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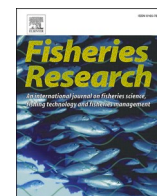
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# A model of size-spectrum dynamics to estimate the effects of improving fisheries selectivity and reducing discards in Mediterranean mixed demersal fisheries

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## ABSTRACT

Size-spectrum models are good candidates to examine the effects of fishery management because predation and fishing are largely body-size dependent. We examine the effects of increasing trawl fisheries' selectivity through the application of a size-spectrum model to a "continental shelf system" in the NW Mediterranean. This system is sustained by detritus, as background resource, and by benthic invertebrates that channel the energy to the fish community. The "continental shelf system" in our model consists of three components: 1) demersal and benthic fish and invertebrate species modelled by size spectrum dynamics, 2) carrion and 3) detritus. The model was able to exemplify the effects of changes in fishing patterns on the different biological components of the shelf system. According to the model outputs, in the short term the main target species, hake and red mullet, would be the main beneficiaries of the increased net selectivity and reduction of fishing effort. Discards reduction would have negligible effects. Despite the positive outcomes, this exercise was not exempt of challenges, mainly due to the data-demanding nature of the approach applied to a system with high diversity of life-histories and feeding strategies of invertebrate and fish species. And yet, our work is a first and crucial step to understand the size-spectrum dynamics of a continental shelf ecosystem subjected to fishery activities.

## 1. Introduction

Trawl fishing activities are responsible for one of the most pervasive impacts on the marine environment, with direct consequences for the populations of target and by-catch species and indirect consequences for the associated habitats and communities (Thrush and Dayton, 2002). The increasing awareness of the negative impacts of trawling activities on marine ecosystems during the previous decade made the European Community enact policy to address this problem as a matter of priority, resulting in the reformed Common Fisheries Policy enforced in January 2014 (EU Regulation No 1380/2013). One of the key elements of this reform was the introduction of a discard ban, with the obligatory landing of the fraction of the catch that is subjected to quotas or minimum conservation reference size (Rochet et al., 2014). Hence, fishers were expected to avoid fishing over particularly vulnerable areas, for instance areas of high concentration of juveniles, because they would need to land all regulated species, incurring in economic losses.

However, numerous authors suggested that a discard ban alone was ineffective in mitigating unwanted catches unless implemented in combination with other regulatory measures, such as the improvement of fishing gear selectivity (Bellido et al., 2014; O'Neill et al., 2019).

Different approaches have been adopted to explore the effectiveness of the proposed fishing management measures. For instance, Heath et al. (2014) used a steady-state, compartment model of the North Sea to show that a landing obligation would be harmful to components of the marine community unless accompanied by increased selectivity. In an Atlantis ecosystem model of Icelandic waters, Sturludottir (2018) found that a ban on discarding cod and haddock had little ecological or economic effects, but increased selectivity in fishing had substantial economic benefits. Celić et al. (2018) found that the landing obligation would give a substantial increase in landings at the cost of greater workload, with little effect on the biomass of fish species in the Northeast Adriatic Sea; this study was based on simulations of the Ecopath-with-Ecosym model with 33 functional groups. While the effects of the landing obligation

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have been assessed from socio-economic (e.g., Guillen et al., 2018; Christou et al., 2019) and stock biomass perspectives, the ecosystem-wide implications of the landing obligation, and related measures (e.g., fishing gear selectivity or fishing effort reductions), have been less explored (but see Celić et al., 2018; Moutopoulos et al., 2018).

Size-spectrum models are designed to describe the dynamics of body-size distributions of species (Andersen, 2019) and they can help us to understand how exploited species respond to changes in fishing. The impacts of improved size selectivity of fishing gear are quantifiable because size-spectrum models do the bookkeeping of biomass as it flows through the ecosystem (Law et al., 2016). This includes impacts on biomass yields and on fisheries-induced evolution (Law and Plank, 2018). The models acknowledge that fish can only grow by eating other organisms, so the (size-based) food web of the ecosystem is at their core. With this in place, it is possible to see how changes in fishing activities spread across the network, impacting on other groups of species, with feedbacks that eventually go back to the target species themselves. However, size-spectrum modelling on benthic ecosystems subjected to trawl fishing is at an early stage of development (Howarth et al., 2020).

Bottom-trawl fisheries are highly non-selective as they capture all demersal and benthic organisms above a certain size, defined by the cod-end mesh size as a first approximation. In the Mediterranean, the small authorized cod-end mesh size (40 mm square) implies capturing a high proportion of by-catch fauna (i.e., many invertebrates and fishes with little or no commercial interest) and unwanted organisms (i.e., undersized commercial fish), a fraction of which is discarded (Tsagarakis et al., 2014). This fishery also has high indirect mortality by the killing of benthic fauna with the passage of the gear (Hiddink et al., 2006). The dead organisms provide food for scavengers, and short-term increases in scavenging fauna densities have been observed in trawled areas (Ramsay et al., 1998). The interaction of trawl fishing with a diversity of benthic and demersal organisms, including different taxonomic groups, feeding strategies and a wide range of sizes, implies that any fishing impact mitigation measure implemented is expected to have effects at the ecosystem level (Prellezo et al., 2016; de Juan et al., 2020; Hinz et al., 2021).

In this work, we examine the ecosystem-wide effects of management measures related to selective trawl fisheries through the application of a size-spectrum model to a “continental shelf system” in the Mediterranean. The species’ trophic interactions on continental shelf systems are highly dependent on the size structure of populations as, for example, hake feeds on small benthic invertebrates in juvenile stages while adults are piscivorous (Cartes et al., 2009).

In the Mediterranean, coastal trawling grounds typically span from 50 to 200 m in depth and are composed of muddy, sandy, or detritic soft bottoms (de Juan et al., 2009). Soft bottoms are characterized by a multidimensional habitat structure where macrofauna living within the sediments interact with epibenthic invertebrates and benthic and demersal fish that feed and reproduce over or near the seabed. The aggregation of all these components is termed the ‘continental shelf ecosystem’ in the present work. The main energy source of the shelf ecosystem is benthic detritus derived ultimately from the pelagic zone and in part created by the recycling of dead mass near the seabed (Pace et al., 1984). In the model presented in this paper, plankton is not considered as background resource, instead detritus is considered. This selection is based on the direct relationship between detritivorous invertebrates, which represent an important fraction of the benthic community, and the organic detritus content of the sediment. It is assumed that a significant fraction of this detritus ultimately comes from plankton. The macrobenthos, those small invertebrates living within the sediments, feed on both benthic detritus and living organisms (e.g., other macrofauna, meiofauna, bacteria); predatory benthic invertebrates and fish feed on macrofauna (de Juan et al., 2007a); and demersal piscivorous fish prey on other fish (Mellon-Duval et al., 2017). Moreover, scavengers consume carrion on the seabed on a time scale of hours to days; therefore, carrion is expected to provide a significant

energy input (Kaiser and Ramsay, 1997; Ramsay et al., 1998). The novelty of the “continental shelf ecosystem” size-spectrum resides in the multi-species, size-spectrum model that incorporates high variability in life-history and feeding strategies of invertebrate and fish species living on or over the seabed.

The continental shelf size spectrum is subjected to a series of ecosystem-based management scenarios in the Mediterranean trawl fisheries. First is the obligation to land all fish of certain species so that fewer are returned dead to the sea; this amounts to about 15 % of the biomass discarded in the north-western Mediterranean before the implementation of the LO (Milisenda et al., 2021). With this obligation, fishers would feel incentivized to adopt more selective fishing gear (Prellezo et al., 2016) or to avoid fishing on areas where juveniles aggregate (Despoti et al., 2020). Second is the introduction of more selective fishing nets to reduce the catch of unwanted fish (Maynou et al., 2021). Third are techniques for catching demersal species with less disturbance to the benthic fauna (Rijnsdorp et al., 2017). Such techniques will reduce the carrion available to scavengers on the seabed and will also allow recovery of benthic invertebrate assemblages by reducing indirect mortality in the benthos. Additionally, with the implementation of the Western Mediterranean Multi-Annual Plan for demersal fisheries (EU Reg. 1022/2019) a limitation of fishing effort (reduction of up to 40 %) is being enforced for the period 2020–2024, which is very relevant to minimize the impact on habitats and on associated biodiversity. The Multi-Annual Plan includes support measures, such as improving fisheries selectivity, to complement effort reduction and achieve the sustainable exploitation of demersal resources by 2025. As Mediterranean trawling targets many invertebrate and fish species living both in the benthic and demersal compartments (Muntadas et al., 2014), any regulation measure is expected to have an impact over the species interaction network, altering the size spectra of communities.

