivore species consuming producers). These webs had connectance of 0.125–0.175, where connectance ( $C$ ) indicates the proportion of realized trophic links ( $L/S^2$ ), with  $L$  representing realized links. Each of the 30 trophic species is assigned a niche value along a single trait axis (interpreted here as body size, see §2c). Species  $i$  preys on species  $j$  if  $j$ 's niche value falls within  $i$ 's feeding range, allowing for potential consumption of species with higher niche values, which accounts for cannibalism. The feeding range of the lowest niche species is set at 0, which prescribes that at least one primary producer be present. Niche values for the 30 trophic species are assigned iteratively, ensuring three criteria are met: (i) there is network connectivity (i.e. there are no isolated nodes/components); (ii) linking each consumer species is linked to a primary producer via a trophic chain; (iii) connectance is achieved within the predetermined range of 0.125–0.175. Fish species are identified among consumer species using a Bernoulli trial ( $p = 0.6$ ), while the remaining species are treated as invertebrates.

## (c) Ecological and economic dynamics

The biomass dynamics of each trophic species within a generated food web is determined by an ordinary differential equation with parameters scaled allometrically by the ATN model. The ATN model has enriched our understanding of food web dynamics by offering flexible approaches to model the biomass dynamics of dozens to hundreds of interacting species while retaining tractability [11,33,35,36,38,40,41]. This model describes the rate of biomass change ( $dB_i/dt$ ) of species  $i$  depending on whether the trophic species is a primary producer equation (2.1) or a consumer equation (2.2) as follows:

$$\begin{aligned} \text{Rate of change in} \\ \text{producer biomass} \quad \frac{dB_i}{dt} &= r_i \left( 1 - \frac{\sum_k \epsilon_{\text{producers}} B_k}{K} \right) B_i - \sum_{j \in \text{predators}} x_j \frac{y_j}{e_{ji}} F_{ji} B_j, \end{aligned} \quad (2.1)$$



**Figure 2.** An example of a simulated time series from a single food web. Before fishing, the biomass of (a) the target species and (c) bycatch species can vary widely before eventually stabilizing (hence the vertical axes are shown in  $\log_{10}$  scale). Fishing begins under various policies (see key), with effects on the (b) target species and (d) bycatch species biomass. For policies with a target species quota (allowing fishing down to the minimum escapement level), harvesting periods are evident from declining target species biomass and non-harvesting periods from increasing target biomass. In open access, biomass for both species declines with harvest, which occurs whenever fishing is profitable.

$$\begin{aligned} \text{Rate of change in} \\ \text{consumer biomass} \end{aligned} \quad \frac{dB_i}{dt} = \underbrace{f_a \sum_{j \in \text{prey}} x_i y_j F_{ij} B_j}_{\text{Gains by consumption}} - \underbrace{f_m x_i B_i}_{\text{Maintenance loss}} - \underbrace{\sum_{j \in \text{predators}} x_j \frac{y_j}{e_{ji}} F_{ji} B_j}_{\text{Loss by predation}} - \underbrace{\frac{H(B_i) E_{ki}}{H(B_i) E_{ki}}}_{\text{Harvest loss}}. \quad (2.2)$$

