

## Investigating fishery and climate change effects on the conservation status of odontocetes in the Northern Ionian Sea (Central Mediterranean Sea)

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### ABSTRACT

A modelling approach applied to the study of ecosystems from a management and conservation point of view allows their complexity to be investigated and represents a tool for meeting sustainability goals, part of the 2030 Agenda for Sustainable Development. Tying into Sustainable Development Goals (SDGs) 13 and 14, the human activities of fisheries and climate change represent two pivotal drivers for the marine environment, acting on keystone predators, such as odontocetes. A calibrated time-dynamic model (Ecopath with Ecosim) was developed to investigate the effects on the odontocetes and their main prey in the Northern Ionian Sea (Central Mediterranean Sea), according to changes in trawl fishery and primary productivity. In particular, the food web of the Gulf of Taranto (GoT) is described by 51 functional groups (FGs), with four odontocetes (striped, common bottlenose, Risso's dolphin and sperm whale) represented as a single FG, and 5 fishing fleets. The calibration of the Ecosim model was carried out during the period 2009–2018 using a combination of automatic and manual fitting procedures. Changes in trawling fishing effort (increases, reductions and bans) and in primary production were tested in the period until to 2040 to detect the effect on the biomass of odontocetes and their main prey. The cumulative effects of the two drivers were assessed using an Interaction Effect Index. Fishery showed negligible effects on all odontocetes, with the exception of the common bottlenose dolphin which respond in a negative way to an increase in fishing effort. The reduction in top-predators due to fishing seems to lead to a reduction in predation pressure on meso-consumers, and thus to an increase in predation pressure on basal prey. Similarly, the bottom-up effect due to increased primary production tends to be diluted towards the top of the trophic network, with slight effects on odontocetes. The trophic interaction pattern tends to mediate the effects tested in the model with a variety of different outcomes on prey. The application of the interaction effects index could contribute to disentangling the effects of fishing and climate on the food web, providing information to address the analysis required by the SDG 14 targets.

### 1. Introduction

The achievement of the UN Sustainable Development Goals (SDGs) represents a key challenge on a global scale in implementing an approach to managing human activities and their interactions with the biosphere in accordance with the principles of sustainability (Claudet et al., 2020; Molony et al., 2022). Among the SDGs, Goal 14 "Life below water" is surely one of the most challenging (United Nations, 2016). Indeed, the complexity of interacting ecological processes in marine

ecosystems, which act at different spatial scales, make it very difficult to direct the management of marine resources and biodiversity conservation towards a condition of sustainability. In addition, several factors play a role in the structure and functioning of marine ecosystems, and these components act in synergistic or antagonistic manner (Halpern et al., 2008).

Considering this complexity, SDG 14 is articulated in a list of targets, which addresses the operational actions towards specific topics of interest for its achievement, such as marine pollution, the management

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and protection of marine and coastal ecosystems, the mitigation of climate changes impacts (e.g., ocean acidification, etc.), the regulation of fishery exploitation, and several other targets (see [Sturesson et al., 2018](#)). In addition, there is relevant interconnection between SDG 14 and SDG 13 “Climate action”, since ocean waters have a huge capacity to absorb the heat gained by the planet ([Zanna et al., 2019](#)).

In the framework of SDG 14, targets define precise interconnected action fields and other SDGs ([Ntona and Morgera, 2018](#)). For example, the topic of habitat and ecosystem conservation (Target 14.2, Protect and restore ecosystems), requires investigation related to features of species ecological roles, community and food web structure, functional diversity, as well as anthropogenic pressures that could lead to impacts and losses of ecosystem functions ([Campagne et al., 2021](#)). From this perspective, fishing often represents a strong impacting stressor on single species, populations and entire ecosystems, requiring strong regulation and limitation actions ([Pauly et al., 2005](#); [Hilborn, 2007](#); [Link and Watson, 2019](#)). Thus, this condition binds Target 14.2 with Target 14.4 (Sustainable fishing), as well as the aims of the Target 14.1 (Marine pollution) addressed to mitigate the pollution induced by human land-based activities, such as marine litter and nutrient pollution. Further consideration concerns the impacts induced by global climate change, which is mainly dealt with in Target 14.3 (Reduce Ocean acidification), as the most important cause of ocean acidification. However, the multiple impacts generated by climate change are pervasive, also affecting the health of marine resources exploited by humans, as well as the ecosystem services provided by marine ecosystems ([Issifu et al., 2022](#)). Therefore, climatic drivers should also be considered in the assessment of components investigated in the previous targets.

The relationships between the SDG 14 targets reflects the complexity of marine ecosystems, which requires integrated approaches to assess their health status, as well as to understand the effects on ecological components induced by several stressors. In this framework, the food web modelling approach is useful to integrate these necessities, thanks to the model’s capacity to encompass the physical and human drivers of change in the entire ecosystem, from plankton to top predators ([Heymans et al., 2020](#)).

The Northern Ionian Sea (Central Mediterranean Sea) represents a very complex environmental context in the Mediterranean Sea, where the extreme northern part (Gulf of Taranto, GoT) is characterized by several critical habitats, and a hot-spot of cetaceans biodiversity, with peculiar environmental conditions that distinguish it from the rest of Northern Ionian Sea ([Carlucci et al., 2017, 2018](#); [Cipriano et al., 2022](#)). At the same time, the area is characterized by an important fishing activity and several anthropogenic pressures impacting the cetaceans in different ways ([Carlucci et al., 2021a](#); [Ricci et al., 2021a](#)). The need to provide time-dynamic models and indicators to predict the biomass trends of cetaceans and the interactive effects of anthropic and environmental factors is becoming urgent. Moreover, the possibility of implementing a time-model able to assess the cumulative impacts of multiple factors, such as climate and fishery ([Serpetti et al., 2017](#)), could support a comprehensive evaluation of the cause-effect relationships, disentangling the more important factors acting on these top-predators. This is particularly important for the study of odontocetes in this Mediterranean area, where they play an important role as keystone species in the ecosystem and in controlling trophic cascades ([Ricci et al., 2019, 2020a](#); [Carlucci et al., 2021b](#)). Investigations on the competition between cetacean-fishery have shown a scarce trophic niche overlap between cetaceans and the fishing fleet, except for the common bottlenose dolphin ([Ricci et al., 2021a](#)). However, these assessments were conducted using a static modelling approach that lacks details on the temporal evolution of trophic interactions. Thus, outcomes provided by a time-dynamic model could be used to address the implementation of cetacean conservation plans and in the management regulation of the fishery in the area ([Carlucci et al., 2022](#)).

In this study, the effects on the odontocetes distributed in the GoT

due to the changes in fishing effort and climate have been assessed through a mass-balance calibrated food-web model. Several scenarios were applied to provide estimates of odontocete biomasses and their main prey in the mid-term future (2035–2040), driven by the cumulative effects of fishing effort (FE) changes, namely increases, reductions and banning, and the increase in net primary production (NPP).

## 2. Materials and methods

### 2.1. Modelling approach

The time-dynamic routine of the Ecosim modelling approach (EwE v. 6.6.5, <http://www.ecopath.org>, [Christensen and Walters, 2004](#)) was applied to an Ecopath static food-web model developed for the assessment of cetacean-fishery competition in an area of 7745 km<sup>2</sup>, included in the depth range of 10–800 m, located within the Gulf of Taranto (GoT, Northern Ionian Sea, [Carlucci et al., 2021b, Fig. 1](#)). This mass-balance model describes the food web through 51 functional groups (FGs, [Table 1](#)) and 5 fishing segments (trawl, longlines, passive nets, other gears and purse seine) using the biomass (B, t km<sup>-2</sup>), production (P/B) and consumption (Q/B) rates, catches (C, as Landings + Discards) and Ecotrophic Efficiency (EE) as input data for each modelled FG (more details are reported in [Carlucci et al., 2021b](#)). The fishing activities are distributed in this bathymetric range, where otter bottom trawls (OTB) were the main fishing fleet, followed by passive nets and longline ([Russo et al., 2017](#)). Four FGs represent the odontocetes occurring in the food web of the GoT. They are the striped dolphin (*Stenella coeruleoalba*), the most abundant and frequent species occurring in the area ([Carlucci et al., 2016, 2018, 2021a](#)); the common bottlenose dolphin (or bottlenose dolphin, *Tursiops truncatus*), the second most frequently observed species both in coastal and pelagic waters ([Santacesaria et al., 2019](#); [Cipriano et al., 2022](#)), as well as the Risso’s dolphin (*Grampus griseus*) and the sperm whale (*Physeter macrocephalus*), an endangered species observed seasonally in the area ([Bellomo et al., 2019](#); [Cipriano et al., 2022](#)).

Starting from a static mass-balance model, the temporal dynamics of the food web can be modelled according to Ecosim routine using the following system of differential equations:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} - (M_i + F_i) \cdot B_i \quad (1)$$

where,  $\frac{dB_i}{dt}$  is the biomass growth rate of group (i) during the interval dt,  $g_i$  the net growth efficiency (production/consumption ratio),  $M_i$  and  $F_i$  the natural and fishing mortality rates of group (i). Migration rates were not considered. The consumption rates  $Q_{ij}$  are calculated based on the “foraging arena” theory (animals balance predation risk with foraging activity) where the prey biomasses are divided into vulnerable and invulnerable components ([Christensen and Walters, 2004](#)).