This work has produced the first dynamic multi-species size-spectrum model capable of describing a continental shelf ecosystem with detritus and carrion at its base. This model will prove useful for the further study of the ecosystem impacts of trawl fisheries. We have made the modelling software that we developed for this work publicly available in the R package *mizerShelf* (<https://sisespectrum.org/mizerShelf/>) to facilitate further research.

## 2. Material and methods

### 2.1. Continental shelf ecosystem in the NW Mediterranean

The continental shelf fished by the Blanes trawling fleet, NW Mediterranean, was selected as a case study to develop the size-spectrum model due to the availability of data and extensive scientific knowledge on the benthic communities and associated trawl fisheries. The Blanes trawling fleet is an important contributor to total landings in the region and their fishing grounds are considered good spatial representatives, with the fleet operating over ca. 2100 km<sup>2</sup> of the continental shelf, which constitutes about 10 % of the shelf in the Catalan region (NE Spain). This section of the continental shelf is principally composed of soft bottoms (i.e., detritic mud alternating with sandy mud) characterized by benthic communities dominated by endobenthic and epibenthic mobile invertebrates (de Juan et al., 2007b). In this area, trawl fishing is multi-specific, with 10–15 principal commercial species whose relative importance varies over the seasons.

The size-spectrum model includes the dominant species in the system, i.e., the species that represent 70–80 % of the abundance or biomass in a NW Mediterranean muddy fishing ground according to previous studies (de Juan et al., 2011; Garcia-de-Vinuesa et al., 2018): a) the macrofauna species that account for up to 80 % of endobenthic community abundance; b) the epifauna species that account for up to 70 % of the community abundance; c) demersal fish sampled with commercial trawlers with the regulation 40 mm square mesh cod-end

(“megafauna”), including most common species in trawl catches in the area.

Red mullet (*Mullus barbatus*) and hake (*Merluccius merluccius*) are the two principal commercial species in the area (Table 1). These species are regulated by minimum landing size (11 cm TL and 20 cm TL, respectively) and fishing mortality targets in the Common Fisheries Policy and the Western Mediterranean Multi-Annual Plan. These two fish differ in their size (hake being larger), feeding strategy (red mullet benthivorous and hake piscivorous) and behavior (red mullet benthic and hake demersal); however, the two species are tightly dependent on the benthic system. Other commercially valuable demersal species in the area, not subject to EU regulations, are among others: blue whiting (*Micromesistius poutassou*), anglerfish (*Lophius* spp.) or cephalopods (different species of octopus and squids) (Table 1).

The (endo)benthic compartment, understood as invertebrates living in the muddy sediments (i.e., macrofauna), is typically surveyed with van Veen grabs that collect sediment samples that are sieved through 1 mm. A typical sample in a muddy fishing ground includes approximately 8.7 g/m<sup>2</sup> (± 3.9) wet weight of macrofauna (de Juan et al., 2011). In this work, the macrofauna species are divided into functional groups to facilitate their incorporation in the size-spectrum model using their biological characteristics, including feeding mode, morphology, position in the sediments and their average maximum size; these traits provide information on the feeding preferences and availability to predators (Table 2). Macrofauna species in a muddy fishing ground comprise approximately 70 % detritivores, 12 % predators, 9 % suspension feeders, and 9 % scavengers of total macrofauna abundance (de Juan et al., 2007b). Polychaete worms contribute approximately to 80% of the abundance of macrofauna, being mainly predators or detritivores. The detritivores worms are particularly important contributors to the detritivore feeding group in the benthos.

The abundance and composition of larger (epi)benthic invertebrates (i.e., epifauna) and fish, living on the sediment surface, is traditionally

**Table 1**

List of target species in the study area, including their adult maximum length, the average annual yield, and the fishing mortality (provided in the regular stock assessment reports). The average annual yield is based on annual catches of the demersal fleets based on Blanes and Palamós (NW Mediterranean), averaged by km<sup>2</sup> for the period 2017–2019. The proportion of the biomass in the catch that is discarded is derived from results of MINOUW project (D1.1, <http://minouw-project.eu/publications-and-papers/>) and other empirical data. The source of the species' parameters is included in Table S3.

Commercial species	Adult maximum length (cm)	Average annual yield (kg/km <sup>2</sup> )	Fishing mortality	Proportion discarded
Red mullet ( <i>Mullus barbatus</i> )	34.5	5.91	1.47	0.05
Striped red mullet ( <i>Mullus surmuletus</i> )	40	3.16	1.47	0.02
Hake ( <i>Merluccius merluccius</i> )	110	19.21	1.74	0.10
Angler fish ( <i>Lophius budegassa</i> )	102	5.2	1.13	0.08
Poor cod ( <i>Trisopterus capellanus</i> )	32	3.69	1.00	0.15
Horse mackerel ( <i>Trachurus trachurus</i> )	70	11.02	1.00	0.15
Blue whiting ( <i>Micromesistius poutassou</i> )	55.5	8.07	1.72	0.25
Horned octopus ( <i>Eledone cirrhosa</i> )	20	5.68	1.00	0.10
Shortfin squid ( <i>Illex coindetii</i> )	26.5	6.70	1.00	0.15

**Table 2**

List of benthic species included in the size-spectrum model: macrofauna, as invertebrates living within the sediments, grouped by their relative size and feeding type (DF: deposit feeding; pred.: predatory); supra-benthos that identified the small crustaceans living above the sediments; epibenthic invertebrates, larger species that live on the sediment surface; benthic fish, species that live on the sediment surface and, due to their small size, are not effectively sampled with trawlers. The average abundance was estimated from experimental surveys in the study area (i.e., continental shelves characterized by muddy bottoms in the NW Mediterranean; (de Juan et al., 2011)). The gear mortality is a per capita rate representing the vulnerability of the organisms to direct gear contact, according to the species' mobility and position in the sediment.

Faunistic group	Taxonomic groups	Adult maximum length (cm)	Average abundance (grams or individuals/m <sup>2</sup> )	Gear mortality (1/year)
Macrofauna	Small DF worms	0.2	279.6 ind.	0
	Small DF crustacea	0.5	79.6 ind.	0
	DF worms	0.5	257 ind.	0.2
	Endobenthic pred. crustacea	0.8	4.95 ind.	0.2
	Endobenthic pred. worms	0.5	199 ind.	0.2
	Large DF worms (bristle worm)	3	95 ind.	0.4
	Suprabenthic crustacea	1	0.03 g	0.2
	Starfish	17	0.118 ind.	0.6
	( <i>Astropecten irregularis</i> )			
	Nut clam ( <i>Nucula nucleus</i> )	5	0.013 ind.	0.4
Supra-benthos	Murex ( <i>Bolinus brandaris</i> )	6	0.063 ind.	0.6
	Angular crab ( <i>Goneplax rhomboides</i> )	3	0.033 ind.	0.6
	Harbour crab ( <i>Liocarcinus depurator</i> )	4	0.027 ind.	0.6
	Red snapping shrimp ( <i>Alpheus glaber</i> )	6	0.026 ind.	0.2
	Spotted flounder ( <i>Citharus linguatula</i> )	31.5	0.061 ind.	0.8
	Black goby ( <i>Gobius niger</i> )	18	0.0126 ind.	1
	Gurnards (Family Triglidae)	17.1	0.239 ind.	1
	Lepidotrigla			
Epibenthic fauna				

estimated with epibenthic dredge samples with a 1 cm mesh size. Some of the largest epibenthic species are also retained by trawling nets and might be commercialized (e.g., the swimming crab *Liocarcinus depurator* or the benthic fish *Citharus linguatula*). The typical epibenthic community in a muddy fishing ground is composed of invertebrates that are selective predators, but they might be also opportunistic scavengers or detritivores (de Juan et al., 2007b).