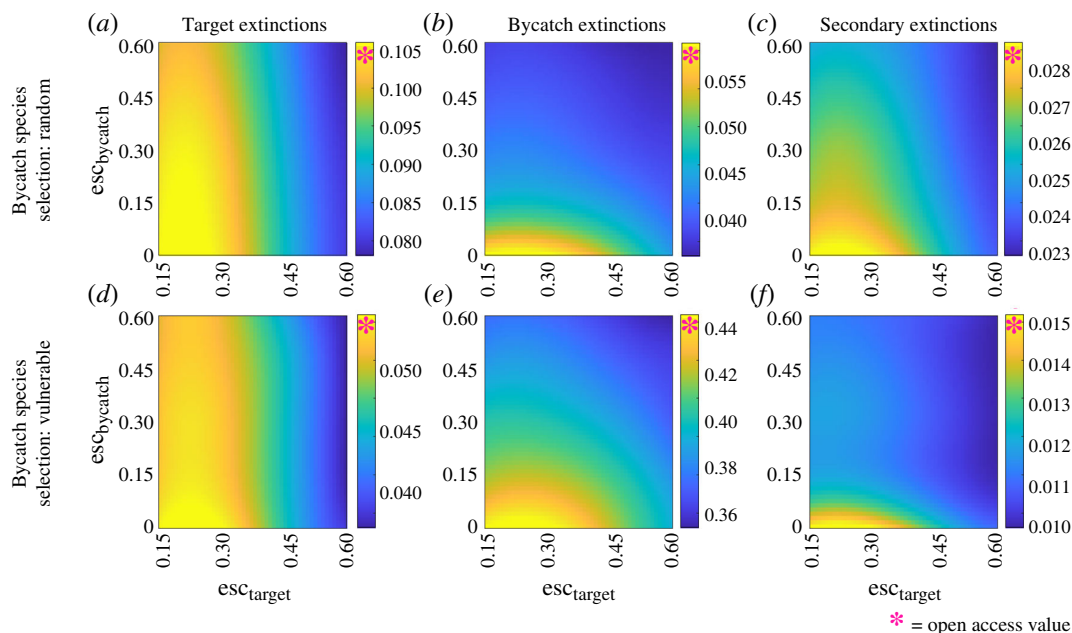
Time-varying variables and constants are indicated by upper- and lower-case fonts, respectively (values and definitions provided in table 1). For variables with two indices (e.g.  $e$  and  $F$ ), the first index represents a consumer species (predator or herbivore) and the second represents its resource species (its prey or primary producer).  $r_i$  is the growth rate of producer species  $i$ . Fractions  $f_a$  and  $f_m$  signify the assimilated carbon used in production and maintenance respiration, respectively, which allows for realistic biomass transfers across trophic levels [62].  $x_i$  is the metabolic rate (rate at which an organism expends energy in physiological processes), defined by  $x_i = a_x/a_r(Z^{T_i-1})^{-0.25}$ , where  $a_x$  is the allometric constant that relates the metabolic rates of consumers to their body size,  $a_r$  is the allometric constant that relates the reproductive rates of producers to their body size,  $Z$  is the body size ratio and  $T_i$  is the trophic level [43,63,64].  $y_i$  represents the maximum consumption rate of species  $i$ , and  $e_{ji}$  represents the efficiency of converting biomass of species  $i$  when consumed by species  $j$  into its biomass.

Dividing 'loss by herbivory (or predation)' by  $e_{ji}$  transforms the biomass assimilated by consumer  $j$  into biomass lost of its resource  $i$  (see [43]).  $F_{ij}$  is the consumer  $i$ 's functional response on  $j$  (i.e. *per capita* consumption rate). Following all prior studies using the ATN framework (e.g. [11,33,35,36,40,41]), we used what it has been called a 'type II.2' (or weak Holling-type III) functional response [65], which has a stabilizing effect on food web dynamics [65,66] and it is supported by general empirical understanding of consumer–resource interactions because this response can capture some of the well-known consumer preference for more abundant resources. This functional response is given by:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_{0,j}^h + \sum_{k \in \text{prey}} \omega_{ik} B_k^h}, \quad (2.3)$$

$B_{0,j}^h$  is  $i$ 's half-saturation biomass for its resource  $j$ .  $\omega_{ij}$  is  $i$ 's preference for its resource  $j$ , calculated as the reciprocal of the total number of  $i$ 's resource species and is re-calculated as resource species become extinct.  $h$  is the hill coefficient, which sets the sensitivity of the functional response to the resource's biomass.

The timescale of the dynamics in each food web is established following Glaum *et al.* [35], where one model time step corresponds to one real-time day. This timescale results from setting the mass-specific growth rate of all producers to  $r_i = 1$ . This rate then normalizes metabolic ( $x_i$ ) and maximum consumption ( $y_i$ ) rates as in most studies using the ATN model (e.g. [11,33,35,36,40,41]). We use an extinction threshold of  $B_{\text{ext}} = 10^{-6}$ , below which we assume a species as locally extinct.



