



# Assessment of cetacean–fishery interactions in the marine food web of the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea)

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Received: 23 January 2020 / Accepted: 1 October 2020  
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**Abstract** The exploitation of fishery resources acts as a driving force on cetaceans both directly, by determining their fishing mortality or injury as by-catch species, and indirectly, through the lowering of the availability of their prey. This competitive overlap between fishing and cetaceans often results in inadequate solutions so that in some cases there have been cases of intentional cetacean culling to maximize fishing production. A modelling approach applied to

investigate the ecological roles of cetaceans in the food web could prove more effective to integrate ecological and fishing aspects and to provide suggestions for management. The comparative analysis carried out in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea) showed that fishing exploitation provides impacts on the investigated food web greater than those due to cetacean predation. Trawling was estimated to be the most negatively impacting fishing gear considering the mortality rates and consumption flows. On the other hand, the striped dolphin was the main impact on the food web due to its highest consumption flows. Analysis showed a negative and non-selective impact on the exploited species due to the fishing gears, while the odontocetes proved to select their prey species and provide a positive impact in the assemblage. In particular, while the fishing gears are primarily size selective, targeting mostly large and economically valuable fish, the

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s11160-020-09623-x>) contains supplementary material, which is available to authorized users.

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The original online version of this article was revised: In the original publication of the article, the given name and surname of the authors are inverted in the author’s affiliation and in the citation of the article. The correct version of authors’ information is provided in this correction. Carlucci R. Capezzuto F. Cipriano G. D’Onghia G. Maiorano P. Sion L. Tursi A. Ricci P. Fanizza C. Libralato S. Maglietta R.

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odontocetes seem to follow a co-evolution process with their prey, developing a specialization in their resources, providing control of the meso-consumers and ensuring a trophic stability in the ecosystem.

**Keywords** Marine mammals · Trophic cascade · Keystone species · Ecological niche · Ecosystem-based fisheries management

## Introduction

The reduction of the conflicting interactions between cetaceans and fisheries represents a target in the management strategies for the conservation of marine ecosystems as well as their regulating and provisional services (Read 2008; Boulton et al. 2016). In fact, considering the fishing gears as multi-trophic and very often unselected consumers, the antagonistic nature of cetacean–fishery interactions can be described as a competition for overlapping resources integrated within a foodweb (Tromeur and Loeuille 2017; Jusufovski et al. 2019). Moreover, the fishery can directly represent a serious threat because of the by-catch or incidental non-targeted catch of marine mammals (eg., Bearzi 2002; Gilman et al. 2006; Mintzer et al. 2018; Hamilton and Baker 2019). Whilst, on the other hand, cetaceans ensure the stability of marine food webs as keystone species (Roman et al. 2014) being top-predators or consumers playing control roles according to the mechanisms of trophic cascade (Estes et al. 2011; Spitz et al. 2018).

The assessment of cetacean–fishery interactions is generally based on reports from fishermen, experimental surveys and acoustic monitoring, or a combination of the above, which must be considered a reductive approach often adopted to assess the negative economic losses caused by cetaceans (Snape et al. 2018 and reference therein). In fact, the use of fishermen’s reports could cause an overestimation of the effective depredation due to dolphin activities (Bearzi et al. 2011a). Moreover, some studies have shown that the conflicting interactions between fishing gears and cetaceans determining economic losses are generally low and are often affected by specific conditions derived from both ecological species features and environmental variability (eg., Silva et al. 2011). Although the direct link between the gear

damage and the occurrence of cetaceans in the fishing areas is highly uncertain, cetaceans have been too often depicted as the fishermen’s “enemies” (Kaschner and Pauly 2005). Consequently, in the past, inappropriate solutions to mitigate possible conflicts were adopted, and the intentional culling of cetaceans was unfortunately applied to maximize fishery production (Gerber et al. 2009; Morissette et al. 2010).