Considering the principles assumed by the “foraging arena” theory ([Ahrens et al., 2012](#)), the interactions between predators and prey are modelled by means of a set of parameters in Ecosim, among which is included the so called “vulnerability”, adopted as a tuning parameter for all functional groups ([Christensen and Walters, 2004](#)). Substantially, only a fraction of the biomass of prey is available to the predator, and this is dynamically described through the vulnerability parameter, specific for each prey-predator interaction ([Walters et al., 2000](#)). In addition, the vulnerability represents the effect of prey and predator density on the consumption by a predator, which identifies top-down and bottom-up processes between predators and prey across the food web ([Walters and Christensen, 2007](#); [Ahrens et al., 2012](#)). The balance condition between top-down and bottom-up controls is represented by a default vulnerability ( $v$ ) equal to 2, while  $v < 2$  and  $v > 2$  represent bottom-up and top-down controls, respectively ([Ahrens et al., 2012](#)). No less important, vulnerabilities are used as a tuning parameter to fit the historical observed data under simulated dynamics forced by primary

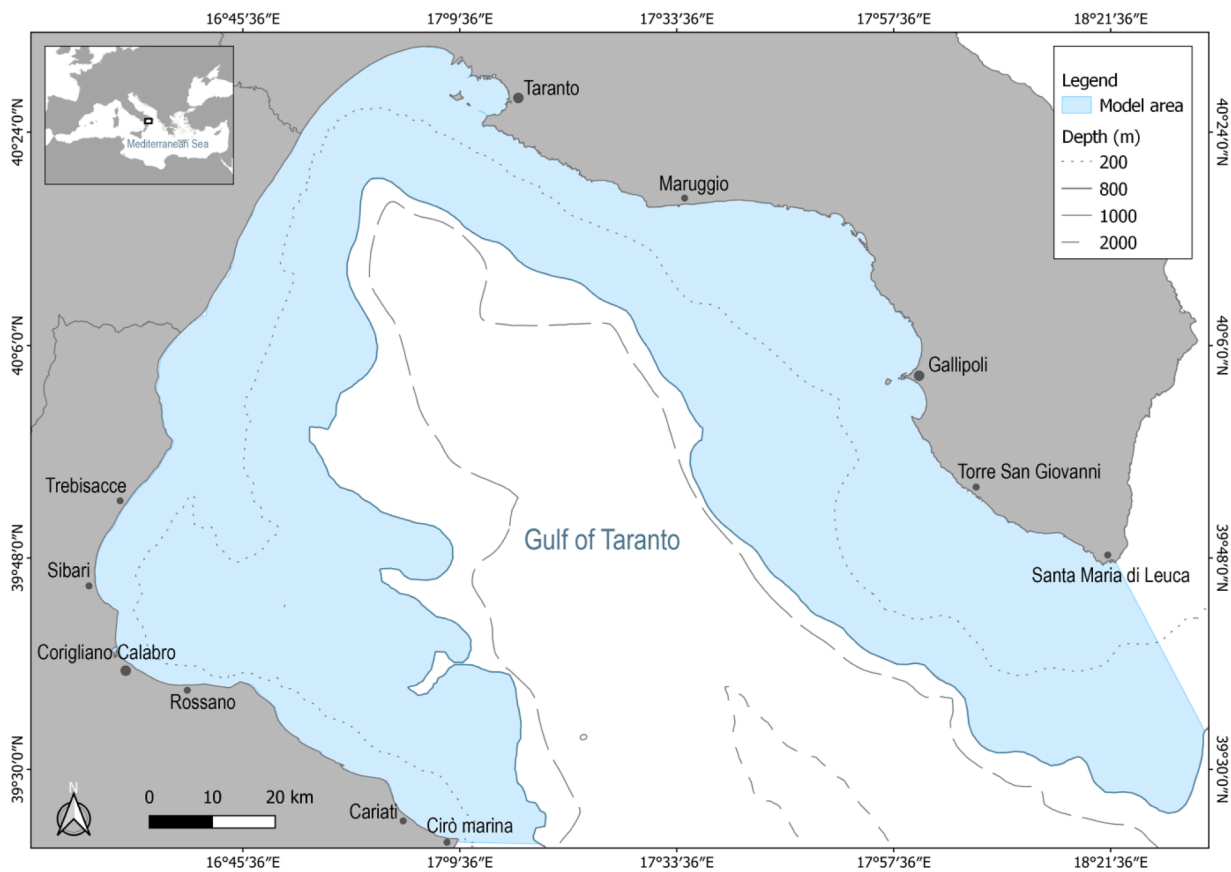


Fig. 1. Map of the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea) displaying the modelled area. The names of the main fishing harbours operating in the study area are reported.

Table 1  
Functional groups name and code used in the Ecosim model.

N.	Functional group	FG code	N.	Functional group	FG code
1	Striped dolphin	S_dolph	27	Hake	Hake
2	Common bottlenose dolphin	CB_dolph	28	Anglers	Anglers
3	Risso's dolphin	R_dolph	29	Slope Squids benthopelagic feeders	SL_Squids
4	Sperm whale	S_whale	30	Shelf Squids benthopelagic feeders	SH_Squids
5	Fin Whale	F_whale	31	Shelf Cephalopods benthic feeders	SH_Ceph
6	Loggerhead Turtle	Log_turtle	32	Slope Octopus and Bobtail Squids benthic feeders	SL_Ceph
7	Seabirds	Seabirds	33	Slope Bobtail Squids benthopelagic feeders	SL_BobSquids_BP
8	Large pelagic fishes	L_pel_F	34	Benthopelagic Shrimps	Shrimps
9	Slope Sharks and Rays benthic feeders	SL_SharksRays_B	35	Slope Decapods Scavengers	SL_Decap_scv
10	Shelf Sharks and Rays benthopelagic feeders	SH_SharksRays_BP	36	Shelf Crabs	SH_Crabs
11	Shelf Sharks and Rays benthic feeders	SH_SharksRaysR_B	37	Deep-water rose shrimp	DWR Shrimp
12	Slope Sharks benthopelagic feeders	SL_Sharks_BP	38	Red giant shrimp	RG Shrimp
13	Slope Demersal fishes generalist feeders	SL_DemFishes_gen	39	Blue and red shrimp	RB Shrimp
14	Shelf Demersal fishes generalist feeders	SH_DemFishes_gen	40	Polychaets	Polychaets
15	Shelf Demersal fish piscivorous	SH_DemFishes_pisc	41	Macrobenthicinvertebrates	Macrobentinv
16	Slope Bathypelagic fishes piscivorous	Bathypel_Fishes_pisc	42	Gelatinous plankton	Gel plank
17	Slope Demersal fishes decapods feeders	SL_DemFishes_decap	43	Suprabenthic crustaceans	Supbentcrust
18	Slope Fishes benthopelagic crustacean feeders	SL_Fishes_BPcrust	44	Macrozooplankton	Macrozooplank
19	Shelf Demersal fishes benthic crustacean feeders	SH_DemFishes_Bcrust	45	Meso and Microzooplankton	Meso_Microzooplank
20	Shelf Demersal fishes benthic invertebrate feeders	SH_DemFishes_Binv	46	Bacterioplankton	Bacterioplank
21	Shelf Fishes zooplanktivorous	SH_Fishes_plank	47	Seagrasses and Macrophytobenthos	Seagrasses and algae
22	Small pelagic fishes	Small_pel_Fishes	48	Phytoplankton	Phytoplank
23	Medium pelagic fishes	Med_pel_Fishes	49	Discards	Disc
24	Macrourids benthic invertebrate feeders	Macrourids	50	Marine snow	M Snow
25	Mesopelagic fishes	Mesopel_Fishes	51	Bottom Detritus	Det
26	Red mullet	R_mullet			

production and/or fishing effort changes (Araújo et al., 2008). Together with trophic interactions modelled through vulnerability, temporal predictions in the model can be adapted to observed data using environmental variables, as well as fishing drivers over time, and these are

represented as forcing functions (Heymans et al., 2016).

The GoT mass-balance model realised for the period 2010–2014 (Carlucci et al., 2021b) was calibrated using a spin-up of 5 years (2005–2009), while the fitting of the dynamic food-web model was

performed for the period 2010–2018 (hindcast) using biological and fishery information organized as a series of yearly data of biomass and catches. Finally, the calibrated model was used to test temporal scenarios of fishery and climate change in the future, up to 2040.

## 2.2. Biological and fishery data and parametrization of the model

Biomass time series for each benthopelagic and demersal FG were obtained from MEDITS data collection (Spedicato et al., 2019), while biomass data on the 4 odontocetes were estimated using abundance data collected through monitoring surveys conducted by Ionian Dolphin Conservation using the distance sampling method (see Carlucci et al., 2017). Abundance data were transformed into biomass using the individual weight of investigated odontocetes using information on body-mass weight available for the study and surrounding areas (Pirioddi et al., 2010; Ricci et al., 2020b; Ingrosso et al., 2022). In the absence of continuous data time series and robust information, other groups belonging to the pelagic (FGs 5–8), benthic and planktonic domains (FGs 40–48) were not used to calibrate the model.

Official annual fishery landings (tonnages, period 2009–2018) by species and gears were obtained from the EU Data Collection Framework provided by the Fisheries and Aquaculture Economic Research for the Ministry of Agricultural Food and Forestry Policies (MIPAAF). Data were standardized on the model area and aggregated into the functional groups according to the taxa.

Discard data of commercial and by-catch groups and species were estimated by means discard rates obtained from the EU Data Collection Framework. Whereas the discard of non-commercial species (or totally discarded species) was estimated through a proportion between their biomass sampled in the MEDITS research program in relation to the biomass of commercial species sampled in the same project and in the official landings (for more details see Ricci et al., 2019). Although the selectivity of the bottom trawl net differs slightly between that of the MEDITS experimental survey and that of professional fishing, the estimation method is a reliable proxy for the quantification of totally discarded species (D’Onghia et al., 2003). Finally, landings and discard data were summed by FGs providing the effective catch data incorporated in the time series used for the calibration.

A total of 67 time series (hereafter also indicated as *complete time series*), composed of 35 and 32 time series of biomass and catch data, respectively) were first revised, in order to erase the outliers reducing potential noise in the calibration process (Figure S1, S2) and then used for a first calibration step (Table S1). Outliers were identified as values higher and lower 1.5 times the interquartile range above the upper and lower quantiles. In addition, a second calibration step was carried out by selecting 61 time series (hereafter referred to as *reduced time series*), in which biomass and catches of following FGs were excluded: SL\_SR\_B (catch data), Bathypel\_Fishes\_pisc (catch data), Mesopel\_Fishes (catch data), SL\_Ceph (catch data), SL\_BobSquids\_BP (biomass and catch data). In fact, said FGs showed unreliable data as they belonged to benthopelagic species that are usually completely discarded by trawl fishery, and not adequately sampled by this type of net.

For both time series, the group info of FGs was set with default values for all variables, except for the feeding time adjust rates of marine mammals, which were fixed to 0.5 according to Christensen et al. (2008).

## 2.3. Fitting procedures and application of forcing functions

In the Ecosim fitting procedure, the model’s hindcast outputs over time against independent observations (FG biomasses and time series of catches) were calibrated for 2009–2018. The goodness of fit was evaluated by the weighted sum of squares (SS), calculated from the deviations of log observed biomasses from log predicted biomasses calculated for each model run (Christensen et al., 2008), the Akaike

information criterion (AIC, Akaike, 1974), and the corrected AIC (AICc, Burnham et al., 2004). A series of trials were performed during the fitting process by changing the vulnerability values and forcing fishing pressure and primary productivity, to find the best fit model characterized by the lowest AICc (Heymans et al., 2016).