Suprabenthic crustaceans, as small crustacean species that live just above the sediment in the water, are an important component of the system as these organisms constitute a significant part of the diet of benthic and demersal species (de Juan et al., 2007a).

The mesh size of sampling gears determines the minimum size of the organisms retained in the samples; this might lead to underestimation of actual abundances. This is taken into account in the size-spectrum model by considering only individuals above a cut-off size.



## 2.2. Modelled interactions in the continental shelf system fished by trawlers

The system studied is characterized by ca. 150 macroscopic species identified in the benthos (de Juan et al., 2011; Muntadas et al., 2014) and the size-spectrum model includes the species that represent 70–80 % of community abundance (Tables 1 and 2). This means that not all species are represented in the system. The selected species represent a diversity of feeding modes that characterize the continental shelf ecosystem, where detritus is considered as the background resource, unlike other studies that consider plankton as the base resource (e.g., Blanchard et al., 2009, 2011). However, the detritus is assumed to arrive mainly from the pelagic zone (Le Loc'h et al., 2008). We treat the pelagic ecosystem as fixed for this work and external to the study system because the shelf ecosystem forms a coherent unit for management. Also, the model does not include meiofauna (e.g., nematodes) and the microbial component that plays a crucial role in the detritus pathway in the size-spectrum (Pace et al., 1984). The role of these two components is considered through the rate at which carrion is decomposed to detritus (Fig. 1).

Fishing discards and dead organisms (killed by the gear) are an important input to the carrion resource. The carrion component is not size-structured as the organisms can feed on carrion independent of their size (i.e., a small species like harbour crab can feed on large dead organisms; Fig. 1). This component is assumed to have a high decomposition rate, as in nature it decomposes fast due to small fauna and microbes (Beasley et al., 2012).

Detritivorous macrofauna, e.g., Polychaeta or small crustaceans, constitute the diet of predatory invertebrates and benthivore fish like red mullet. Predatory invertebrates feed on other invertebrates and eggs and larvae. The larger demersal fish (e.g., hake) and cephalopods (e.g., short-fin squid) prey on smaller fish or epibenthic invertebrates. Additionally, some invertebrate species, e.g., decapod crustaceans or starfish, feed on the dead organic matter arriving at the seabed (Fig. S1). The species' interaction matrix (Fig. 1 in supplementary material) assumes that not all species interact with each other. The interaction depends on the size of the species, on their feeding preferences (i.e., a detritivore does not prey upon other species), but also on their potential overlap in the three-dimensional space of the benthic system, with some species

with a preference for the suprabenthic zone, e.g., poor cod, and other species that can dig in the sediments for prey, e.g., goby fish (Fig. 1).

## 2.3. Size spectrum model

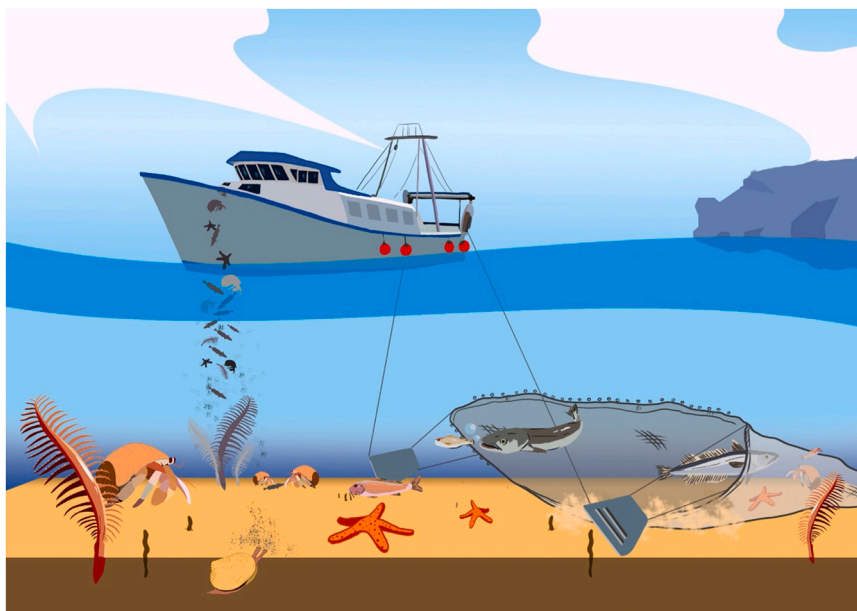
The model consists of three components: 1) 25 species modelled by size spectrum dynamics, 2) carrion and 3) detritus. The model is implemented using the R package 'mizerShelf' (Delius et al., 2022b) that was developed for this work. This software adds the dynamics of the detritus and carrion components to the size-spectrum dynamics that is already implemented in the R package 'mizer' (Scott et al., 2014; Delius et al., 2022a). The software allows to examine the effects of fisheries' management scenarios: the landing obligation, the change in net selectivity, and the change in fishing effort. The model is introduced below, and a detailed explanation with equations is given in the [supplementary material](#).

### 2.3.1. Species size-spectrum

The model assumes that an individual can be characterized by its weight  $w$  and its species number  $i$ . The model aims to calculate the size spectrum  $N_i(w)$ , understood such that the number of individuals in a size range is the area under the number density  $N_i(w)$ . The time evolution of the number density  $N_i(w)$  is described by the McKendrick-von Foerster equation, which is a transport equation describing the transport of biomass from small to large individuals, with an additional loss term due to fish mortality (eq. 1 in supplementary material). The individual growth and mortality rates depend on the density of other species of other sizes, as well as the carrion and detritus biomasses, making the size-spectrum dynamics non-linear. For the smallest size class, instead of a rate of growth into the size class, there is a rate of reproduction of new individuals into that size class.

### 2.3.2. Growth

Consumers can grow only by consuming prey, carrion and/or detritus. The rate at which a predator encounters food is determined by summing over all prey species and integrating over all prey sizes, weighted by the selection factors, and (where relevant) adding the encounter rates of carrion and detritus (eq. 2 in supplementary material). The species' interaction matrix (Fig. 1 in supplementary material)



**Fig. 1.** Illustration of the continental shelf ecosystem, with detritus as background resource and invertebrates living within and on the sediments channelling the energy to the benthic and demersal fish community. Trawl fishing is directly (by extracting and damaging fauna) and indirectly (through the input of dead organisms) affecting this system (art by Llorenç Vidal).

sets the interaction strength between predator and prey species. The size selectivity is encoded in the predation kernel; for principal predatory fish included in our model (e.g., hake, angler fish, poor cod, and blue whiting) we use a power-law kernel with sigmoidal cut-offs (eq. 3 and 4 in supplementary material).

Only a proportion of the encountered prey is consumed depending on the level of satiation, and then only a proportion of that consumed biomass is retained, while a proportion is expelled in the form of feces that contribute to the detritus. Part of the retained biomass is used to fuel the needs for metabolism, activity, and movement. The remaining energy, if any, is then available for growth and reproduction (eqs. 5–10 in supplementary material). When food supply does not cover the requirements of metabolism and activity, growth and reproduction stop, i.e., there is no negative growth.

### 2.3.3. Mortality

An individual's mortality rate has four sources: predation, external, fishing, and excess gear mortality. All consumption by fish translates into corresponding predation mortalities on the ingested prey individuals, which is a function of size and the species' interaction (in eqs. 11–15 in supplementary material).

The fishing mortality rate is the product of the species- and size-dependent selectivity of the gear, the species-specific catchability (Table 1), and the fishing effort. We use sigmoidal selectivity curves described by the parameters L50 (the length where 50 % of the individuals are selected) and L25 (the length at which 25 % are selected). Some species (e.g., macrofauna and small epifauna like nut clam and red snapping shrimp) experience no fishing mortality. However, the fishing gear also causes mortality on benthic organisms due to direct contact (Table 2). This mortality is assumed not to be size-specific, but it depends on the position of the species in or above the sediments and their mobility. This mortality is denoted as excess gear mortality and it contributes to carrion production.