According to ecosystem-based fisheries management (Jusufovski et al. 2019), several international bodies have expressly recommended implementing an ecosystem approach in fisheries management to quantify to what extent fishing operations overlap with the endangered, threatened or protected cetacean species on a local and wider scale (eg., ACCOBAMS-ECS-WK Threats 2017). In fact, all species and the fishing gears are connected through a complex ecosystem trophic structure, in which the exchanges of energy and matter are influenced by predation/harvesting activities (FAO 2018; Agnetta et al. 2019). Therefore, simplifying the issue to the elemental pairs of the interaction, or thinking of the cetaceans as exclusively harmful to fishing, clearly seems to be an inadequate assumption. On the contrary, a modelling approach applied to investigate the ecological roles of cetaceans in the food web could prove more effective to integrate ecological and fishing aspects and to provide suggestions for the management system (Matthiopoulos et al. 2008). In fact, top predators do not only consume their favourite prey, but also their prey’s consumers (Punt and Butterworth 2001). Consequently, according to the specific case, the fishery could be favoured by beneficial predation, which excludes competitors of fishing resources (Kaschner and Pauly 2005). Competition for resources between cetaceans and fishing could be lower than that expected, because of the feeding flexibility of cetaceans, their predation on non-target species, or in areas excluded from fishery exploitation (Trites et al. 1997; Kaschner et al. 2001; Morissette et al. 2012; Breen et al. 2016). On the contrary, the competition between cetaceans and fishing could even increase when the fishing resources are overfished, posing serious threats for their conservation and for the functional integrity of the marine ecosystem and the services provided (Jennings et al. 2016).

According to the EU Marine Strategy Framework Directive (MSFD) and Maritime Spatial Planning Directive (MSPD), the conservation status of

cetaceans makes a significant contribution to the assessment of the marine ecosystem health condition. In particular, anthropogenic pressures should not adversely affect cetacean population dynamics or their long-term maintenance (EU Commission Decision n. 848/2017) to meet targets under the range of several international agreements such as the Habitats Directive (Annex IV), the Barcelona Convention (Annex II) and the Convention on Biological Diversity.

In the Mediterranean Sea, the exploitation of fishery resources acts as a driving force on top predators both directly, by determining their fishing mortality or injury as by-catch species, and, indirectly, through the lowering of the availability their prey (Colloca et al. 2017; Mazzoldi et al. 2019). For example, the common bottlenose and the short-beaked common dolphin populations declined in North-eastern Ionian Sea also because of the depletion of their prey harvested by fishery (Piroddi et al. 2010). The prey abundance and their spatial distribution influence the cetaceans in their choice of preferential habitats (Cañadas et al. 2002; Giannoulaki et al. 2017), proving to be a critical factor in the analyses based on food web modelling approaches.

The odontocetes *Stenella coeruleoalba*, *Tursiops truncatus*, *Grampus griseus* and *Physeter macrocephalus*, as well as the mysticetes *Balaenoptera physalus*, have all been regularly recorded in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea) (Dimatteo et al. 2011; Fanizza et al. 2014; Carlucci et al. 2017). However, the ecological roles of these cetaceans and their overlapping with the fishing resources within the food web have not yet been fully and appropriately investigated. In fact, the only assessment on the dolphins-fishery interactions (Lauriano et al. 2009) was carried out by means of fishermen's reports aggregating data at an inappropriate administrative scale rather than considering ecological overlapping between species and fleet displacement. This could lead to inaccuracy and overestimations of the interactions between cetaceans and the fishery, making this assessment not useful for the implementation of management actions. In addition, dolphin species could show different interactions with the fishing gears, such as in the case of *T. truncatus* and *S. coeruleoalba* with trawling in the Gulf of Taranto (Carlucci et al. 2016). Not less important, a comparison between fishermen's