**Figure 3.** Extinction probabilities (shading) for the target (a,d), bycatch (b,e) and secondary (c,f) vary across a range of the target ( $esc_{\text{target}}$ ) and bycatch ( $esc_{\text{bycatch}}$ ) minimum escapement levels (i.e. minimum biomass allowed to escape the fishery used in policy, see §2). Extinction probabilities are calculated as the fraction of simulations resulting in their extinction after 5 years of fishing across all 400 food webs. The colour bars showing extinction rates differ by subplot, with the marker ‘asterisk’ representing the value obtained in open access. Plots were produced by running model simulations for each food web with values [0.15, 0.30, 0.45, 0.60] for each target and bycatch escapement levels (and all their combinations) and then using spline interpolation to fill the extinction values across a broader continuous range of  $esc_{\text{target}} \in [0.15, 0.60]$  and  $esc_{\text{bycatch}} \in [0, 0.6]$ .

Biomass loss owing to harvesting ( $H(B_i, E_{ki})$  in equation (2.2)) is dependent on the biomass of the harvested species  $i$  ( $B_i$ ) and the fishing effort of fisher  $k$  on species  $i$  ( $E_{ki}$ ) as follows:

$$H(B_i, E_{ki}) = \begin{cases} \sum_{k \in \text{fishers}} \gamma_k E_{ki} q_i B_i & \text{if } i \text{ is target} \\ \sum_{k \in \text{fishers}} (1 - \gamma_k) E_{ki} q_i B_i & \text{if } i \text{ is bycatch} \\ 0, & \text{otherwise} \end{cases} \quad (2.4)$$

Effort is a measure of the amount of harvesting resources used in a fishery. Depending on the specific fishery, effort can be a measure of the number of fishing lines, boats, workers or work hours dedicated to harvesting. The results presented here do not qualitatively depend on the specific details of the fishing effort. Each fisher extracts biomass of two species in each food web, one as a target and the other as a bycatch. The ability of fisher  $k$  to allocate their effort towards catching target (and simultaneously avoiding bycatch) is given by  $\gamma_k$ . Fishers differ in their ability to catch the target while simultaneously avoiding bycatch. This heterogeneity among fishers could be owing to different levels of skill or access to information on species concentration (as facilitated by information sharing among fishers). We model five fishers with  $\gamma_k \in [0.70, 0.75, 0.80, 0.85, 0.90]$ .  $q_i$  is the catchability of species  $i$ .

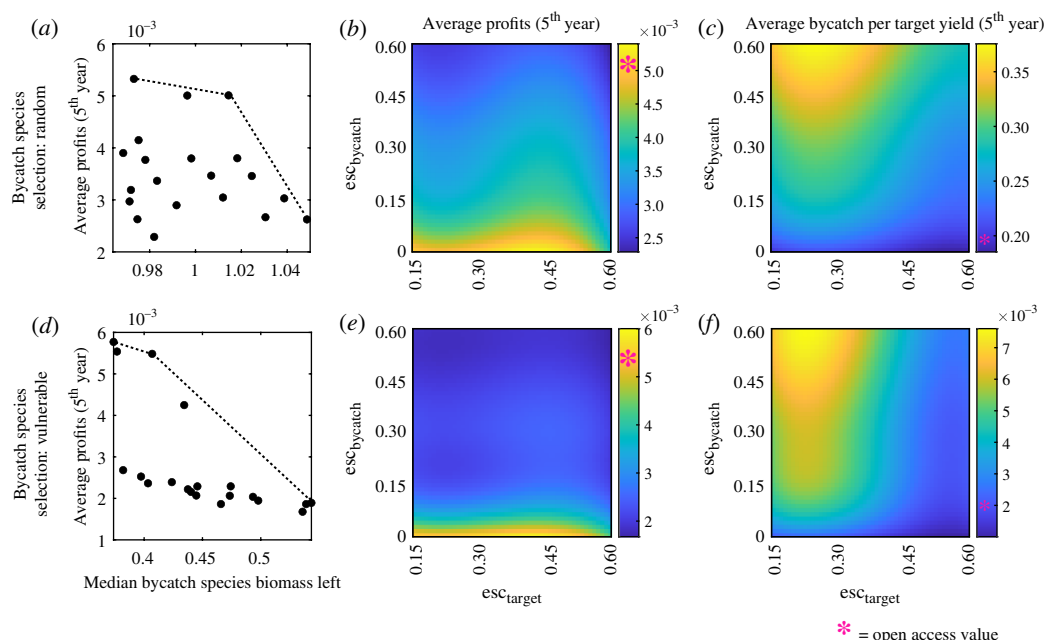
Within a fishing season, fisher  $k$  harvest the biomass of the target species  $i$  ( $B_{\text{target}}$  onwards, with  $i = \text{target}$ ) at a constant maximum effort ( $E_{\text{max}}$ ) as long as fishing is profitable. That is, as long as gross profits per unit effort ( $\gamma_k p q_{\text{target}} B_{\text{target}}$ ) are greater than marginal costs of fishing effort ( $c_0$ ), as follows:

$$E_{k\text{target}} = \begin{cases} E_{\text{max}}, & \text{if } \gamma_k p q_{\text{target}} B_{\text{target}} > c_0 \\ 0, & \text{otherwise} \end{cases} \quad (2.5)$$

Whether it is profitable for fisher  $k$  to harvest the target species ( $E_{k\text{target}} = E_{\text{max}}$ ) or not ( $E_{k\text{target}} = 0$ ) depends on their ability to catch the target species ( $\gamma_k$ ), market price ( $p$ ), catchability of target species ( $q_{\text{target}}$ ), the biomass of the target-species at that instant ( $B_{\text{target}}$ ) and the marginal costs of effort ( $c_0$ ):

$$c_0 = \psi p q_{\text{target}} B_{\text{target}}(t=0), \quad (2.6)$$

where  $\psi$  is a scaling parameter ranging between 0 and 1. Note that, instead of using a fixed value (given by  $c_0 = \psi p q_{\text{target}}$ ), we made the marginal costs of fishing dependent on the biomass of the target species before fishing starts ( $B_{\text{target}}(t=0)$ ). We chose this setup because every simulated network is unique in the biomasses of its constituent species, ranging over a few orders of magnitude. Thus, under a fixed value of marginal costs of fishing, some networks have no fishing at all because the costs are higher than the gross profits per unit of fishing effort (when the target species has low initial biomass; see equation (2.5)), whereas some networks have excess of fishing (when target species has high initial biomass). Therefore, equation (2.6) ensures that there is initial fishing in every network and allows us to compare various levels of marginal fishing costs across networks.



**Figure 4.** Economic results for two alternative scenarios of selecting the bycatch species: randomly (*a–c*) and the most vulnerable species (i.e. species with the lowest biomass, *d–f*). Average profits (*a*) and median remaining biomass of the bycatch species (*d*) were calculated across the 5 fishers and 400 food webs, with all possible target–bycatch combinations considered within each food web. Each point corresponds to a given level set for  $esc_{target}$  and  $esc_{bycatch}$ . The dashed lines trace out the frontier determining the maximum profit for a given unit of bycatch species’ biomass left (or alternatively the maximum bycatch species’ biomass achievable for a given profit). The colour bars showing extinction rates differ by subplot, with the marker ‘asterisk’ representing the value obtained in open access. All results are for the final (fifth) year of fishing to mitigate transient effects apparent in early periods when fishing is first initiated.

## (d) Policies

We incorporated two different policy scenarios and compared our findings with base reference open access, where there is no policy in place:

- Open access: Fishing occurs while the fishery is profitable and the target species is not extinct (i.e. biomass of target species is not 0).
- Shared target quota: A quota is set equal to the current biomass less a minimum escapement level ( $B_{target}^{esc}$ ) for the target species. Fishers harvest until either the quota is exhausted or the profit is negative. The minimum escapement level is the minimum number of fish that are allowed to escape the fishery and spawn to ensure their long-term sustainability and avoiding extinctions.
- Shared target and bycatch quota: In addition to the shared target quota defined above, a shared quota is similarly set for bycatch species according to a minimum escapement level ( $B_{bycatch}^{esc}$ ).