In our approach, the stepwise fitting routine (Scott et al., 2016) was applied adopting both “*by predator*” and “*by predator-prey*” strategies to estimate vulnerability multipliers (Christensen et al., 2008). These strategies are based on searching the vulnerability multipliers to fit predictions to observed data. In the search for “*by predator*” vulnerabilities, a single multiplier is applied homogeneously across all prey for a predator functional group, while in searching for “*by predator-prey*” vulnerabilities, different multipliers are estimated for the most sensitive predator–prey binary interactions (those which have the greatest impact on the model fit, Bentley et al., 2020). In addition, a further fitting step was performed using the manual searching routine based on the “*by predator-prey*” strategy according to the approach of Bentley et al. (2020), in which a hybrid approach using both “*by predator*” and “*by predator-prey*” strategies were adopted, in order to resolve the binary predator-prey interactions and improve the model fitting. The number of vulnerability multipliers changed in the fitting procedures should not exceed the number of independent time-series to avoid over-parameterization (Mackinson et al., 2009).

The annual fishing effort by fishing gears during the period 2009–2019 was obtained from the European Fleet Register (<http://ec.europa.eu/fisheries/fleet/index.cfm>, accessed on 12 January 2022), as the number of vessels calculated considering a total of 11 fishing harbours distributed in the modelled area (Fig 1). The choice of using the number of vessels as an indicator of fishing pressure, rather than other fishing indicators, is due to the need to better describe this driver in the modelled area. In fact, other fishing indicators, such as fishing days or hours, are officially available on a geographical sub-area scale (GSA 19, more than 16,000 km<sup>2</sup>), which is wider than the GoT. Thus, adopting other indicators could have risked overestimation of fishing pressure. The relative fishing effort value, adopted as a forcing function by the Ecosim routine, was calculated as the ratio between the number of vessels in the considered year and the mean FE in the time span 2009–2018 (Fig. 2.a; Table S2).

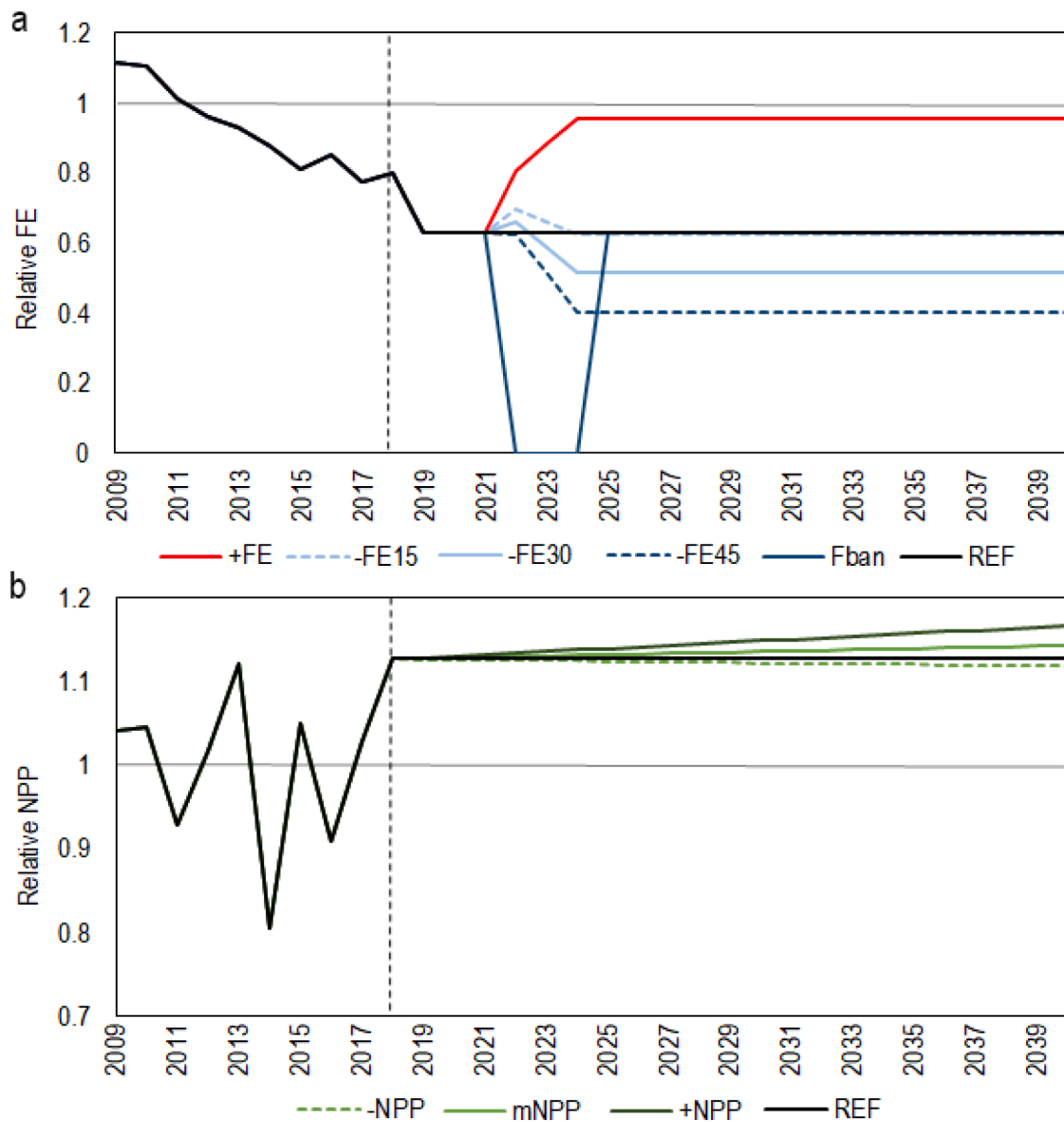
Finally, the annual NPP was estimated by Copernicus Marine Service (CMEMS) and used as a bottom-up forcing function in the model (Fig. 2. b; Table S2). Original geo-referenced CMEMS data, expressed as gCm<sup>-3</sup>, were extracted for the studied area, in the period 2009–2018, and integrated over depth (10–200 m) to obtain the NPP referred to the surface unit in the photic zone (Cossarini et al., 2021). NPP, extracted from Copernicus database (CMEMS, Mediterranean Sea Biogeochemistry Reanalysis, MEDSEA\_MULTIYEAR\_BGC\_006\_008; Cossarini et al., 2021), was chosen as an indicator of energy input in the system to force the bottom-up effects in the food web; as phytoplankton in this model is represented by only one group that encompass different phytoplankton taxa (Carlucci et al., 2021b), NPP was selected as a proxy for production that better represents different turnover rates across phytoplankton taxa than phytoplankton biomass. Moreover, for our study area Copernicus was not providing data for different phytoplankton sizes.

## 2.4. Tested scenarios

The effects of fishery and climate change on the cetaceans and the entire food web were assessed by means of temporal simulations based on the best fit model selected through the calibration process. The simulation period corresponds to approximately two decades in the future (2019–2040), and a total of 10 scenarios were set to represent plausible conditions of changes in the supposed fishing effort and primary production in the investigated food web (Table 2, Fig 2.a, b).

The reference scenario (REF) was set with constant FE and NPP values observed at the end of the hindcast period (2018).

A total of 5 scenarios were applied to assess the impact of changes of



**Fig. 2.** a, b: Relative values of a) Fishing effort (FE) and b) net primary production (NPP) used as forcing functions in the Ecosim model. Vertical dashed line separates the observed trends (2009–2018) and the future scenarios (2018–2040). Codes and details of tested scenarios in the legend are reported in Table 2.

trawl fishing fleet effort (Table 2). The total reduction and increasing tested were equal to -15%, -30%, -45%, and +30%, changing gradually across three years (2022–2024) with respect to the 2017–2019 mean effort value. After 2024, the FE level was kept constant to 2024 value. In all FE scenarios, NPP was set constant to 2018 value. The ranges of the FE scenario tested were chosen considering the context of multi-annual management plans of the fishery in the Mediterranean Sea (Common Fishery Policy, 2013), simulating realistic applications of the effort reduction adopted within several Mediterranean regions (Regulation EU, 2019/1022; Recommendation GFCM/43/2019/5). Thus, the scenarios analysed in this study are a preliminary trade-off of more plausible conditions occurring in the conservation and management plans.

Climate scenarios consisted in 3 simulations, in which NPP changes were set using the projection of RCP 8.5 for the Eastern Mediterranean Sea (Reale et al., 2022), adopting the mean value (mNPP), and minimum (-NPP) and maximum (+NPP) values obtained from the standard deviation ( $\pm$ SD) from Reale et al. (2022) model predictions. Therefore, PPN values increased from 2019 up to 2040, and the percentage of changes was calculated.

Finally, the cumulative scenario was the combination of fishing effort reduction (-FE10) and climate change represented by trend of the mNPP.

To assess the quality of the input data in terms of sensitivity and uncertainty of the best-fitted model, Monte Carlo simulations were performed (Heymans et al., 2016) testing the uncertainties propagation assuming 10% changes of Ecopath basic inputs (B, P/B, Q/B and EE). Thus, a total of 100 Monte Carlo simulation trials for each investigated FG were carried out for the REF scenario (2009–2040) and 5% and 95% confidence intervals were calculated.

### 2.5. Assessment of scenario outputs

The impact of the scenarios tested was assessed in terms of changes of biomasses of target odontocetes and their main preys, defined as the food items corresponding to a cumulative dry weight equal to at least 60% in each odontocetes' diet (Table S3).

Temporal trends of species biomasses across scenarios were visualised as relative changes.

For the reference scenario (keeping trawling fishing effort and NPP

**Table 2**

Summary of scenarios used for the modelling analysis, and the features of the OTB Fishing Effort (FE) and Net Primary Production (NPP) applied into the simulations (to see main text for details).

Scenario	Code	FE (applied during 2022–2024)	NPP (2019–2040)
Reference scenario	REF	constant at 2018 value	constant at 2018 value
FE increasing	+FE	Increasing of 30% for OTB	constant at 2018 value
FE decreasing	-FE15	reduction of 15% for OTB	constant at 2018 value
FE decreasing	-FE30	reduction of 30% for OTB	constant at 2018 value
FE decreasing	-FE45	reduction of 45% for OTB	constant at 2018 value
Fishing ban	Fban	Fishing ban for OTB	constant at 2018 value
Climate max NPP	+NPP	constant at 2018 value	RCP_8.5 (+3.58%)
Climate mean NPP	mNPP	constant at 2018 value	RCP_8.5 (+1.44%)
Climate min NPP	-NPP	constant at 2018 value	RCP_8.5 (−0.76%)
Cumulative	CUM	-FE10	mNPP

as in 2018), percentage of changes (and standard deviations) were evaluated for the short term (or near future, 2026–2030) and for the medium term (or mid future, 2036–2040) in relation to the REF 2018 values.