### 2.3.4. Reproduction

The total rate of energy investment into reproduction is obtained by integrating the contribution from all mature individuals of a species, each of which invests a proportion of their available energy (eq. 16 in supplementary material). The model parameters that determine the efficiency with which this invested energy is converted to biomass of new offspring are chosen so that the level of reproduction leads to the observed abundances given in Tables 1 and 2.

Three important density-dependent mechanisms widely assumed in fisheries models are automatically captured in the *mizer* model, which lead to an emergent stock-recruitment relationship: i) high density of spawners leads to a reduced food income of the spawners and consequently reduced per-capita reproduction; ii) high density of larvae leads to slower growth of larvae due to food competition, exposing the larvae to high mortality for a longer time, thereby decreasing the survivorship to recruitment size; iii) high density of fish leads to more predation on eggs and fish larvae by other fish species or by cannibalism. However, there are other sources of density dependence that are not explicitly modelled mechanistically in *mizer*. An example would be the limited carrying capacity of suitable spawning grounds and other spatial effects. This requires additional density-dependent contributions to the stock recruitment. In *mizer*, this type of density dependence is modelled through constraints on egg production and survival (eq. 17 in supplementary material). In our model we assumed that maximum recruitment for commercial species would be twice the recruitment observed at present, based on the highly depleted state of Mediterranean fish stocks, with spawning stock biomass at 5 % or lower than virgin spawning stock biomass (Vasilakopoulos et al., 2014), and a Beverton-Holt stock recruitment function with a steepness value of  $h = 0.7$ .

### 2.3.5. Carrion

Feeding on carrion by scavengers is not size based, therefore we do

not need to model its size distribution but only its total biomass. The rate of change in the total carrion biomass is the difference between the rate at which carrion biomass is produced and the rate at which it is consumed (eqs. 18–20 in supplementary material). Carrion is consumed by scavengers, but it is also decomposed by bacteria and other processes. The rate at which carrion biomass is consumed is assumed to be proportional to the available carrion biomass. The rate at which carrion biomass is produced by the ecosystem has contributions from three sources: a proportion of external mortality, excess gear mortality and discards (eqs. 21–24 in supplementary material). The external mortality comes from animals that have died by natural causes other than predation. The excess gear mortality comes from animals killed by the fishing gear that is not taken up to the fishing vessel but are left dead in the sea. The discards come from discarding a proportion of the catch biomass (Table 1).

### 2.3.6. Detritus

We describe the detritus as a size-spectrum described by a power law up to a maximum size. The rate of change in the total detritus biomass is the difference between the rate at which detritus biomass is produced and the rate at which it is consumed eqs. 25–27 in supplementary material). The consumption rate is assumed to be proportional to the available detritus biomass, and total consumption depends on the abundance of consumers and their preference for detritus (eqs. 28 and 29 in supplementary material). The detritus production has contributions from three sources: feces, decomposing carrion, and external input (eqs. 30–32 in supplementary material). The feces come from the biomass that is consumed but not assimilated by the predators. The decomposing carrion is the carrion biomass that is decomposed to detritus at a fixed rate. The external input is the rate at which detritus enters the system from external sources. This will mostly be detritus sinking in from the pelagic zone. This rate is a model parameter independent of any other model component and determined to achieve the steady state of the model.

## 2.4. Biological parameters: model input

The model shelf ecosystem has two broad groups of species with variable data availability: i) macrofauna, such as worms and crustaceans, living within the sediments. These species are very much understudied and only some biological parameters will be known with some accuracy (e.g., von Bertalanffy growth rate  $k$ , adult max. size, standing stock biomass, egg size). Aiming to encompass the diversity of strategies exhibited by macrofauna, the principal taxonomic groups in our environmental context are divided into groups defined by size categories and principal feeding mode (e.g., large predatory crustaceans, small deposit feeding polychaetes; ii) "large fauna", or megafauna living on the sediment surface or near the surface. For our model purposes, it includes two sub-components: a) epifauna, as non-commercial species (starfish, some bivalves, some crustaceans, two gobies), and b) species of commercial interest (mostly finfish but also some cephalopods in our area). For these species, certain parameters can be determined accurately (e.g.,  $k$ , max size, maturity size, standing stock biomass, the size at which the organism enters our system, fisheries selectivity, and catchability).

The values of the parameters for the model were tuned to the shelf ecosystem off the coast of Blanes in the NW Mediterranean (Table 1 to 15 in the supplementary material). There are different data sources available: i) data from experimental surveys on benthic communities that provide information on biodiversity inventories and relative abundances of macrofauna (endobenthic, epibenthic, and suprabenthic); ii) fishing surveys onboard commercial trawlers that provide information on relative biomasses, catchability, and size-frequency of megafauna (commercial fish and invertebrates, e.g., MINOUW project; regular annual monitoring surveys of the EU Data Collection Framework program (DCF)); iii) open-source databases (e.g., (Muntadas et al.,

2014), for fishes, and SeaLifeBase, for megafaunal invertebrates and the *add\_my\_pet* database for small macrofauna) and published literature was consulted when local case-study data was not available. Moreover, commercial fish parameters were obtained from iv) annual fisheries stock assessments that are performed over the commercially most important fish species (e.g., red mullet, hake, mackerel) by the Scientific, Technical and Economic Committee for Fisheries (<https://stecf.jrc.ec.europa.eu/reports>) and the General Fisheries Commission for the Mediterranean ([www.fao.org/gfcm/](http://www.fao.org/gfcm/)).

There is a set of parameters that are assumptions based on expert knowledge and these parameters might control the sensitivity of the system. This was explored by selecting different values of these parameters to assess their impact on the model outcome: i) the reproduction level (set at 0.5; Fig. S2); ii) the carrion lifetime (1/365 years by default); iii) detritus lifetime (1 year by default); and iv) the proportion of the carrion production that is caused by fishing (0.2 by default). The selection of different parameters did not significantly alter the outcome of the scenarios, in terms of the direction of changes of biomass (Fig. S2).

## 2.5. Scenario analyses

The scenarios are based on current regulation proposals for the Mediterranean trawl fisheries, and these include increased selectivity of the fishing gear, a reduction of discards of key species and a reduction in fishing effort. The change in selectivity, from a regulatory 40 mm cod-end to a more selective 50 mm cod-end, will affect all target species in the system (Table 3). The reduction of discards affects current discards of hake and red mullet, from a current average rate of 15 % to a 0 % discard rate, as all unwanted fish traditionally discarded (i.e., hake and red mullet individuals below the minimum landing size or that have been damaged during the fishing activity) must be landed and their use is restricted to purposes other than direct human consumption (Christou et al., 2019). The change in fishing effort follows the newest regulation (West Med MAP) that calls for a reduction in fishing effort by up to 40 % between 2020 and 2024.

In the selectivity scenarios for commercial species (Table 3), we use parameters of a sigmoidal curve (in length) averaged over studies in D2.4 of the MINOUW project (<http://minouw-project.eu/publications-and-papers/>). No data were available for a couple of species, and we used an L50 of 15 cm and L25 of 14 cm for all non-commercial species retained by the current SM40 trawl net.

## 3. Results

The size-spectrum of the continental shelf system in its steady state

**Table 3**

Data input for the management scenarios: selectivity, including original parameters (L25 and L50 with current mesh sizes – SM40 trawl net) and new parameters (L25 and L50 with SM50 trawl net); a reduction of the discards for hake, from current estimates of 15 % of hake catch discarded to 0 discards; a 40 % reduction in trawling effort.