We simulate a range of target and bycatch quotas that follow from a minimum biomass escapement policy, which is specified in each new simulation as a share of the biomass at the onset of fishing:  $B_{target}^{esc} = esc_{target} \cdot B_{target}(t = \text{onset of fishing})$  and  $B_{bycatch}^{esc} = esc_{bycatch} \cdot B_{bycatch}(t = \text{onset of fishing})$ . To explore a range of policy stringencies, we consider a set of escapement shares ( $esc_{target}$ ,  $esc_{bycatch}$ ) given by the vector [0.15, 0.30, 0.45, 0.60]. Figure 2*b,d* shows an example of how different policies manifest in a given simulation, while figure 2*a,c* shows the transient dynamics in biomass of the target and bycatch species, respectively, until the steady state before fishing starts. After fishing begins, the shared target quota allows the target species to recover its biomass substantially during non-harvesting periods (i.e. when the fishery is closed; figure 2*b*) and slows down the biomass decline of the bycatch species compared with open access (figure 2*d*). Adding the shared bycatch quota allows for recovery of bycatch species whenever it falls to its minimum escapement level (figure 2*d*). Thus, as expected, having both target and bycatch quotas results in higher bycatch and target species populations in general.

## 3. Results

We first analyse the effects of different policies on mitigating ecological extinctions of target, bycatch and all other species in the food web, which we call secondary species. Figure 3 shows the average probability of those extinctions for different minimum escapement levels of target ( $esc_{target}$ ) and bycatch ( $esc_{bycatch}$ ). As the minimum escapement level for the target quota is raised above around 0.3, the probabilities of all extinctions begin to fall. Adding a bycatch policy ( $esc_{bycatch} > 0$ ) has a limited impact on target species (figure 3*a,d*), but it effectively reduces bycatch (figure 3*b,e*) and secondary (figure 3*c,f*) extinctions once the minimum escapement level of bycatch increases above around 0.10. Interestingly, the effect of high minimum escapement levels for both target and bycatch have a similar effect in reducing target and secondary extinctions is similar to that of setting a

**Table 1.** Parameter definitions, values and sources. Units are indicated for parameters, except when they are unitless.

|                              | description                                                                                      | value (units)                                          | source  |
|------------------------------|--------------------------------------------------------------------------------------------------|--------------------------------------------------------|---------|
| <b>ecological parameters</b> |                                                                                                  |                                                        |         |
| $r_i$                        | growth rate of species $i$                                                                       | $1(\text{time}^{-1})$                                  | [35]    |
| $K$                          | carrying capacity                                                                                | $1(\mu\text{gC/L})$                                    | [41]    |
| $e_{ji}$                     | assimilation efficiency of predator $j$ given that prey consumed $i$ is a carnivore or herbivore | carnivore: 0.85, herbivore: 0.45                       | [41]    |
| $a_r$                        | allometric constant relating reproductive rates of producers to their body size                  | variable                                               | [41]    |
| $a_x$                        | allometric constant relating metabolic rates of consumers to their body size                     | variable                                               | [41]    |
| $a_x/a_r$                    | allometric constant                                                                              | invertebrate: 0.314, fish: 0.88 ( $\text{time}^{-1}$ ) | [41]    |
| $y_i$                        | maximum consumption rate of species $i$ relative to its metabolic rate                           | invertebrate: 8, fish: 4                               | [41]    |
| $Z$                          | body size ratio                                                                                  | 100                                                    | [41]    |
| $B_0$                        | half-saturation biomass                                                                          | $0.2 (\mu\text{gC/L})$                                 | Assumed |
| $h$                          | hill coefficient                                                                                 | 1.2                                                    | [59]    |
| $B_{\text{ext}}$             | extinction threshold biomass (used in simulations)                                               | $10^{-6} (\mu\text{gC/L})$                             | [60]    |
| $\omega_{ij}$                | preference of species $i$ for species $j$                                                        | variable                                               |         |
| $F_{ij}$                     | functional response of predator species $i$ for prey species $j$                                 | variable                                               |         |
| $f_m$                        | factor for maintenance respiration                                                               | 0.4                                                    | Assumed |
| $f_a$                        | fraction of assimilated carbon used for production                                               | 0.4                                                    | [61]    |
| $x_i$                        | metabolic rate of species $i$                                                                    | variable ( $\text{time}^{-1}$ )                        |         |
| <b>economic parameters</b>   |                                                                                                  |                                                        |         |
| $E_{\text{max}}$             | maximum effort                                                                                   | 1                                                      | assumed |
| $q_{\text{target}}$          | catchability coefficient for target species                                                      | 0.002                                                  | assumed |
| $q_{\text{bycatch}}$         | catchability coefficient for bycatch species                                                     | 0.002                                                  | assumed |
| $\psi$                       | threshold for profitable fishery                                                                 | 0.25                                                   | assumed |
| $p$                          | market price                                                                                     | 1                                                      | assumed |