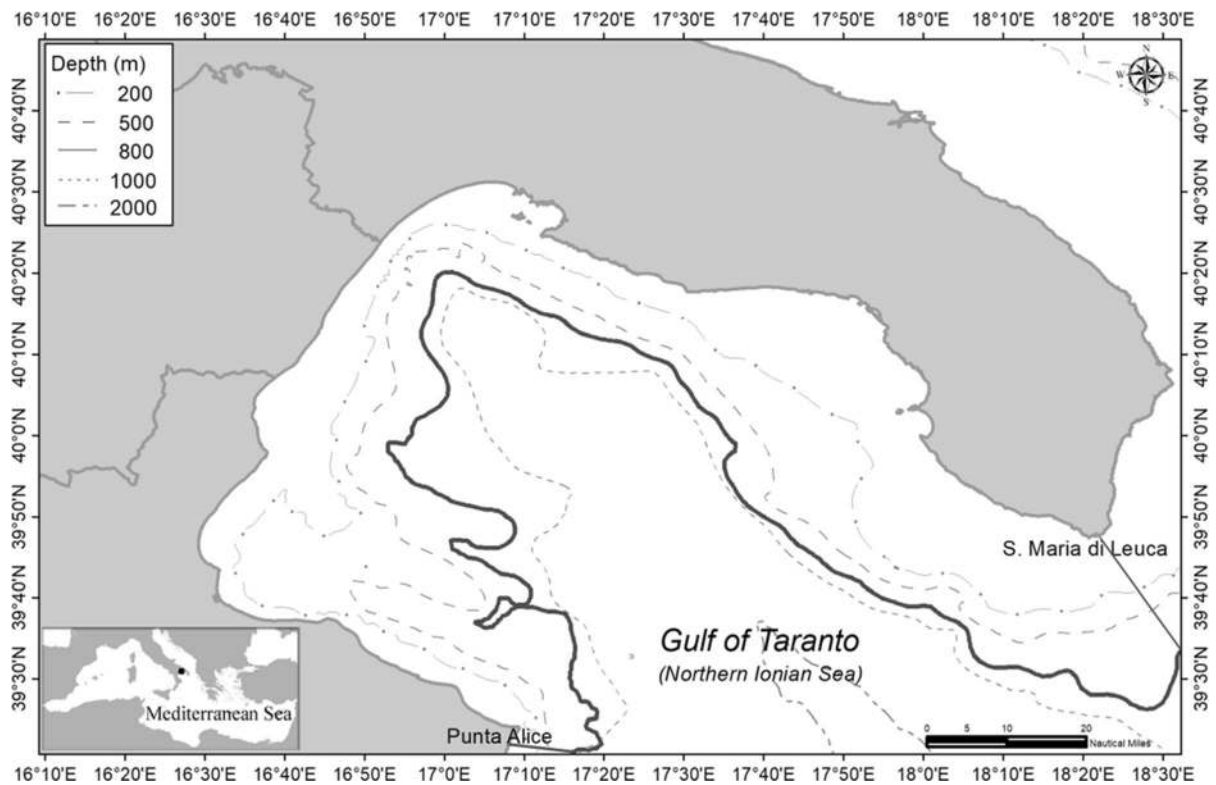
interviews and independent visual boat surveys carried out on the dolphin and fishery interactions in the Gulf of Taranto highlighted mismatching results (Bearzi et al. 2011a). The goal of this study is to provide new information on the ecological role of the cetaceans and to assess the cetacean-fishery interactions in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea) through a food web modelling approach based on Ecopath with Ecosim (EwE) (Christensen et al. 2008). In particular, a set of ecological and fishing indicators were used to compare the impacts of cetaceans and the fishery on the marine food web assessing the overlapping between the cetaceans' prey and the harvested resources.

## Materials and methods

### Study area

The Gulf of Taranto (GoT) extends over an area of about 14,000 km<sup>2</sup> from Santa Maria di Leuca to Punta Alice in the Northern Ionian Sea (Central Mediterranean Sea) (Fig. 1). A NW–SE submarine canyon called the 'Taranto Valley' characterizes the area with bathyal grounds down to 2200 m (Harris and White-way 2011). This singular geo-morphology involves a complex distribution of water masses with a mixing of surface and dense bottom waters with the occurrence of high seasonal and decadal variability in upwelling currents (Bakun and Agostini 2001; Civitarese et al. 2010). The Gulf of Taranto includes a complex set of coastal and offshore habitats among which the deep cold-water coral province offshore from Santa Maria di Leuca (SML CWC) and the Amendolara shoal (Capezzuto et al. 2010; D'Onghia et al. 2016a; Carlucci et al. 2018a).