Scenarios	Original parameters (cm)		New parameters (cm)	
<b>Increase selectivity</b>	L25	L50	L25	L50
hake	15.8	16.9	18	21.5
red mullet	11.1	12.2	15.13	17.28
striped red mullet	11.1	12.2	15.13	17.28
angler fish	13.5	15.00	14.00	18.00
poor cod	7.6	8.74	8.10	9.50
horse mackerel	14.5	15.9	15.20	17.00
blue whiting	17.8	19.2	18.80	22.25
shortfin squid	14.00	15.00	14.20	16.50
horned octopus	14.00	15.00	14.20	16.50
<b>Reduce hake and red mullet discards</b>	0.15 (15 % biomass)		0	
<b>Reduce effort</b>	1		0.6 (40 %)	

(i.e., year 0) shows a system dominated by high biomass density of small organisms (Fig. S3) that are interconnected through their trophic interactions (Fig. S1). The fisheries management scenarios explored modify this steady state size-spectrum and projects changes in the yield for the commercial species. These changes are a consequence of changes in the size-spectrum of the benthic ecosystem. A timeframe of 15 years is considered as relevant for fisheries management.

A change in fisheries selectivity to a more selective net (Table 3) leads to an initial increase in the biomass of all species, except for poor cod and horse mackerel. However, at year 5, the biomass for most target species decrease to close to initial values (e.g., short-fin squid or blue whiting), or even decrease (e.g., angler fish). The species that benefit the most from a change in selectivity are the two mullets and hake (Fig. 2a). In terms of the species' yield, there is an initial decrease in all the commercial species, however, in the case of hake and the two mullets the yield exceeds initial values after year 2 and remains approximately constant at high values after year 10 (Fig. 2b). On the other hand, the yield of the other target species stabilizes at lower values (Fig. 2b).

The discard reduction scenario, from 15 % of estimated hake and red mullet discards to 0 discards for these species (Table 3), has practically no effects on the biomass or yield of the species in the case study (Fig. 3).

The effort reduction scenario (Table 3) influences all the commercial species in the study area. Commercial species like hake, mullets and angler fish show an increase of biomass (Fig. 4a). However, after a general initial increase in biomass, some species (horned octopus and blue whiting) decrease to values lower than the initial biomass. For the yield, we observe an initial decrease of 40 % in all species (Fig. 4b), later stabilizing at lower (e.g., blue whiting and shortfin squid) or higher (e.g., hake) values compared to initial values. A sustained increase in the yield over the 15 years projection is only observed for hake, angler fish and the two mullets.

This scenario also has a strong effect on the non-commercial invertebrates in the study area (Fig. 5), with some benthic fish and invertebrates benefiting from the measure (e.g., harbour and angular crab, and small deposit feeding crustacea). On the other hand, abundant invertebrates in the area like starfish (a scavenger species) decrease in biomass because the reduction in fishing effort has led to a reduction in excess gear mortality and hence a reduction in carrion. The reduction of effort tends to have small impact on the biomass of small-bodied but highly abundant worms, while species in the middle of the trophic web tend to have progressively larger positive (e.g., harbour crab) or negative effects (e.g., starfish, black goby).

In summary, of the three fishery management scenarios explored, the two main commercial species (hake and red mullet) would mainly benefit from the increased selectivity, with the positive effects on mullet being more marked (Fig. 6). Effort reduction has a positive effect on hake in particular; however, it should be noted that this scenario has effects on all components of the system, with positive and negative changes in the different components (Fig. 5).

## 4. Discussion

In this work, we have developed a multispecies size-spectrum model with detritus and carrion components to investigate the ecological dynamics of fishing grounds in the north-western Mediterranean continental shelf. The current work is motivated by the need to understand the effects on the marine ecosystem of regulatory measures for the trawl fisheries in the Mediterranean, beyond the effects on target species that are usually considered (Maynou et al., 2021). The Multi-Annual Plan for the Mediterranean fisheries includes support measures, such as improving fisheries selectivity, to complement effort reduction and achieve the sustainable exploitation of demersal resources by 2025. This plan will affect the system through the size of the catches, through discard modification, and a reduction of fishing pressure over the target species, but also non-target benthic communities. We explored the changes caused by these support measures on the continental shelf

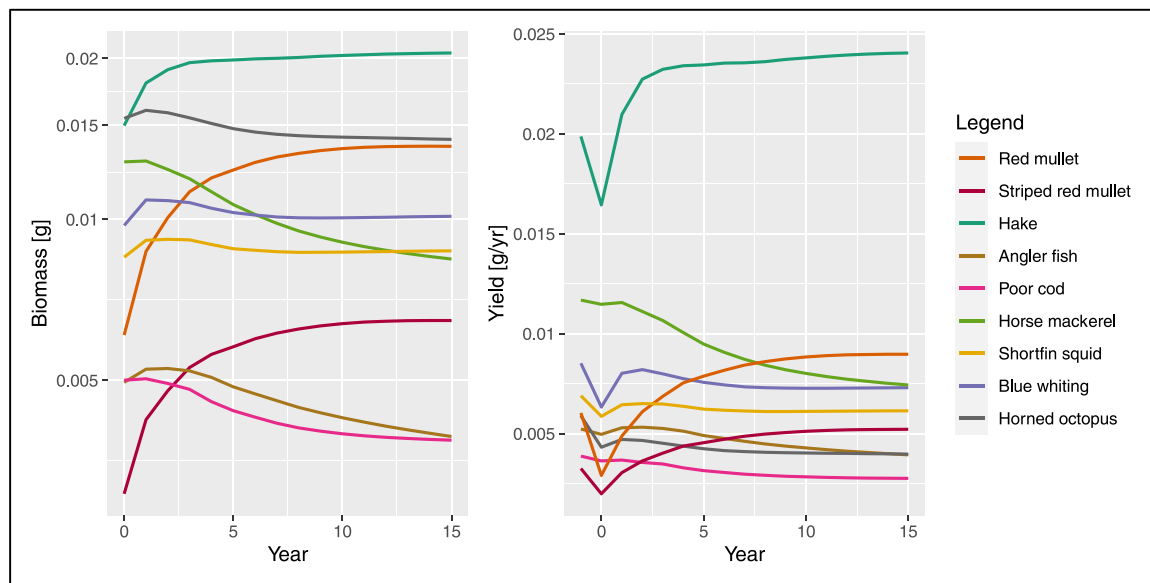


Fig. 2. Projected changes in the biomass (a) and yield (b) of the commercial species after an increase in the fishing net selectivity (Table 3).

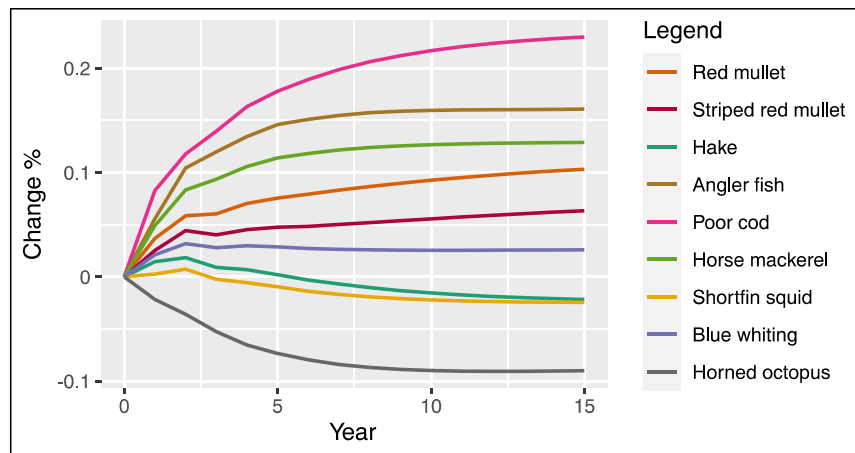


Fig. 3. Percentage change in the biomass of the commercial species after the implementation of 0 discards for hake and red mullet. Note that the % of change in biomass with respect to the initial state is  $< \pm 0.3\%$  for all species.

system with a size-spectrum model because predation and fishing are largely body-size dependent.