high minimum escapement level for target alone. Furthermore, the effect of setting medium–low target and bycatch minimum escapement levels has similar effect on reducing bycatch and secondary extinctions is similar to that of setting a medium–high target escapement level alone. For example, figure 3e shows that the probability of bycatch extinctions at target and bycatch escapement levels of 0.25 and 0.15, respectively, is similar to the one achieved by setting a target escapement level of 0.45. Overall, simulations in which the bycatch species is chosen as the species with the lowest biomass in the food web before fishing starts (i.e. the most vulnerable species) exhibit higher extinctions than those where the bycatch species was chosen randomly.

We then analyse the economic results of our model in year 5, to exclude transient dynamics in the first 4 years stemming from the initiation of fishing. We calculated average profits as:

$$\frac{1}{N} \sum_{k=1}^N \frac{1}{365} \sum_{t=1}^{365} E_{k,t} (\gamma_k p q_{\text{target}} B_{\text{target},t} - c_0), \quad (3.1)$$

where  $E_{k,t}$  is the effort of  $k$ th fisher on day  $t$  and  $B_{\text{target},t}$  is the biomass of target species at day  $t$ . Figure 4a,d shows profits for each combination of policy scenario (given by  $\text{esc}_{\text{target}}$  and  $\text{esc}_{\text{bycatch}}$ ) against the median of the fraction of initial unfished bycatch species biomass that survived after 5 years of fishing. We use the median for the bycatch species biomass left given the strong skew of this distribution (across the simulated collection of 400 food webs, with all possible target–bycatch combinations considered within each food web). The frontier of these values (dotted lines) illustrates the set of feasible best options, where for a given level of bycatch biomass preserved, the expected profits are maximized. Note that we cannot combine the economic and conservation objectives because the bycatch species is not valued in monetary terms here. We found that the typical biomass remaining (median) of the bycatch species is near its unfished biomass (1.0) when the bycatch species is chosen randomly (figure 4), but it is typically less than half of its unfished biomass when the most vulnerable species is caught as bycatch (figure 4b).

Average profits (figure 4b,e) are highest when there is no constraint on bycatch ( $\text{esc}_{\text{bycatch}} = 0$ ) and the minimum target escapement level is in a middle range. At such a policy combination, the average profits are higher than in open access (the ‘asterisk’ indicator for open access is below the maximum profit level). This profit-maximizing point is associated with some

reduction in extinct risks across all species (see [figure 3](#)). Limiting bycatch via a quota reduces extinctions but also expected profits ([figure 4b,e](#)). This tradeoff is stronger when the bycatch species is vulnerable ([figure 4e](#)) rather than randomly chosen ([figure 4b](#)). Finally, we find that the policy zone that minimizes bycatch per unit of target species harvested (top-left corners of [figure 4c,f](#)) is different from the zone that minimizes extinctions (top-right corners of all panels in [figure 3](#)). Furthermore, we find that the bycatch per unit of target species can be worse (higher) than that achieved in open access, specifically when there is no constraint on bycatch but the constraint on target species harvest is stringent (high  $esc_{\text{target}}$ ). More generally, we find that the bycatch species yield per unit target species yield first increases and then decreases with increasing target escapement levels. In contrast, increasing bycatch escapement levels leads monotonically to more bycatch species yield per unit target species yield.