Relative changes between each tested scenario and REF were assessed comparing the mean biomass ratio calculated at the near and mid-term future (Agnetta et al., 2022). Therefore, mean biomass ratios lower than 1.00 indicate a reduction in the scenario tested whilst values higher than 1.00 represent a biomass increase. Moreover, catches of the main preys of the target odontocetes were also assessed for the tested scenarios (Red Mullet, Small pelagic fishes, SHB Squids, SH Cephalopods).

The interactive effects between fishery and climate on FG biomass were estimated according to the Interaction Effect Index (IEI, Allgeier et al., 2011; Villar-Argaiz et al., 2018), expressed in the following equation:

$$IEI = \ln \left[ \text{Abs} \left( \frac{\text{effect Cumulative}}{\text{effect}(-FE) + \text{effect}(+NPP)} \right) \right] \quad (2)$$

where Abs = absolute value, effect Cumulative = effects of the combination scenario, effect -FE = effect of fishing effort reduction scenario, and effect +NPP = effect of the Climate scenario.

IEI allows us to identify synergistic effects (IEI > 0), antagonistic effects (IEI < 0) or purely additive effects (IEI = 0) due to the different impacts of fisheries and climate tested in the scenarios (Agnetta et al., 2022).

### 3. Results

#### 3.1. Fitting and validation of the model

Unfitted models showed an SS = 1580.9 and AICc = 580.5 for the complete time series, and an SS=744.1 and AICc=162.0 for the reduced time series, with an SS improvement of 52.9% (Table 3). Therefore, the stepwise fitting was carried out using the reduced time series, and the best fit model (SS = 662.2 and AICc = 122.3) was obtained by means of a “by predator” strategy forcing the fishing effort in the automatic fitting procedure, with a total of 12 vulnerabilities changed. This best fit model was used for the second calibration step based on the manual searching, obtaining the last best fit model (SS = 644.4, AICc = 84.7) through a “by predator-prey” strategy, with a change of 48 vulnerabilities in total after 3 rounds of manual searching. The improvement in SS of this last model was of 59.2% with respect to the initial unfitted model. The fitting

**Table 3**

Time series used in the model fitting as all available time series (Complete) or time series with the selection of discard time series (Reduced), the fitting type as automatic (A) or manual (M), the strategy adopted in the fitting of trophic relationships as predator (P) or predator-prey (Pp), the number of parameters (K) adopted during the fitting steps, the number of vulnerabilities changed (Vs), Sum of Square (SS), corrected Aikaike Information criterion (AICc) and the improvement in SS (SS imp.%) during the automatic-manual fitting procedure. The best fit model (in bold) is reported for manual fitting, taken from the automatic procedure and the number of vulnerabilities changed in this model.

Time series	Fitting type	Strategy	K	Vs	SS	AICc	SS imp. %
Complete	No-fit	–	–	–	1580.9	580.5	–
Complete	A	P	66	10	1452.9	549.1	+8.1
Complete	A	Pp	66	5	1488.6	553.6	+5.8
Reduced	No-fit	–	–	–	744.1	162.0	+52.9
<b>Reduced</b>	<b>A</b>	<b>P</b>	<b>60</b>	<b>12</b>	<b>662.2</b>	<b>122.3</b>	<b>+58.1</b>
Reduced	A	Pp	60	5	688.6	129.1	+56.4
Reduced	M1 P v = 12	Pp	48	24	652.3	132.9	+58.7
Reduced	M2 P v = 12	Pp	24	18	646.1	121.4	+59.1
<b>Reduced</b>	<b>M3 P v = 12</b>	<b>Pp</b>	<b>6</b>	<b>6</b>	<b>644.4</b>	<b>84.7</b>	<b>+59.2</b>

results of the main functional groups analysed in the study are reported in Supp. Mat. (Figure S3).

#### 3.2. Scenario analysis

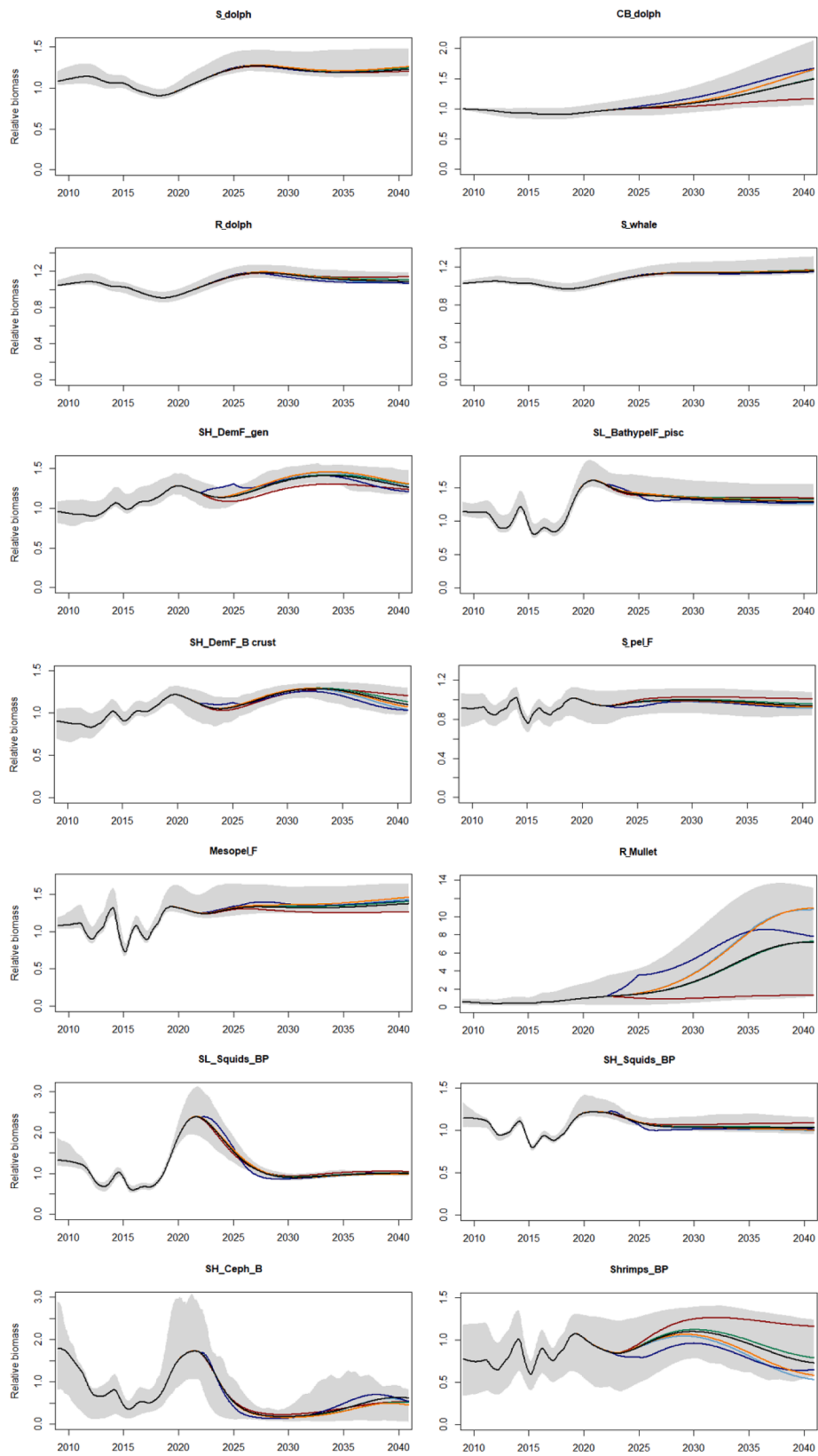
In Fig. 3 outputs for all investigated odontocetes and their main preys were visualised only for selected scenarios for the sake of clarity (REF, +FE, -FE30, Fban, mNPP and CUM). Outputs for other scenarios (-FE15, -FE45, +NPP and -NPP) showing similar overlapping results are reported in Table S4. In all scenarios, odontocetes showed trends characterized by increases in biomass in the future, with the mean value in the 2036–2040 period higher than in 2018. In particular, CB\_dolph showed a regular increase in biomass up to the end of simulations, while other odontocetes were characterized by a general stabilisation of biomass values from the 2024–2027 period onwards.

#### 3.3. REF scenario

In the REF scenario (keeping trawling fishing effort and NPP as in 2018), odontocetes biomass showed an increase in the mid-term future, with the highest positive change observed for bottlenose dolphin (+53.5% compared to 2018) (Table 4). In addition, the striped dolphin showed a positive change in mean biomass equal to +33.1% compared to 2018, and the Risso’s dolphin and the sperm whale showed increases in biomass of around 18–20%. Furthermore, starting from the 2024–2027 period, the biomass of the Risso’s dolphin showed a weak decreasing trend, while that of the sperm whale was weak increasing (Fig. 3). Considering the main prey in the REF scenario, all FGs showed an increase in mean biomass in the mid-term future compared to the 2018 value, except for SH\_Ceph, Shrimps\_BP and Small\_pel\_F, which were characterized by percentage decreases in biomass of −25.2%, −18.8% and −3.5%, respectively (Table 4). The highest positive change in biomass in the 2036–40 period compared to 2018 was estimated for the R\_mullet, with an increase in biomass of +795%, followed by Bathypel\_Fishes\_pisc, with an increase in biomass of +21.1, and SH\_DemFishes\_gen with an increase in biomass of 12.5% compared to 2018.

#### 3.4. Fishing effort changes scenarios

In the -FE30 and Fban scenarios (reduction and ban in fishing pressure, respectively), the estimated mean biomass for the bottlenose



**Fig. 3.** Trends of relative biomass predicted by the Ecosim model in the GoT (2009–2040) for each tested scenario (black = REF, red = +FE, light blue = -FE30, dark blue = Fban, green = Climate mNPP, orange = CUM). 95% and 5% percentiles calculated for the REF scenario are plotted (grey area). The names of odontocetes and their prey are coded in [Table 1](#).

**Table 4**

Changes in mean biomasses ( $\pm$  standard deviation) estimated in the REF scenario during near and mid-term future compared to 2018. Shades of blue represent different levels of percentage increase in biomass, shades of red represent biomass decrease.