In the continental shelf, different taxonomic and functional groups interact, as fish can feed on benthic fauna or prey on other fish. These interactions can change over the life of an organism, depending on their size (Sánchez-Hernández et al., 2019). Bottom trawling can change food availability for benthivorous demersal species by (i) changing benthic prey composition through physical seabed impacts and (ii) by removing overall benthic consumer biomass, thereby increasing the net availability of benthic prey for remaining individuals. All these changes are likely to be size-dependent. Moreover, a diversity of benthic and demersal organisms is opportunistically taking advantage of the dead organic matter input in fishing grounds. In consequence, the model described here strips a complicated ecosystem down to a level that just holds in place the detritus-based food chain, including the growth in body size of detritivores and predators from feeding.

The novelty of this work resides in the multi-species approach that incorporates high variability in life-history and feeding strategies of invertebrate and fish species living on or over the seabed. The simplest applications of size-spectrum models to benthic (detritus-based) ecosystems aggregate all individuals within a single size spectrum

regardless of their feeding strategy (e.g., Blanchard et al., 2009, 2011). But this is simplistic, as organisms with different strategies (e.g., detritivores and predators) are expected to exhibit different responses to pressures (Howarth et al., 2020). Benoit et al. (2022) applied a multi-species size spectrum model to a freshwater community and observed that changes in fishing mortality caused changes in species' interaction, including competition and predation, varying across life stages.

The fishery management scenarios we explore are based on current regulation proposals for the Mediterranean trawl fisheries, such as the change in selectivity, from a regulatory 40 mm cod-end to a more selective 50 mm cod-end. According to the model outputs, in the short term, hake and red mullet are the main beneficiaries of the increased selectivity of trawl fishing, while some other valuable species, e.g., angler fish, experience a decrease relative to the initial yield over the 15 years. An initial rapid response in the biomass is likely due to the survival of small individuals which escape through the more selective net and can recruit to the fished population over the next few years. These projections are in accordance with Maynou et al. (2021) that show that the implementation of more selective fishing gear that avoids catching undersize hake would result in substantial increases in the biomass of this species. However, the higher abundance of species that benefit from



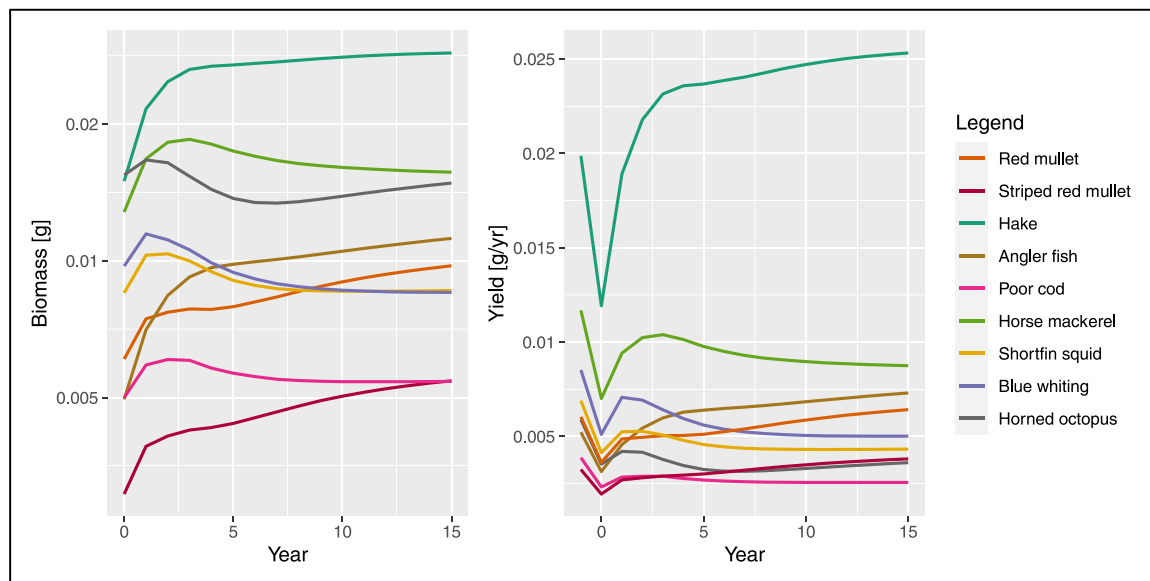


Fig. 4. Projected changes in the biomass (a) and yield (b) of the commercial species after a reduction of fishing effort (Table 3).

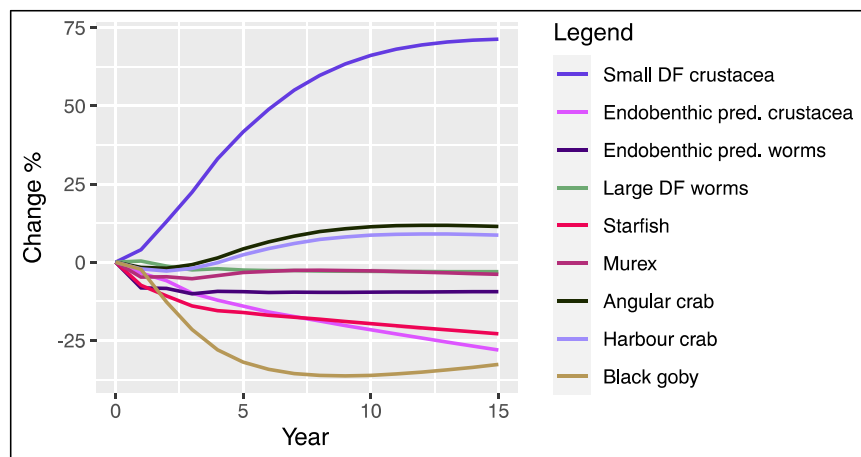


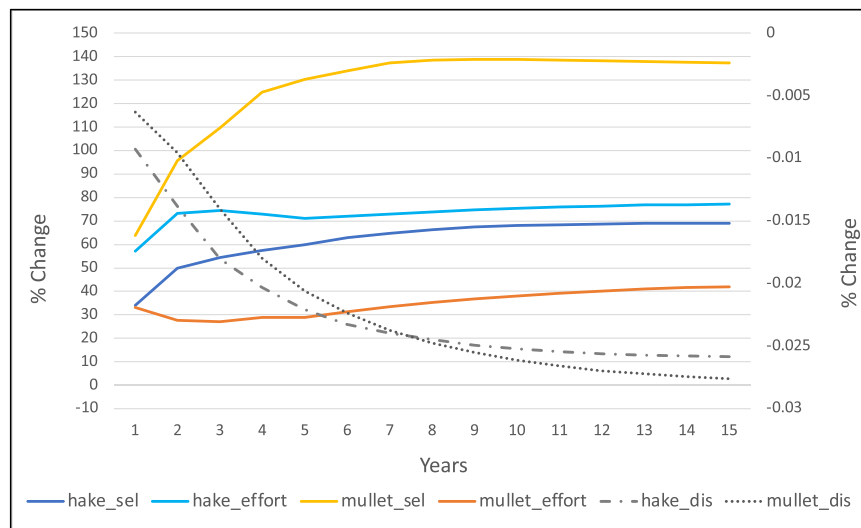
Fig. 5. Example of the effect of fishing effort reduction on non-commercial benthic invertebrates and fish. Data as a percentage change in biomass relative to year 0.

improved selectivity (e.g., hake) would increase trophic pressure on the entire ecosystem due to a potential higher predation impact of hake (i.e., a carnivore, aggressive species) on the system, undercutting the resources available to other species with similar diets (e.g., blue whiting, García-Rodríguez et al., 2021). Therefore, according to the size-spectrum model, in the mid and long term (i.e., 10 or more years) increasing the selectivity has positive effects on the target species (e.g., hake and red mullet), but the effect is less positive for other species also of commercial value.