## 4. Discussion

One of the factors that aid the extensive use of single-species-based management (and its subsequent effectiveness in mitigating fishery collapses) is the abundance of theoretical work, which forms the basis for effective prediction and management [67]. However, there are few theoretical studies that address the dynamic interaction of all species in the marine food web—including impacts from human harvest—while considering policy design. We aim to fill this gap by presenting a novel framework that merges ecological networks and bioeconomic elements to facilitate a quantitative assessment of fishery management policies, furthering an integrative EBFM approach [9,26]. We extend the ATN framework in fishery studies by incorporating bycatch species, fisher heterogeneity and annual harvestable quotas for target and bycatch species, which leads to limited fishing periods. We show the effects of target and bycatch quotas on ecological outcomes (species local extinction)—which are relevant, especially for vulnerable bycatch species—and economic outcomes (profits and bycatch per unit target yield), which are of primary interest in commercial fishing of the target species.

Having a low minimum escapement level for the target species alone can reduce extinctions in target, bycatch and secondary species. This is consistent with previous analyses [35,36] showing that the effects of harvesting target species propagate through the ecological network impacting non-target species. While those works focused solely on take of target species, we add realism by including unintentional take of bycatch species as part of fishing. Specifically, our model allows us to quantify how harvest policies regarding target species and bycatch species (given by escapement levels) mitigate species extinctions. Having medium–low target and bycatch escapement levels mitigates bycatch and secondary extinctions in a similar way to having a medium–high target escapement level alone. Furthermore, having high target and bycatch escapement levels reduces extinctions in target and secondary extinctions in a similar way to having a very high harvest policy for target escapement ([figure 3a,c,d and f](#)). High escapement levels can lead to smaller fishing opportunities in a fishery, potentially driving out fishers and leading to excessive bycatch in other fisheries, as shown in previous literature [68]. Our model aids in better understanding the benefits of these fishery policies for reducing species extinctions and could potentially aid with setting escapement levels that align with the goals of specific fisheries. Delving into the economic results, we show that there is a combination of target and bycatch species harvest policies (among all escapement combinations possible) that maximizes average profits, for any given level of bycatch species preserved ([figure 4a,d](#)). For some combinations along this frontier, the average profit incurred is higher than under open access ([figure 4b,e](#)), although this involves a trade-off with the conservation of bycatch and secondary species.

A key benefit of our modelling approach is that it allows for the assessment of a wide range of fishery policy stringencies (on constraining removal of target and bycatch species biomass) based on how they perform across a large set of potential food web configurations. Such configurations are rarely exhaustively characterized in practice. And we are aware of no examples in which the biomass level of each species in an extended food web is regularly assessed to inform fishery management. Such information would be valuable but prohibitively costly to assess carefully on an ongoing basis. Such food webs are also likely to vary over space and time. For the time being, given that managers will not have the luxury of full information about the state of a given food web on a regular basis, there is value in identifying harvest policies for target species and bycatch species that achieve objectives in a manner robust to an array of potential food web realities.

There are several avenues for future exploration. While we studied a scenario where a single target and bycatch were harvested, the model's flexibility allows for the harvesting of multiple species (target or bycatch), which mimics the functioning of most fisheries around the world. Concepts like the maximum economic yield from single-species models are difficult to extend to multiple species [69] effectively. And even when done, such attempts to maximize profits over constraints on multiple species often leads to overexploitation of harvested species [70]. We provide an alternative framework that addresses both of those problems. We could constrain fishing on multiple species by setting escapement levels specifically for each of them in our model, leading to newer insights into profit maximization amidst the constraints imposed by multiple species. Lastly, the model's structure can be extended to encompass a broader array of policies—such as setting individual limits on target and bycatch species yield for every fisher (as opposed to a shared annual limit determined by the excess of target and bycatch biomasses above escapement levels, as implemented in our study) and/or penalties when fishers exceed their individual quota [71,72]—or more complex fisher efforts, which might dynamically grow or shrink in response to the profits incurred from the fisheries [73]. Our model paves the way for including the complex interactions of different species in the marine food web and their interactions with fishers and policymakers in multi-species fishery, thus furthering our insights into achieving sustainable fisheries.

**Ethics.** This work did not require ethical approval from a human subject or animal welfare committee.

**Data accessibility.** All codes and data used for this project can be found here [74].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** A.K.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; M.R.S.: conceptualization, methodology, project administration, supervision, writing—original draft, writing—review and editing; F.S.V.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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