FGs	2018	2026-2030	Near future	2036-2040	Mid-term future
S_dolph	0.04	0.05 $\pm$ 0.001	38.3%	0.05 $\pm$ 0.001	33.1%
CB_dolph	0.01	0.01 $\pm$ 0.0002	17.1%	0.01 $\pm$ 0.0005	53.5%
R_dolph	0.01	0.01 $\pm$ 0.0001	29.5%	0.01 $\pm$ 0.00001	20.7%
S_whale	0.02	0.02 $\pm$ 0.0001	17.4%	0.02 $\pm$ 0.0001	18.7%
SH_DemFishes_gen	0.41	0.45 $\pm$ 0.022	9.7%	0.46 $\pm$ 0.014	12.5%
SH_DemFishes_B crust	0.61	0.65 $\pm$ 0.030	5.8%	0.63 $\pm$ 0.025	2.7%
Bathypel_Fishes_pisc	0.32	0.40 $\pm$ 0.005	27.0%	0.39 $\pm$ 0.002	21.1%
Small_pel_Fishes	1.41	1.43 $\pm$ 0.003	0.8%	1.36 $\pm$ 0.012	-3.5%
Mesopel_Fishes	1.53	1.64 $\pm$ 0.005	7.2%	1.67 $\pm$ 0.017	9.3%
R_mullet	0.11	0.32 $\pm$ 0.076	197.4%	0.97 $\pm$ 0.049	795.5%
SL_Squids	0.08	0.09 $\pm$ 0.011	6.4%	0.09 $\pm$ 0.001	6.0%
SH_Squids	0.13	0.13 $\pm$ 0.001	1.5%	0.13 $\pm$ 0.0001	0.5%
SH_Ceph	0.17	0.05 $\pm$ 0.010	-72.5%	0.13 $\pm$ 0.015	-25.2%
Shrimps_BP	1.49	1.61 $\pm$ 0.057	8.1%	1.21 $\pm$ 0.089	-18.8%

dolphin and striped dolphin showed positive changes, which were more marked for the former (-FE30/REF ratio = 1.08  $\pm$  0.015; Fban/REF ratio = 1.13  $\pm$  0.004) than for the latter (-FE30/REF ratio = 1.01  $\pm$  0.003; Fban/REF ratio = 1.02  $\pm$  0.005) (Fig. 3, Table 5). Differently, the Risso's dolphin showed a negative response to fishery reduction or a fishing ban, with mean biomass ratios lower than 1.00 in the 2036–40 period. Similarly, the sperm whale showed a mean biomass ratio lower than 1.00 in the mid-term future of the Fban scenario.

In the +FE scenario (increase in trawl fishing effort between 2022 and 2024), the bottlenose dolphin mean biomass in the mid-future was lower than that estimated in the REF scenario (+FE/REF ratio = 0.82  $\pm$  0.028), and the striped dolphin also showed a slight decrease in 2036–40 (+FE/REF ratio = 0.99 $\pm$ 0.006). On the other hand, the Risso's dolphin and sperm whale showed a positive response to an increase in fishing effort, which was more pronounced for the former (+FE/REF ratio = 1.04 $\pm$ 0.005) than the latter (+FE/REF ratio = 1.01 $\pm$ 0.002).

The odontocetes' prey showed different responses to the trawling fishing effort changes. In the mid-term future, increased trawling effort had a negative effect on the mean biomass of R\_mullet, SH\_Ceph, Mesopel\_Fishes and SH\_DemFishes\_gen (Table 5). Differently, a relevant positive effect due to an increase in fishing effort was detected for the Shrimps\_BP, with the highest increase (+FE/REF ratio = 1.48 $\pm$ 0.083),

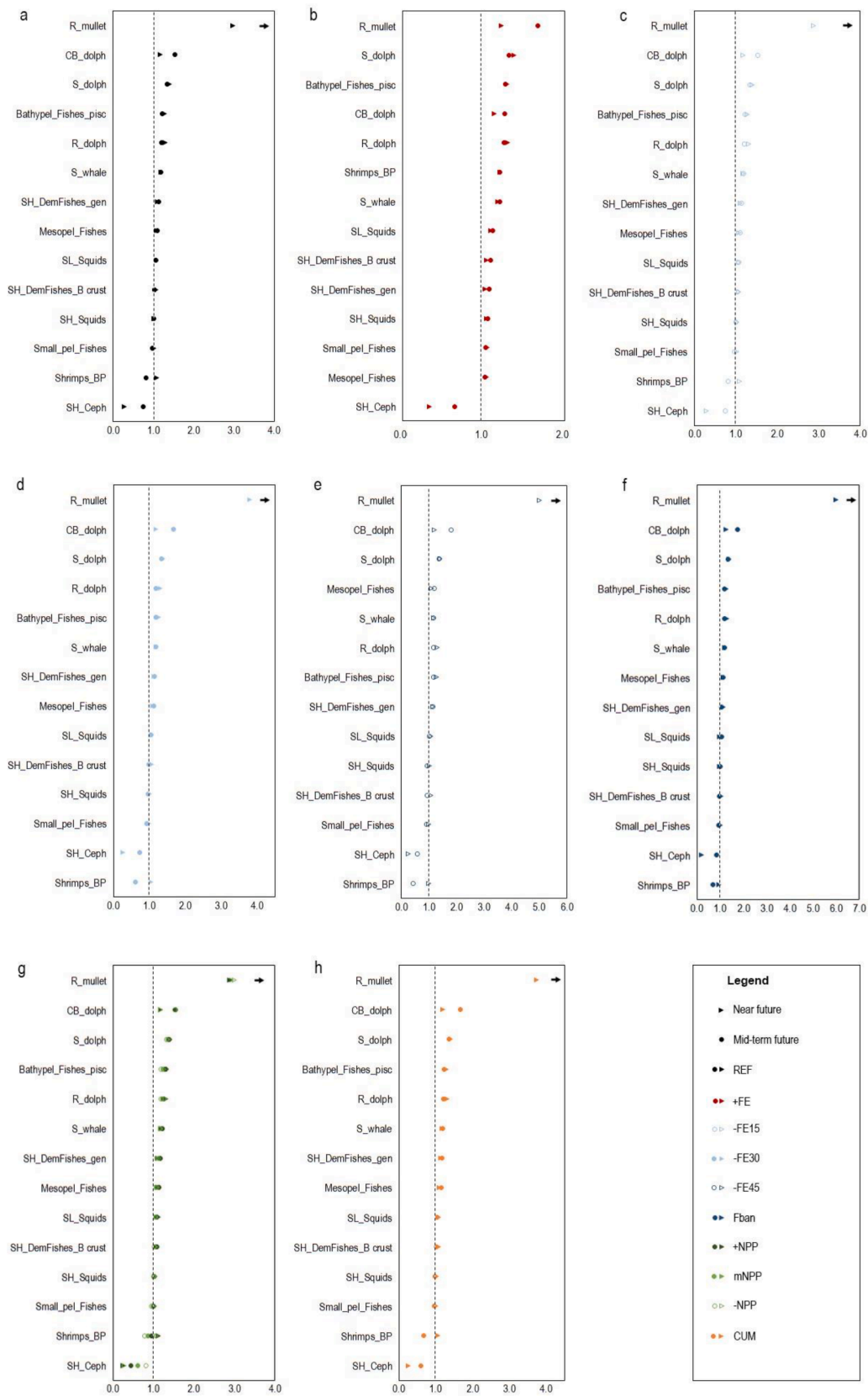
followed by Small\_pel\_Fishes and SH\_DemFishes\_B crust (Table 4). Some prey showed a similar response in both fishing effort reduction scenarios, such as SH\_DemFishes\_B crust, Bathypel\_Fishes\_pisc, Small\_pel\_Fishes, SH\_Squids and Shrimps\_BP with a slight reduction in biomass (between a mean value of 0.93 and 0.99). On the other hand, R\_mullet and Mesopel\_Fishes showed an increase in biomass both in -FE30 and Fban scenarios, with the highest increase in -FE30/REF ratio = 1.51 ( $\pm$  0.006) for the former species (Table 5). In addition, some cephalopod groups showed opposite responses in the two fishery reduction scenarios, with an increase in the mean biomass in the Fban scenario, and vice versa.

The mean biomass values of the two future spans, as relative to 2018, are displayed in Fig. 4b–d. Considering the +FE scenario, the investigated FGs showed a mean biomass increase of 1.16  $\pm$  0.223, with the maximum and minimum values showed by R\_mullet (1.67) and SH\_Ceph (0.64), respectively (Fig 4b). Considering the -FE30 scenario, FGs showed a mean biomass increase of 1.97 $\pm$ 3.336 with a maximum increase of 13.53 for R\_mullet and a minimum value of 0.62 Shrimps\_BP (Fig 4c). Similarly, in the Fban scenario a mean value of 1.80 $\pm$ 2.616 was displayed, which ranged between 10.84 for R\_mullet and 0.67 for Shrimps\_BP (Fig 4d). In addition, the FGs SHB\_Squids feed, SH\_DemFishes\_B crust, Small\_pel\_Fishes and SH\_Ceph showed a decrease in

**Table 5**

Mean biomass ratios ( $\pm$  SD) of each investigated FG calculated by comparing tested scenarios with the REF at the endpoint in the mid-term future (2036–2040). Shades of red/blue in each row indicate ratios lower/higher than 1. FG names are reported in Table 1, and scenarios details are explained in Table 2.