Intense fishing exploitation occurs from the coastal waters to about 800 m in depth. The small-scale fishery (gillnets, trammel nets, set long lines, traps) is characterized by vessels with a length-over-all (LOA) of 6–12 m limiting operation to the coastal grounds, while the bottom otter trawls (LOA of 12–18 m) mainly exploit the shelf break and slope (Russo et al. 2017). Most of the boats are registered as polyvalent fishing vessels, because they often change type of gear, according to the season and sea/weather conditions, as well as the variable availability of resources and market demand. Trawlers represent about 21% in



**Fig. 1** Map of the modelled area located in the Gulf of Taranto. Bold line marks the modelled area of 7745 km<sup>2</sup> from S. Maria di Leuca to Punta Alice included in a depth range between 10–800 m

number, 64% in gross tonnage and 56% in engine power in the whole Northern Ionian Sea fleet (Maiorano et al. 2010). The main target species in the trawl commercial catches are the European hake (*Merluccius merluccius*), red mullets (*Mullus barbatus* and *M. surmuletus*), cuttlefish (*Sepia officinalis*), octopus (*Octopus vulgaris*), common pandora (*Pagellus erythrinus*), deep-water rose shrimp (*Parapenaeus longirostris*), giant red shrimp (*Aristaeomorpha foliacea*), and blue and red shrimp (*Aristeus antennatus*) (Russo et al. 2017). Considering the effect of trawling, and to a lesser extent, other fishing gear, the General Fishery Commission for the Mediterranean (GFCM FAO) created a new legal category of Fishery Restricted Area (FRA) on the SML CWC, recommending the prohibition of towed gears (D'Onghia et al. 2010, 2012, 2016b; Vassallo et al. 2017; Capezzuto et al. 2018).

Although the Gulf of Taranto is characterized by a marked anthropogenic presence and intense fishing exploitation (Carlucci et al. 2016), the occurrence of cetacean species, such as the striped dolphin (*Stenella*

*coeruleoalba*), the common bottlenose dolphin (*Tursiops truncatus*), the Risso's dolphin (*Grampus griseus*), the sperm whale (*Physeter macrocephalus*) and the fin whale (*Balaenoptera physalus*) makes this area eligible for the establishment of a Specially Protected Area of Mediterranean Importance (SPAMI), according to the SPA/BD Protocol (Carlucci et al. 2018b, c; Maglietta et al. 2018; Azzolin et al. 2020). In particular, the striped and common bottlenose dolphins are the most frequent and abundant species distributed throughout the Gulf of Taranto (Carlucci et al. 2016, 2018b). The Risso's dolphin is distributed in the range depth between 400–1000 m (Carlucci et al. 2020), whilst the sperm whale has been observed between 550–1200 m usually in summer and autumn (Bellomo et al. 2019). Lastly, the fin whale occurs with few individuals on the continental slope waters (Dimatteo et al. 2011; Fanizza et al. 2014).

In order to represent the spatial area with the highest overlap between cetaceans and the fishery, the modelling of trophic structure within the GoT was

performed on an area of 7745 km<sup>2</sup> included between 10 and 800 m of depth, delimited by Santa Maria di Leuca to the east and Punta Alice to the west (Fig. 1).