The discard practices are one of the critical pillars of unsustainable fishing worldwide, including the Mediterranean (Tsagarakis et al., 2014). Over the past decade, policy makers worked towards the elimination of discard practices to achieve a more sustainable fishery. However, the elimination of discards might have unexpected consequences at the ecosystem level as discarded fish are food for a range of scavenging species (Heath et al., 2014). According to our size-spectrum model, the changes in the yield, being either positive or negative changes, are negligible for all species of commercial interest. Our results show that the projection of management measures targeting specific regulated species (e.g., discards ban on undersize hake) can differ between the traditional fisheries models and models that consider emerging ecosystem properties, such as *mizerShelf*. For instance, we

showed here that not discarding the approximately 15 % of undersize hake and red mullet has barely perceptible effects on the evolution of biomass and yield of the commercial species of the continental shelf ecosystem, probably due to the proportionally overall low amount of biomass represented by undersize hake in the ecosystem.

A reduction of fishing effort is considered crucial to limit the ecosystem-wide impacts of trawl fisheries, as less effort not only implies less pressure on target and non-target species, but also less impact over the seabed (Hiddink et al., 2006). According to our size-spectrum model scenario, in the short term, most commercial species benefit from the effort reduction, but, after an initial important increase in certain species (e.g., blue whiting, shortfin squid or horse mackerel), their biomass projection would remain near their initial values. The most important and sustained increases in the yield are observed for angler fish, hake, and red mullet. This scenario also has a stronger effect on the non-commercial invertebrates in the study area with some invertebrates benefiting from the measure (e.g., endobenthic crustaceans and harbour crabs), while abundant invertebrates in the area like starfish (a scavenger species) decrease in biomass. An effect of the effort reduction on a wider species' spectra is expected as trawling activities physically disturb the seabed and the benthic fauna (i.e., gear mortality) and indirectly alters the system due to the extraction of the target species'



**Fig. 6.** Percentage change in biomass relative to year 0 for the two principal commercial species in the 3 fisheries management scenarios in a 15 years' projection. Left axis represents the positive change of the selectivity and effort reduction scenarios for hake and mullet (hake\_sel, hake\_effort, mullet\_sel, mullet\_effort). Right axis represents the slightly negative change for the discard scenarios for the two species (hake\_dis, mullet\_dis).

biomass and the input of additional organic matter through discards (Thrush and Dayton, 2002; Kaiser et al., 2006). This effect can be anticipated with a model such as *mizerShelf*, with ecological interactions, but not with traditional fisheries models that project management measures as simple changes to fishing mortality of single species (Prellezo et al., 2016).

The model presented shows that measures applied to fisheries influence the entire system, with winners and losers, due to the network of trophic interactions on the continental shelf. There is no single measure that benefits all commercial species in the medium term, and probably the combination of different measures is the most effective, including a discard ban extended to all the species. Additionally, it must be taken into account that we are studying a system historically modified by trawling. The composition of the benthic community considered in this work is an example of a trawl bottom community, dominated by small, endobenthic and opportunistic species (de Juan et al., 2009). A change in the level of effort or in the amount of discards will modify the contribution of organic matter to the benthos, with possible alteration of the composition of the benthic fauna, currently adapted to high organic matter inputs. On the other hand, this exercise has not considered the temporal dimension of the ecosystem in a trawl bottom, where the recovery rates of benthic fauna and migration from other nearby systems (Hiddink et al., 2017) have an impact on the composition of the benthos (and therefore, of demersal species) in the long term.

Despite the observed advantages of the application of a size-spectrum model, this exercise was not exempt of challenges due to the limited available knowledge of species life-history. This was partly addressed by selecting a subset with the dominant, and generally best-known, species to represent the continental shelf system. In these systems, over 150 species of fish and invertebrates have been identified (Muntadas et al., 2016; de Juan et al., 2020) and, in consequence, some interactions are not captured in the model. For example, the “small fauna”, or endobenthic macrofauna, such as worms and crustaceans, are very much understudied and only some biological parameters are known with some accuracy (e.g., von Bertalanffy growth rate  $k$ , adult max. size, standing stock, and egg size). To represent the variability in biological traits exhibited by this community, and encompass as many species types as possible, this component is described by their biological traits and principal taxonomic group (e.g., large predators/scavenging crustaceans). With this approach, our model was able to incorporate a diversity of taxa, functional strategies, and size ranges; thus, so far, this is the most representative size-spectrum model done for a benthic

system.

Despite the aforementioned limitations, the model presented in this paper allows us to explore the direction of the effects of fishery regulation measures on species of commercial interest, illustrating as well as possible according to the existing information the complex relationships in the benthic system of a trawl bottom. The management of Mediterranean demersal fisheries should move beyond implementing conservation measures based on single-species advice and consider the wider ecosystem effects of fishing. Reducing fishing pressure on juvenile fish by improving selectivity or adopting area closures on recruitment bottoms can benefit certain highly overexploited target species, such as European hake, but will not necessarily lead to ecologically or economically more productive fisheries on NW Mediterranean fishing grounds, due to the highly multispecies nature of these fisheries and to cascading effects across the trophic web.

We have made the *mizerShelf* R package, which we developed to implement the model described in this paper, publicly available. This makes it easy to explore further the effect of conservation policies. Also, the package allows researchers to create models for other continental shelf ecosystems.

#### CRedit authorship contribution statement

**Silvia de Juan:** model conceptualization and development (supporting); Writing – original draft (lead); Writing – review & editing (lead). **Gustav Delius:** model conceptualization and development (lead); Writing – review & editing (supporting). **Francesc Maynou:** conceptualization of work (lead); model conceptualization and development (supporting); Writing – review & editing (supporting).

#### Declaration of Competing Interest

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

#### Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2023.106764](https://doi.org/10.1016/j.fishres.2023.106764).