FGs	+FE	-FE30	Fban	mNPP	CUM	-F15	-F45	+NPP	-NPP
S_dolph	0.99 $\pm$ 0.006	1.01 $\pm$ 0.003	1.02 $\pm$ 0.005	1.02 $\pm$ 0.001	1.02 $\pm$ 0.002	1.00 $\pm$ 0.000	1.02 $\pm$ 0.006	1.04 $\pm$ 0.001	0.99 $\pm$ 0.000
CB_dolph	0.82 $\pm$ 0.028	1.08 $\pm$ 0.015	1.13 $\pm$ 0.004	1.00 $\pm$ 0.001	1.09 $\pm$ 0.16	1.00 $\pm$ 0.000	1.18 $\pm$ 0.032	1.01 $\pm$ 0.002	1.00 $\pm$ 0.001
R_dolph	1.04 $\pm$ 0.005	0.99 $\pm$ 0.002	0.98 $\pm$ 0.003	1.02 $\pm$ 0.001	1.00 $\pm$ 0.002	1.00 $\pm$ 0.000	0.97 $\pm$ 0.005	1.04 $\pm$ 0.002	0.99 $\pm$ 0.000
S_whale	1.01 $\pm$ 0.002	1.00 $\pm$ 0.001	0.99 $\pm$ 0.001	1.01 $\pm$ 0.001	1.01 $\pm$ 0.001	1.00 $\pm$ 0.000	0.99 $\pm$ 0.002	1.03 $\pm$ 0.002	0.99 $\pm$ 0.000
SH_DemFishes_gen	0.95 $\pm$ 0.016	1.01 $\pm$ 0.006	0.95 $\pm$ 0.008	1.02 $\pm$ 0.006	1.03 $\pm$ 0.001	1.00 $\pm$ 0.000	1.02 $\pm$ 0.009	1.05 $\pm$ 0.013	0.99 $\pm$ 0.003
SH_DemFishes_B crust	1.06 $\pm$ 0.026	0.96 $\pm$ 0.011	0.93 $\pm$ 0.006	1.02 $\pm$ 0.006	0.98 $\pm$ 0.005	1.00 $\pm$ 0.000	0.90 $\pm$ 0.018	1.05 $\pm$ 0.014	0.99 $\pm$ 0.003
Bathypel_Fishes_pisc	1.05 $\pm$ 0.003	0.98 $\pm$ 0.001	0.99 $\pm$ 0.005	1.03 $\pm$ 0.002	1.01 $\pm$ 0.002	1.00 $\pm$ 0.000	0.96 $\pm$ 0.001	1.07 $\pm$ 0.006	0.98 $\pm$ 0.001
Small_pel_Fishes	1.07 $\pm$ 0.006	0.97 $\pm$ 0.002	0.98 $\pm$ 0.007	1.02 $\pm$ 0.002	0.99 $\pm$ 0.001	1.00 $\pm$ 0.000	0.94 $\pm$ 0.002	1.04 $\pm$ 0.004	0.99 $\pm$ 0.001
Mesopel_Fishes	0.93 $\pm$ 0.007	1.04 $\pm$ 0.004	1.03 $\pm$ 0.004	1.02 $\pm$ 0.001	1.06 $\pm$ 0.005	1.00 $\pm$ 0.000	1.08 $\pm$ 0.009	1.05 $\pm$ 0.002	0.99 $\pm$ 0.000
R_mullet	0.19 $\pm$ 0.007	1.51 $\pm$ 0.006	1.21 $\pm$ 0.104	1.00 $\pm$ 0.011	1.51 $\pm$ 0.011	1.00 $\pm$ 0.006	2.19 $\pm$ 0.018	0.98 $\pm$ 0.022	1.00 $\pm$ 0.006
SL_Squids	1.05 $\pm$ 0.005	0.98 $\pm$ 0.001	1.01 $\pm$ 0.009	1.01 $\pm$ 0.001	0.98 $\pm$ 0.0003	1.00 $\pm$ 0.000	0.95 $\pm$ 0.007	1.02 $\pm$ 0.003	1.00 $\pm$ 0.001
SH_Squids	1.05 $\pm$ 0.002	0.97 $\pm$ 0.004	0.99 $\pm$ 0.003	1.01 $\pm$ 0.001	0.98 $\pm$ 0.004	1.00 $\pm$ 0.000	0.93 $\pm$ 0.011	1.02 $\pm$ 0.002	1.00 $\pm$ 0.001
SH_Ceph	0.86 $\pm$ 0.037	0.97 $\pm$ 0.052	1.14 $\pm$ 0.184	0.82 $\pm$ 0.007	0.80 $\pm$ 0.040	0.99 $\pm$ 0.009	0.80 $\pm$ 0.159	0.60 $\pm$ 0.020	1.10 $\pm$ 0.004
Shrimps_BP	1.48 $\pm$ 0.083	0.77 $\pm$ 0.030	0.83 $\pm$ 0.031	1.07 $\pm$ 0.011	0.83 $\pm$ 0.023	1.01 $\pm$ 0.002	0.51 $\pm$ 0.050	1.17 $\pm$ 0.029	0.96 $\pm$ 0.005



**Fig. 4.** a–h. Mean biomass ratios for each investigated FG by comparing tested scenarios with the start point of predictions (2018, dashed line) across the near and mid-term future. Tested scenarios are a) REF; b) +FE; c) -FE15; d) -FE30; e) -FE45; f) Fban g) +NPP, mNPP and -NPP; and h) CUM. The FG names are reported in Table 1.

biomass (relative values < 1) in both fishery reduction scenarios compared to 2018. Notably, the CB\_dolph was the only odontocete with a visible difference in mean biomasses between the near and mid-term future, where the biggest difference was in the Fban scenario.

Mean biomass values obtained by -FE15 and -FE45 scenarios showed similar trends and variations to that of -FE30 scenario (Fig. 4c-d, Table 5). At the mid future, the Fban scenario showed mean biomass ratios lower than those estimated by -FE30 and -F45 scenarios.

The outputs estimated for the fishing catches of main commercial FGs showed a similar pattern for Small\_pel\_Fishes, SH\_Squids, which was characterized from the highest values in +FE scenario (Fig. 5a-d). On the contrary, the highest catches for the R mullet were estimated in -FE30, CUM and Fban scenarios, with values around 0.500 t km<sup>-2</sup> at endpoint of simulations (Fig. 5b). Differently, the +FE scenario showed stable catch values for the entire simulation period, similar to those observed in 2018 (about 0.100 t km<sup>-2</sup>), but very lower than those of REF scenario. Finally, no relevant differences were estimated for the SH\_Ceph, where small positive effects on the catches were detected in the Fban scenario at mid-future (Fig. 5c).

### 3.5. Climate change scenario

The main climate change scenario (represented by an increase in mNPP), showed a slight general increase in biomass for all odontocetes, compared to those estimated in the REF scenario (Table 5). In particular, S\_dolph and R\_dolph showed an increase of 1.02±0.001 (mNPP/REF ratio), while it was an even slimmer changes for S\_whale (1.01±0.001) and CB\_dolph (1.00±0.001). The odontocetes' prey also showed a general increase in biomass in this scenario, generally in the range between 1.01±0.001 for SL\_Squids and SH\_Squids, and 1.07±0.011 for Shrimps\_BP. Only SH\_Ceph showed a decrease in mean biomass with a mNPP/REF ratio of 0.82±0.007.

Considering the relative biomasses in the mid-term future,

odontocetes and their prey altogether showed a mean increase of 1.67 ±2.102 with respect to 2018, with the maximum value of 8.93 showed by R\_mullet and the minimum value of 0.62 showed by SH\_Ceph (Fig 4e). Small\_pel\_Fishes and Shrimps\_BP also showed a decrease in biomass (0.98 and 0.87, respectively) compared to 2018. On the other hand, all odontocetes benefitted from the increase in mNPP, showing mid-term future/2018 ratios between 1.20 for S\_whale and 1.54 for CB\_dolph.

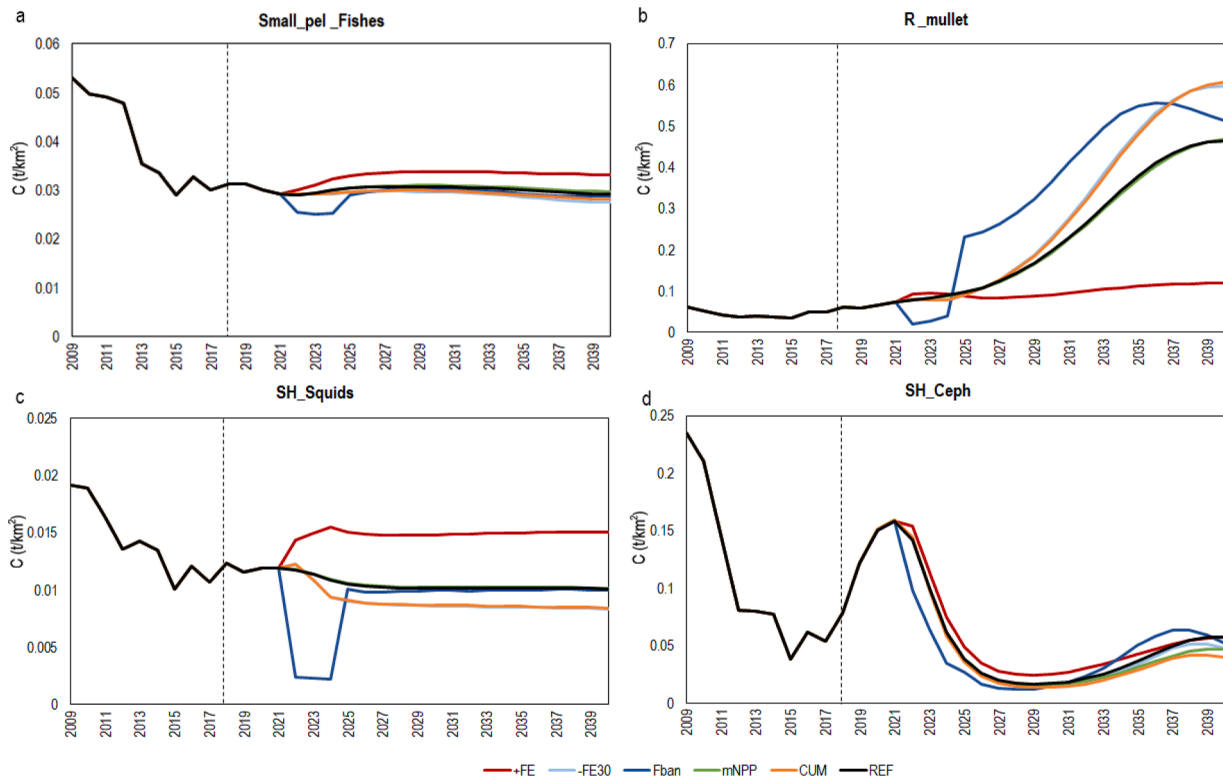
Considering the outputs estimated from -NPP and +NPP scenarios, a general overlap was estimated with results of mNPP for the most of FGs (Fig. 4e). Some slight changes were detected at mid-future for SH\_Ceph, Shrimps\_BP indicating a higher sensibility of these FGs.