### The Ecopath modelling approach

The Ecopath with Ecosim (EwE) modelling approach (Christensen et al. 2008) was used to describe the energy balance of the food web in the GoT. Food webs are described by means of Functional Groups (FGs elsewhere also termed nodes or groups), each representing a group of species with similar trophic, ecological and life-history traits, a single species or a life stage of a species. The FGs in the food web can represent consumers, autotrophs and non-living compartments, such as forms of organic matter, and links between FGs are formally described by a set of linear equations, one for each FG, representing the balance of energy and matter expressed as:

$$B_i \cdot \left(\frac{P}{B}\right)_i * EE_i - \sum_{j=1}^n B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} - Y_i - E_i - BA_i = 0 \quad (1)$$

where  $B_i$  is the biomass of group (i),  $(P/B)_i$  is the production of (i) per unit of biomass; the consumption i by the other FGs of the food web is then represented through  $(Q/B)_j$ , the consumption per unit of biomass of all j predators the proportion of (i) in the diet composition of predator (j) in terms of biomass ( $DC_{ij}$ ); other losses on group i are represented by fishery catches,  $Y_i$ , the net migration rate  $E_i$  and, eventually, the biomass accumulation  $BA_i$ . The parameter  $EE_i$  represents the ecotrophic efficiency, i.e., the proportion of the production of group (i) which is utilized within the system modelled (Christensen and Walters 2004). Energy balance for each group is also ensured by equating its consumption ( $Q/B_i$ ) with the sum of production ( $P/B_i$ ), respiration ( $R/B_i$ ) and unassimilated food ( $U/Q * Q/B_i$ ). The system of equations is solved according to several ecological constraints by providing EwE with diet composition, the unassimilated food, the catches and the exports for each group as well as three of the basic parameters  $B_i$ ,  $(P/B)_i$ ,  $(Q/B)_i$  and  $EE_i$  (Christensen et al. 2008). The solution provides a snapshot of the trophic flows within the ecosystem (further details on EwE

modelling approach can be found in review literature such as Christensen and Walters 2004; Heymans et al. 2014).

### Model structure: definition of functional groups

The demersal and benthopelagic domains were described by a total of 276 species aggregated in 29 FGs, according to the methods applied in Ricci et al. (2019) (Table 1). Some species of particular commercial interest within the demersal and benthopelagic groups have been considered as individual FGs: the European hake (*M. merluccius*), the red mullet (*M. barbatus*), the anglers (*Lophius budegassa* and *L. piscatorius*), the deep-water shrimps (*A. foliacea*, the red giant shrimp, *A. antennatus*, the blue and red shrimp and *P. longirostris*, the deep-water rose shrimp). The 29 FGs were named using a trinomial nomenclature, reporting indications on the bathymetric layer (first code, Shelf-SH, Shelf Break-SHB, Slope-SL), the taxonomy of group (middle part) and the characteristic feeding habits of the group (last part) (Table 1, Online Resource 1, Table S1). Moreover, 14 other living FGs describing several components of the ecosystem were added, namely the planktonic domain (the phytoplankton, the bacterioplankton, the macrozooplankton, the meso-microzooplankton and the gelatinous plankton), the pelagic domain (the loggerhead turtle, the seabirds and the large, medium and small pelagic fishes) and the benthic domain (the macrobenthic invertebrates, the polychaetes, the suprabenthic crustaceans and the benthic primary producers, such as seagrasses and seaweeds). A total of 5 FGs were dedicated to the striped dolphin (*S. coeruleoalba*), the common bottlenose dolphin (*T. truncatus*), the Risso's dolphin (*G. griseus*), the sperm whale (*P. macrocephalus*) and the fin whale (*B. physalus*). Thus, the GoT food web model was described by a total of 51 FGs, including 3 groups of non-living matter (detritus, discards and marine snow) (Table 1).