## References

- Andersen, K.H., 2019. Fish ecology, evolution, and exploitation. In: *Fish Ecology, Evolution, and Exploitation*. Princeton University Press.
- Beasley, J.C., Olson, Z., DeVault, T., 2012. Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos* 121, 1021–1026 (Wiley Online Library).
- Bellido, J., Carbonell, A., Garcia, M., Garcia, T., González, M., 2014. The obligation to land all catches—consequences for the Mediterranean. European Parliament, Directorate-General for Internal Policies Policy Department B: Structural and Cohesion Policies, 52.
- Benoit, D.M., Chu, C., Giacomini, H.C., Jackson, D.A., 2022. Size spectrum model reveals importance of considering species interactions in a freshwater fisheries management context. *Ecosphere* 13, e4163 (Wiley Online Library).
- Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J., Benoit, E., 2009. How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* 78, 270–280 (Wiley Online Library).
- Blanchard, J.L., Law, R., Castle, M.D., Jennings, S., 2011. Coupled energy pathways and the resilience of size-structured food webs. In: *Theoretical Ecology*, 4. Springer, pp. 289–300.
- Cartes, J.E., Hidalgo, M., Papiol, V., Massutí, E., Moranta, J., 2009. Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. In: *Deep Sea Research Part I Oceanographic Research Papers*, 56. Elsevier, pp. 344–365.
- Celić, I., Libralato, S., Scarcella, G., Raicevich, S., Marčeta, B., Solidoro, C., 2018. Ecological and economic effects of the landing obligation evaluated using a quantitative ecosystem approach: a Mediterranean case study. In: *ICES Journal of Marine Science*, 75. Oxford University Press, pp. 1992–2003.
- Christou, M., De Juan, S., Vassilopoulou, V., Stergiou, K.I., Maynou, F., 2019. Monitoring the environmental, social and economic dimensions of the landing obligation policy. *Front. Mar. Sci.* 6, 594 (Frontiers Media SA).
- Delius, G., de Juan, S., Maynou, F., 2022a. mizerShelf: Mizer Models with Carrion and Detritus Components Suitable for Continental Shelf Ecosystems. (<https://sizespectrum.org/mizerShelf/>).
- Delius, G., Scott, F., Blanchard, J., Andersen, K., 2022b. mizer: Multi-Species Size Spectrum Modelling in R. (<https://sizespectrum.org/mizer/>).
- de Juan, S., Cartes, J.E., Demestre, M., 2007a. Effects of commercial trawling activities in the diet of the flat fish *Citharus linguatula* (Osteichthyes: Pleuronectiformes) and the starfish *Astropecten irregularis* (Echinodermata: Asteroidea). *J. Exp. Mar. Biol. Ecol.* 349, 152–169.
- de Juan, S., Demestre, M., Sanchez, P., 2011. Exploring the degree of trawling disturbance by the analysis of benthic communities ranging from a heavily exploited fishing ground to an undisturbed area in the NW Mediterranean. *Sci. Mar.* 75, 507–516.
- de Juan, S., Demestre, M., Thrush, S.F., 2009. Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: a Mediterranean case study. *Mar. Policy* 33, 472–478.
- de Juan, S., Hinz, H., Sartor, P., Vitale, S., Bentes, L., Bellido, J.M., Musumeci, C., et al., 2020. Vulnerability of demersal fish assemblages to trawling activities: a traits-based index. *Front. Mar. Sci.* 7, 44 (Frontiers Media SA).
- de Juan, S., Thrush, S.F., Demestre, M., 2007b. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Mar. Ecol. Prog. Ser.* 334, 117–129.
- Despoti, S., Milisenda, G., Ligas, A., Bentes, L., Maynou, F., Vitale, S., Garofalo, G., et al., 2020. Marine spatial closures as a supplementary tool to reduce discards in bottom trawl fisheries: examples from southern European waters. *Fish. Res.* 232.
- García-de-Vinuesa, A., Sola, I., Quattrocchi, F., Maynou, F., Demes, M., 2018. Linking trawl fleet dynamics and the spatial distribution of exploited species can help to avoid unwanted catches: the case of the NW Mediterranean fishing grounds. *Sci. Mar.* 82, 165–174.
- García-Rodríguez, E., Vivas, M., Bellido, J.M., Esteban, A., Torres, M.A., 2021. Ontogenetic shifts and feeding strategies of 7 key species of Gadiformes in the western Mediterranean Sea. *Fish. Bull.* 119, 50–65.
- Guillen, J., Holmes, S.J., Carvalho, N., Casey, J., Dörner, H., Gibin, M., Mannini, A., et al., 2018. A review of the European Union landing obligation focusing on its implications for fisheries and the environment. *Sustainability* 10, 900 (MDPI).
- Heath, M.R., Cook, R.M., Cameron, A.I., Morris, D.J., Speirs, D.C., 2014. Cascading ecological effects of eliminating fishery discards. *Nat. Commun.* 5, 3893.
- Hiddink, J.G., Hutton, T., Jennings, S.R., Kaiser, M.J., 2006. Predicting the Effects of Area Closures and Fishing Effort Restrictions on the Production, Biomass, and Species Richness of Benthic Invertebrate Communities, 63, 822–830.
- Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D., et al., 2017. Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc. Natl. Acad. Sci. USA* 114, 8301–8306 (National Acad Sciences).
- Hinz, H., Törnroos, A., de Juan, S., 2021. Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. *Ecol. Indic.* 126, 107692.
- Howarth, L.M., Somerfield, P.J., Blanchard, J.L., Waggett, J.J., Allender, S., Hiddink, J. G., 2020. The effects of trawling and primary production on size-structured food webs in seabed ecosystems. *Can. J. Fish. Aquat. Sci.* 77, 1659–1665. NRC Research Press 1840 Woodward Drive, Suite 1, Ottawa, ON K2C 0P7.
- Kaiser, M.J., Ramsay, K., 1997. Opportunistic feeding by dabs within areas of trawl disturbance: possible implications for increased survival. *Mar. Ecol. Prog. Ser.* 152, 307–310.
- Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C., Somerfield, P.J., Karakassis, I., 2006. Global analysis of response and recovery of benthic biota to fishing. *Mar. Ecol. Prog. Ser.* 311, 1–14.
- Law, R., Plank, M.J., 2018. Balanced harvesting could reduce fisheries-induced evolution. *Fish. Fish.* 19, 1078–1091 (Wiley Online Library).
- Law, R., Plank, M.J., Kolding, J., 2016. Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish. Fish.* 17, 281–302 (Wiley Online Library).
- Le Loc'h, F., Hily, C., Grall, J., 2008. Benthic community and food web structure on the continental shelf of the Bay of Biscay (North Eastern Atlantic) revealed by stable isotopes analysis. *J. Mar. Syst.* 72, 17–34 (Elsevier).
- Maynou, F., García-de-Vinuesa, A., Sánchez, P., Demestre, M., 2021. Bioeconomic impacts of two simple modifications to trawl nets in the NW Mediterranean. *Ocean Coast. Manag.* 213, 105853 (Elsevier).
- Mellon-Duval, C., Harmelin-Vivien, M., Métral, L., Loizeau, V., Mortreux, S., Roos, D., Fromentin, J.M., 2017. Trophic ecology of the European hake in the Gulf of Lions, northwestern Mediterranean Sea. *Sci. Mar.* 81, 7–18.
- Milisenda, G., Garofalo, G., Fiorentino, F., Colloca, F., Maynou, F., Ligas, A., Musumeci, C., et al., 2021. Identifying persistent Hot Spot areas of undersized fish and crustaceans in southern European waters: implication for fishery management under the discard ban regulation. *Front. Mar. Sci.* 8, 610241.
- Moutopoulos, D.K., Tsarakis, K., Machias, A., 2018. Assessing ecological and fisheries implications of the EU landing obligation in Eastern Mediterranean. *J. Sea Res.* 141, 99–111 (Elsevier).
- Muntadas, A., Demestre, M., de Juan, S., Frid, C.L.J., 2014. Trawling disturbance on benthic ecosystems and consequences on commercial species: a northwestern Mediterranean case study. *Sci. Mar.* 78, 53–65.
- Muntadas, A., de Juan, S., Demestre, M., 2016. Assessing functional redundancy in chronically trawled benthic communities. *Ecol. Indic.* 61, 882–892 (Elsevier Ltd).
- O'Neill, F.G., Feekings, J., Fryer, R.J., Fauconnet, L., Afonso, P., 2019. Discard avoidance by improving fishing gear selectivity: helping the fishing industry help itself. *The European Landing Obligation*. Springer, Cham, pp. 279–296.
- Pace, M., Glasser, J., Pomeroy, L., 1984. A simulation analysis of continental shelf food webs. *Mar. Biol.* 82, 47–63 (Springer).
- Prellezo, R., Carmona, I., García, D., 2016. The bad, the good and the very good of the landing obligation implementation in the Bay of Biscay: a case study of Basque trawlers. *Fish. Res.* 181, 172–185 (Elsevier).
- Ramsay, K., Kaiser, M.J., Hughes, R.N., 1998. Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *J. Exp. Mar. Biol. Ecol.* Vol. 224, 73–89.
- Rijnsdorp, A.D., Eigaard, O.R., Kenny, A.J., Hiddink, J.G., Hamon, K., Piet, G.J., Sala, A., et al., 2017. Assessing and mitigating of bottom trawling. Final BENTHIS Project Report, Benthic Ecosystem Fisheries Impact Study, Seventh Framework Programme.
- Rochet, M.-J., Catchpole, T., Cadrin, S., 2014. Bycatch and discards: from improved knowledge to mitigation programmes. In: *ICES Journal of Marine Science*, 71. Oxford University Press, pp. 1216–1218.
- Sánchez-Hernández, J., Nunn, A.D., Adams, C.E., Amundsen, P.-A., 2019. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. *Biol. Rev.* 94, 539–554 (Wiley Online Library).
- Scott, F., Blanchard, J.L., Andersen, K.H., 2014. Mizer: an R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods Ecol. Evol.* 5, 1121–1125 (Wiley Online Library).
- Sturludottir, E., 2018. Exploring the effects of discarding using the Atlantis ecosystem model for Icelandic waters. *Sci. Mar.* 82S1, 51–62 (Departamento de Publicaciones del CSIC).
- Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 33, 449–473.
- Tsarakis, K., Palialexis, A., Vassilopoulou, V., 2014. Mediterranean fishery discards: review of the existing knowledge. *ICES J. Mar. Sci.* 71, 1219–1234 (Narnia).
- Vasilakopoulos, P., Maravelias, C.D., Tserpes, C., 2014. The alarming decline of Mediterranean fish stocks. *Curr. Biol.* 24, 1643–1648.