### 3.6. Cumulative changes scenario

A cumulative scenario (CUM) simultaneously simulating a decrease in fishing effort and an increase in mNPP was also investigated in this food-web model. In this scenario, the odontocetes showed a higher biomass compared to the REF scenario, in the mid-term future (Table 5). In particular, CB\_dolph showed the highest value of the CUM/REF ratio equal to 1.09±0.002, followed by S\_dolph (1.02±0.002), S\_whale (1.01 ±0.0001), while R\_dolph biomass overlapped with its biomass predicted in the REF scenario.

On the other hand, the odontocetes' prey showed a prevalent negative response in this scenario. In particular, Small\_pel\_Fishes, SH\_Dem-Fishes\_B crust, SL\_Squids and SH\_Squids showed a CUM/REF ratio between 0.98 and 0.99, and the lowest biomasses were estimated for SH\_Ceph and Shrimps\_BP, with values equal to 0.80±0.040 and 0.83 ±0.023, respectively.

Considering the mid-term future/2018 biomass ratios of the odontocetes and their prey overall, a mean increase of 1.98±3.339 was found, with the maximum value of 13.55 shown for R\_mullet and the minimum value of 0.59 shown for SH\_Ceph (Fig 4f). In addition, Small\_pel\_Fishes and Shrimps\_BP also showed a decrease in biomass



**Fig. 5.** a–d. Trends of catches ( $C$ , t km<sup>-2</sup>) of the main commercial FGs predicted by the Ecosim model in the GoT (2009–2040) for each tested scenario (see the legend and Table 2 for more details). FGs considered are a) Red mullet, b) Small pelagic fishes, c) SHB Squids, d) SH Cephalopods. Vertical dashed line separates the observed trends (2009–2018) from future scenarios (2018–2040).

(0.96 and 0.81, respectively) compared to 2018. On the other hand, all odontocetes showed a benefit effect from the combined action of fishery and mNPP changes, with mid future/2018 ratios between 1.19 (S\_whale) and 1.67 (CB\_dolph).

### 3.7. Assessment of interaction effects between fishery and climate on the odontocetes

The evaluation of the interaction effects between the two scenarios (-FE and mNPP) tested individually and cumulatively showed slight antagonistic effects for all investigated odontocetes (Table 6). In particular, R\_dolph showed the highest negative IEI value.

Considering the odontocetes' prey, Mesopel\_Fishes and SH\_DemFishes\_gen showed an increase in biomass in all scenarios with slightly synergic effects. The R\_mullet showed an increase in biomass in both fishery reduction and cumulative scenarios, while a biomass reduction was predicted in the climate scenario, with a very slight synergic effect. Bathypel\_Fishes\_pisc was characterized by an antagonistic effect, whereas biomass increased in both climate and cumulative scenarios, and it decreased in the fishery reduction scenario. SL\_Squids, SH\_Squids, Shrimps\_BP, Small\_pel\_Fishes and SH\_DemFishes\_B crust were characterized by reduction of biomasses in the CUM and -FE30 scenarios, while their biomasses increased in the +NPP scenario. All groups showed synergic effects, except for the SH\_DemFishes\_B crust group, which showed an IEI value of -0.02 (slight antagonistic effect). Finally, the group of SH\_Ceph was characterized by decrease in biomass in all tested scenarios, with a value of IEI indicating a slight antagonistic effect.

## 4. Discussion

This study provides the first temporally dynamic food-web model in the Northern Ionian Sea, with a well detailed trophic structure and a focus on the odontocetes in a fishery-exploited ecosystem. The main aim was to investigate the individual and cumulative effects of changes in bottom trawling effort and primary production (a proxy of climate change) simulating top-down and bottom-up controls on the food web.

In the calibration step, the functional groups with a time series of information were equal to 73% of the total functional groups described in the Ecopath model. The hybrid fitting approach applied (by adopting both the "by predator" and "by predator prey" strategies consecutively) extended the calibration capability of the stepwise fitting routine (Scott et al., 2016) reaching the full potential of the fitting strategies in Ecosim and avoiding overparameterization (Bentley et al., 2020). With this study, such a fitting strategy is applied for the first time on a food web

**Table 6**  
Assessment of increasing (+) or decreasing (-) mean biomass ratio (2036–2040) of odontocetes (Odo) and their main FGs prey in response to the different scenarios (-FE30 = Fishing Effort reduction, mNPP = Climate scenario, CUM = Cumulative scenario). Interactive Effect Index (IEI) values are reported by indicating synergistic (positive values), additive (zero values) and antagonistic (negative values) effects between effort reduction and climate changes on FGs.

Category	FG	IEI	-FE30	mNPP	CUM
Odo	S_dolph	-0.02	+	+	+
	CB_dolph	-0.01	+	+	+
	R_dolph	-0.13	-	+	+
	S_whale	-0.01	-	+	+
Prey	SH_DemFishes_gen	0.02	+	+	+
	Mesopel_Fishes	0.01	+	+	+
	R_mullet	0.01	+	-	+
	Bathypel_Fishes_pisc	-0.07	-	+	+
	SH_DemFishes_B crust	-0.02	-	+	-
	S_pel_Fishes	0.03	-	+	-
	SL_Squids	0.05	-	+	-
	SH_Squids	0.01	-	+	-
	Shrimps_BP	0.04	-	+	-
	SH_Ceph	-0.02	-	-	-

model realised in the Mediterranean Sea.

Furthermore, the calibration procedure was tested on two alternative time series, modified with respect to a sensitive component of the data. The changes made with the removal of less accurate discard time series resulted in a great improvement in the fitting of the model. This aspect should be taken into consideration in future calibrations on time series data showing similar characteristics of non-target species for considered sampling gear.

A future improvement in the modelling approach could be represented by the comparison of different fishing effort indicators as a forcing function. In this analysis, the selection of the fishing effort indicator has been elaborated considering the peculiarity of both the study area and trawling fishing fleet. Indeed, the study area is mainly characterised by trawling that exploits deep resources and only a few areas on the shelf are exploited (Russo et al., 2017; Maiorano et al., 2022). In addition, the fleet has been subject to an evolution over the time achieving a structure characterized by two main size segments (LOA 15–18 and 18–24 m), which occur in similar number sharing the same fishing grounds (Carlucci et al., 2022). For this reason, a segmentation of trawling fleet was not assumed as not relevant for the analysis. Taking into consideration the choice of fishing effort indicators, the use of spatial fishing effort data, acquired from Vessel Monitoring System (VMS) and the Automatic Identification System (AIS), are increasingly used (Russo et al., 2018). However, some critical points can arise when the study areas are not overlap to management spatial units (e.g., GSAs), which are adopted as reference for this kind of data (Russo et al., 2019). Thus, spatial contexts different from those of GSAs require adaptations, which could contribute to bias and more uncertain estimation of fishing effort. Since the goal of this study is focused on cetacean conservation, the final choice of a nominal fishing effort indicator was addressed towards a trade-off in the representativeness of temporal fishing effort trends and the available data. In particular, the nominal fishing effort in the GSA 19 have showed a coherent behaviour with VMS and AIS trends (Russo et al., 2019), indicating that fishing capacity indicator could be assumed as a proxy for this first study. Overall, future comparisons for the selection of fishing effort indicators to support the fitting procedure in the model could be performed to increase the model performances.

### 4.1. Fishery effects

In the REF scenario, where fishing effort of the trawl fleet is kept in the simulation at the same intensity as 2018, the general increase in biomass of all investigated FGs is very probably due to the ongoing decrease in fishing effort. In fact, fishing effort in the GoT area experienced a reduction of around 30% in terms of number of active trawling vessels from 1995 to 2020 (Carlucci et al., 2018; Maiorano et al., 2022), causing direct positive effects on the target species and indirect effects on the entire food web, in the long run. The results visible at the endpoint in the mid-term future reflect several effects, resulting from changes in the forcings functions implemented in the scenario and trophic interactions occurring in the food web. Indeed, the outcome of the fishing pressure is diversified for the investigated FGs, depending on the trophic level and the ecological role (e.g., apex predators, mesoconsumers, etc.) they play in the food web (Heithaus et al., 2008; Ferretti et al., 2013).

Overall, the fishery variations seem to have negligible effects on all odontocetes, with the exception of the common bottlenose dolphin, which is the species characterized by the largest variety of responses as a result of changes in fishing effort. This outcome is to be expected, considering that it has the most interaction with fishery in the Mediterranean basin (Bearzi, 2002) and Ionian region (Carlucci et al., 2021a, b; Ricci et al., 2021a), mainly due to its feeding habits and diet bound to demersal resources strongly affected by bottom-trawling (Blanco et al., 2001). Similar responses by bottlenose dolphin to the fishing effort changes have been observed on the Rías Baixas shelf (North-West Spain) through the same modelling approach (Giralte Paradell et al., 2021). No

relevant variations were found for the other odontocetes across the scenarios tested, as changes are strongly mediated by the interactions occurring in the underlying trophic levels, which mitigated the impacts on cetacean biomasses driven by changes in fishing effort. Thus, the increase in fishing pressure on some prey, or its release on others, does not show a directly proportional effect on the analysed FGs, due to the top-down, bottom-up controls, and competition that occur simultaneously in the food web. For instance, the Risso's dolphin shows a higher biomass in the scenario of increased fishing effort, probably since its main prey, bathyal squids, are not highly impacted by the trawl fishery in the study area (Ricci et al., 2021a). This can be seen as an example of an indirect effect of top-down control of fishing, which impacts on the competitors of Risso's dolphin prey, with a beneficial effect on them (Crowder et al., 2008; Hočevar and Kuparinen, 2021). As for the apex predators, for the same reasons, there appears to be no substantial difference between the two fishing effort reduction scenarios. If, on the other hand, we consider the odontocete's prey, the effects of changes in fishing effort can be summarised in two main aspects. In the first instance, the FGs scarcely impacted by trawling, such as small pelagic fishes and benthopelagic shrimps (*Plesionika* spp., *Pasiphea* spp.), benefit from the increase in fishing pressure on their predators or competitors (Ricci et al., 2021b). The second instance is mainly represented by demersal FGs, such as the Red mullet and shallow benthic cephalopods (*Octopus vulgaris*, *Sepia* spp., *Eledone* spp.), which are mostly directly impacted by trawl fishing activities and respond in a similarly direct and predictable manner to the increase in fishing. In particular, predictions of the benthic cephalopod biomass show a critical decrease in biomass in all fishery scenarios. This condition can be attributed to the large catches operated by small scale fishery, such as passive nets, which represent over 50% of the catches in the Ecopath model in the GoT (Carlucci et al., 2021b), and they are not affected by the fishing effort changes in tested scenarios. No less important, the decrease in benthic cephalopods could be due to a higher vulnerability to the bottom trawling than squids and cephalopods characterized by benthopelagic habits. Although most commercial landings of these cephalopod species can be attributed to bottom trawling (Jereb et al., 2015), regional variations in the Mediterranean Sea could occur where small scale fishing gears assume a predominant role (Quetglas et al., 2015; Geraci et al., 2021). In addition, several studies indicate the importance of environmental factors impacting on cephalopod growth and recruitment, affecting population dynamics (Sobrinho et al., 2002; Rodhouse et al., 2014).