### Model parametrization: initial conditions and time series

The GoT model was developed for a period of 4 years (2010–2014) using a wide set of input data obtained from several data collections. The input parameters, the diet composition matrix and data sources of FGs

**Table 1** The list of the functional groups (FG) with the corresponding FG Code adopted in the main text

No.	Functional group	FG code	No.	Functional group	Code FG
1	Striped dolphin	S dolph	17	Slope Demersal fishesdecapod feeders	SL_DemF_Decap
2	Common bottlenose dolphin	CB dolph	18	Shelf Break-Slope Fishes benthopelagic crustacean feeders	SHB_F_BP crust
3	Risso's dolphin	R dolph	19	Shelf-Shelf Break Demersal fishes benthic crustacean feeders	SH_DemF_B crust
4	Sperm whale	S whale	20	Shelf-Shelf Break Demersal fishes benthic invertebrate feeders	SH_DemF_Binv
5	Fin Whale	F whale	21	Shelf Break Fishes zooplanktivorous	SHB_F_plank
6	Loggerhead Turtle	Log turtle	22	Small pelagic fishes	S pel F
7	Seabirds	Seabirds	23	Medium pelagic fishes	M pel F
8	Large pelagic fishes	L pel F	24	Macrourids benthic invertebrate feeders	Macrourids
9	Slope Sharks and Rays benthic feeders	SL_SR_B	25	Mesopelagic fishes	Mesopel F
10	Shelf-Shelf Break Sharks and Rays benthopelagic feeders	SH-SHB_SR_BP	26	Red mullet	R mullet
11	Shelf Sharks and Rays benthic feeders	SH_SR_B	27	Hake	Hake
12	Slope Sharks benthopelagic feeders	SL_Sharks_BP	28	Anglers	Anglers
13	Shelf Break-Slope Demersal fishes generalist feeders	SHB-SL_DemF_gen	29	Slope Squids benthopelagic feeders	SL_Squids_BP
14	Shelf-Shelf Break Demersal fishes generalist feeders	SH-SHB_DemF_gen	30	Shelf Break-Slope Squids benthopelagic feeders	SHB_Squids_BP
15	Shelf-Shelf Break Demersal fish piscivorous	SHB_DemF_pisc	31	Shelf-Shelf Break Cephalopods benthic feeders	SH_Ceph_B
16	Slope Bathypelagic fishes piscivorous	SL_BathypelF_pisc	32	Slope Octopus and Bobtail Squids benthic feeders	SL_Ceph_B
33	Shelf Break-Slope Bobtail Squids benthopelagic feeders	SHB_BobSquids_BP	43	Suprabenthiccrustaceans	Supbentcrust
34	Benthopelagic Shrimps	Shrimps_BP	44	Macrozooplankton	Macrozooplank
35	Slope Decapods Scavengers	SL_Decap_Scav	45	Meso and Microzooplankton	Meso_Microzooplank
36	Shelf and Shelf Break Crabs	SHB_Crabs	46	Bacterioplankton	Bacterioplank
37	Deep-water rose shrimp	DWR Shrimp	47	Seagrassesand Macrophytobenthos	Seagrasses and algae
38	Red giant shrimp	RG Shrimp	48	Phytoplankton	Phytoplank
39	Blue and red shrimp	BR Shrimp	49	Marine snow	Disc
40	Polychaets	Polychaets	50	Discards	M Snow
41	Macrobenthicinvertebrates	Macrobentinv	51	Bottom Detritus	Det
42	Gelatinus plankton	Gel plank			

The bathymetric layers are abbreviated as Shelf (SH), Shelf-Break (SHB) and Slope (SL). Species names by FG are listed in Online Resource 1, Table S1

are reported in Online Resources 1 (Tables S1, S2). The diets adopted for the striped dolphin, common bottlenose dolphin and Risso's dolphin in the Gulf of