Similar trends have been detected for the Red mullet in the GSA 19 and surrounding areas during the period 1994–2015 (see Tserpes et al., 2019), as well as in the EwE model of the Strait of Sicily (SoS), in response to reduced fishing effort and increased primary production (Agnetta et al., 2022). Notably, the high increase in biomass of this target species observed in all scenarios could be influenced by considering the species as a single functional group in the GoT model, instead of representing the population in different age classes, as applied in the SoS model. This difference in the modelling of species could amplify the positive response of species to the fishery reduction. In addition, the Red mullet seems to show a rapid positive response to the fishery reduction and ban, as reported in other modelling approach applied in the GSA 19 (Russo et al., 2017). In this scenario, the trawling ban was applied for three months of the year, resulting in a near doubling of the standing stock biomass of the species over the seven-year simulation period. Since in our simulations the fishery ban is fully fixed for three years, the effect on the biomass increase could be amplified. Future analysis should be carried out to better understand the response mechanisms.

Similarities of GoT scenarios with those of SoS food web model was also found for the odontocetes which show little change in biomass for the mid-term future predictions. In general, it has been observed that a reduction in top-predators due to fishing may lead to a reduction in predation pressure on meso-consumers, and thus to an increase in predation pressure on basal prey (Gislason, 2003; Ferretti et al., 2013). It should be emphasised that the effect of fishing on trophic relationships

in the whole ecosystem can be complex to interpret. This is because the non-selective nature of some fishing gears, such as trawls (Vitale et al., 2018), can result in mixed effects of control on species and the food web, as well as interacting with the effects of environmental variables (Agnetta et al., 2019). Furthermore, the shift in fishing pressure towards intermediate trophic level resources could result in control mechanisms, such as wasp-waist control (Cury et al., 2000; Hunt and McKinnell, 2006). Nevertheless, in the Mediterranean basin, the indirect release effect of fishing pressure on non-target species has been observed in other food web models, such as in the Gulf of Gabes and the Adriatic Sea (Halouani et al., 2015).

A last consideration should be carried out for the several levels of fishing effort reduction tested in the analysis. Although further analyses are required to select several efficient indicators of the fishing effort, our results suggest the FGs response to both FE 30% and 45% reductions is more sensible than that to the fishing ban. This can be an expected behaviour because the trawling FE effort values from 2024 come back to the level of 2018 for the Fban scenario, maintaining a fishing pressure higher than other reduction scenarios. From a fishery management point of view, this aspect should be taken in careful consideration, because the fishing closure seem to lose the effectiveness after 10 years. Indeed, for some demersal species, such as the Red Mullet, a reduction of biomass and catches was observed in Fban scenario after 2035, with lower values than those observed in other fishery reduction scenarios. Although this issue is not the focal point of this study, however future analysis should be developed also in the fishery management field.

#### 4.2. Climate effects

In the climate scenario, a bottom-up effect on the FGs of the food web was simulated through an increase in energy input into the system through the net primary production change. For similar reasons to the dynamics explained above for the fishing effort, several mechanisms and interactions intervene in the food web to mediate and dilute the effect of the increase in primary production as it moves up towards the apex levels. In fact, all cetaceans mildly benefit from the increase in the energy input simulated in the climate scenario. A similar response has also been observed in the SoS model for the mid-term future period (Agnetta et al., 2022). Similarly, the increase in primary production generally triggers amplified responses in primary consumers (Christensen, 2013; Chust et al., 2014; Armengol et al., 2019), and consequently positive responses in the odontocetes' prey, due to their position in the food web. Only benthopelagic shrimps and benthic cephalopods show a slightly negative response to the increase in primary production in the mid-term future. The negative effects on these two preys could be linked trophic interactions pattern, which could be favourable to an increase in biomass of both their predators (e.g., odontocetes, sharks) and competitors (e.g. mesopelagic and bathypelagic fishes, small pelagic fishes) as was found in other ecosystems (Alexander et al., 2015). In particular, benthopelagic shrimps play an important trophic role within the benthic-pelagic coupling, as prey of many deep-sea and shelf consumers (Ricci et al., 2022), potentially suffering from high predation mortality in the long term, as observed in our scenarios. A similar condition could explain the dynamics of benthic cephalopods, which occupy a position of keystone mesoconsumers and are affected by both predation and fishing mortality (Coll et al., 2013). Notably, in a higher energy condition of the food web, as simulated in the climate scenario, benthic cephalopods also show a critical condition, which could indicate the need for high attention on their stock management (Geraci et al., 2021).

The NPP tested in this scenario is a proxy of climate change that directly intervenes in food web dynamics. However, climate change could mean seawater temperature and salinity changes (causing water mass circulation and stratification changes, as well as thermocline variations), acidification, sea level variations, and it is known how cetaceans are susceptible to these changes (Simmonds and Elliott, 2009; Nunny et al., 2019). In particular, the Northern Ionian area is subject to

fluctuations in deep-water circulation on a ten-year scale (Bimodal Oscillating System, Liu et al., 2022), involving very complex chemical-physical and biological aspects (Civitaresse et al., 2010). The interaction of different environmental variables (temperature, salinity, nutrients,) have effects on trophic flows and benthopelagic coupling patterns with spatial variations in the Ionian basin (Ricci et al., 2022). Therefore, for a comprehensive assessment of the impacts of climate change on cetaceans and the trophic structure, the modelling of temperature in Ecosim scenarios should be performed also considering the depth gradient in the study area in future analysis, as well as other environmental drivers (Serpetti et al., 2017).

#### 4.3. Assessment of interaction effects between fishery and climate

The assessment of interaction effects is a useful tool to understand whether the implementation of a regulation, such as fishing reduction, can be effective in the context of interaction with other environmental or anthropogenic variables over time (Nogues et al., 2021). From our analysis, the combined interactions between fishery reduction and primary production increase seem to have slightly antagonistic effects on the predicted biomass of the odontocetes. This indicates that the effects of fishing regulation may lose some of their effectiveness due to climatic effects and the interaction of the two components within the trophic network. Certainly, more in depth analyses should be aimed at assessing the effects on the whole food web and, from a management point of view, on the fishery catch yield through modelling approaches able to analyse single and cumulative effects.

The antagonistic effects of the investigated odontocetes estimated in our study are very similar to those obtained for the single functional group of marine mammals (IEI = -0.10) in the SoS model by Agnetta et al. (2022). The only difference observed concerns the response in the fishing effort reduction scenario, where the marine mammals in the SoS model show biomass changes in line with those of the Risso' dolphin and the sperm whale modelled in the GoT. Therefore, in our model, the higher detail on the description of odontocetes species allows better understanding of the different pattern of response of these species in cumulative scenarios.

It should be highlighted that the Ecosim routine supports the spatial modelling of top predators in the food web dynamics interacting with anthropogenic pressures acting at different levels of impacts (Serpetti et al., 2021). In the Gulf of Taranto, where the cetacean distribution is affected by other human threats, such as noise, vessel traffic and Italian Navy activities (Carlucci et al., 2022), the assessment of their conservation status through an integrated ecosystem modelling approach could represent a future challenge in the management of the biodiversity and resources.

#### 4.4. Insights to support SDG 14 through trophodynamic modelling

In the framework of SDG 14, the methodological approach applied in this study responds to the necessity to investigate the effects of single factors and their combination, which can support the knowledge required by several SDG 14 targets. Indeed, the modelling of the food web interactions with effects of fishing and climatic drivers is an attempt to investigate the dynamics between keystone predators, fishing regulations and a potential climate effect. The totality of these components is the subject of several interconnected SDG 14 targets, which require ecosystem-based modelling approaches according to a management point of view (Heymans et al., 2020). Presumably, from an ecological point of view, a simplification of the food web and a focus on certain prey-predator relationships could help to better understand some of the processes derived from cumulative effects by improving knowledge on the topic. However, ecological information provided by simplified models should be integrated, in order to describe the complexity of marine ecosystems to satisfy management requirements.

Potential enhancements and upgrades to the model may include the

implementation of new environmental variables such as temperature, to better describe climate change and investigate its impacts on the food web in the GoT (Corrales et al., 2018). Furthermore, a future challenge will be the reconfiguration of the structure of the food web modelled for the study area, in order to highlight new FGs of individual species with the role of preferential prey of cetaceans and fishing targets, at different stages of their biological cycles. These changes could result in a more detailed model that can easily meet the evaluation requirements included Sustainable Development Goal 14 Life Below Water.

The application of the interaction effects index could contribute to disentangling the effects of fishing and climate on odontocetes in a complex trophic structure. In our study, the interactive effects were assessed for the reduced fishing effort scenario and the climate scenario, which are modelled according to realistic indications provided by the Multiannual Fishery management plan (Common Fishery Policy, 2013) and projection of RCP\_8.5 (Reale et al., 2022). The results obtained by this first modelling are a baseline to implement new simulations testing other potential fishery regulations and climate prediction.

In conclusion, our analysis suggests that fishing effort change is the driver that determines the most relevant impacts on the marine ecosystem in the GoT, as shown in a preliminary analysis in the same area (Cascione et al., 2022). Improved representation of the fishing effort as a driver in the model, e.g. by detailing fleet size, using also different FE capacity indicators (Tidd, 2013), could help improve simulations under various scenarios. Ecosystem-scale modelling of fishery dynamics in the food web is crucial to achieve the demands of SDG 14. The study reported here confirms the validity of these food web models which can be exploited for their potential to simulate cumulative scenarios and to do so as many drivers and variables affecting the system as possible need to be integrated at the same time.

#### CRediT authorship contribution statement

**P. Ricci:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **N. Serpetti:** Formal analysis, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **D. Cascione:** Data curation, Formal analysis, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **G. Cipriano:** Investigation, Writing – review & editing. **G. D'Onghia:** Writing – review & editing. **D. De Padova:** Data curation. **C. Fanizza:** Funding acquisition, Investigation, Project administration, Resources. **M. Ingresso:** Data curation, Writing – review & editing. **R. Carlucci:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft.

#### 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.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2023.110500.

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