Taranto were mostly derived from the stomach contents analysed in the North Aegean Sea (Milani et al. 2017). Starting from these diets used as a

baseline, additional food items were also integrated from the literature, when available, to improve the robustness of the input information. In fact, for *T. truncatus* and *G. griseus* food items were added from the Western Mediterranean areas (Blanco et al. 2001, 2006), whilst for *S. coeruleoalba* from the Ionian Sea and Ligurian Sea (Bello 1993; Würtz and Marrale 1993). The diet information for the sperm whale was derived from the Ligurian Sea (Garibaldi and Podestà 2014), integrating food items from the Greek seas (Roberts 2003). Food items from the North Atlantic, North Pacific and Mediterranean Sea were integrated for the input diet of *B. physalus* (Pauly et al. 1998; Piroddi et al. 2017). Observations recorded in the GoT reported that all the investigated cetacean species forage on a depth range wider than 800 m (Carlucci et al. 2018b; Maglietta et al. 2018). Consequently, a proportion of prey distributed below this limit in their diet was considered as imports (Lassalle et al. 2014). Biomass estimates (in  $t\ km^{-2}$  of wet weight) for many fish species, cephalopods and crustaceans were obtained from the MEDITS trawl surveys carried out in the North-Western Ionian Sea in the period 1995–2015. In order to determine more accurate absolute species abundance, the standardized biomass data from surveys were corrected using a catchability factor by species, estimated by means of the literature whenever possible, or by comparison of MEDITS estimates with other data sources (eg., benthic samples, other fishing gears, stock assessments) (Ricci et al. 2019). The biomasses of large pelagic fishes and seabirds were derived from the literature (ICCAT 2010; Zenatello et al. 2014) and models developed in the Greek Ionian Sea and the Strait of Sicily, which are both close to the study area (Moutopoulos et al. 2013; Agnetta et al. 2019). Fin whale and loggerhead turtle biomasses were estimated from abundance data ( $N\ km^{-1}$ ) obtained from the OBIS SeaMap database (Halpin et al. 2009) and values of mean individual weight adopted in other models (see Piroddi et al. 2010). The biomass estimates of the 4 investigated odontocetes were derived from data collected during monitoring surveys carried out in the Gulf of Taranto since 2009 (eg. Carlucci et al. 2018c, 2020; Maglietta et al. 2018). The meso-microzooplankton productivity and consumption were estimated by averaging the results obtained for the area of study from the OPATM-BFM Mediterranean biogeochemical model (Lazzari et al. 2012). The

biomasses of the zooplanktonic groups, the polychaetes, the suprabenthic crustaceans and the benthic primary producers were estimated by setting the EE values (Table 2).

Production and consumption rates (P/B and Q/B) were obtained from empirical relationships based on local data or other EwE models (Online Resources 1, Tables S1, S3). The FG values were calculated as weighted averages of the values for the species belonging to the group, where the proportion of species biomass within the group was used as a weighting factor (Libralato et al. 2010).

Official fishery landings by species from 2006 to 2015 were obtained from the EU Data Collection Framework. Landings are detailed for bottom otter trawls (OTB), set long lines (LLS), passive nets (GTR), other gears (drifting long lines, driftnets, pots, traps and beach seines) (MIX) and purse seines (PS).

Discards of the trawl fishery by species (undersized individuals and non-commercial species) were calculated using the locally estimated discard rates (D’Onghia et al. 2003). Differently, the discards for the remaining gears were obtained from the literature (see Tsagarakis et al. 2014 and the Online Resources 1, Table S3).

In order to balance the model, a pre-balancing analysis (PREBAL, Link 2010) was carried out to assess the coherence of the input data with the basic thermodynamic laws, rules and principles of ecosystem ecology at the system level (Heymans et al. 2016). For more details on the balancing steps, see the procedure in Online Resources 1 (Fig. S1).

#### Model analysis and ecosystem indicators

Ecological indices were used to analyse the ecological role of the cetaceans and impacts of fishing based on trophic flow analysis and indicators based on thermodynamic concepts and network theory (Christensen and Walters 2004).

#### *Ecological indicators of the cetaceans’ role*

In order to assess the overall quality of the model, the “pedigree” of each input data was calculated on the basis of the source of data and its accuracy (whether it was taken from a model or original field sampling, from the studied system or from a similar system). The

**Table 2** Data input and output of the GoT model for each FG: Biomass (B t km<sup>-2</sup> year<sup>-1</sup>), Production/Biomass (P/B y<sup>-1</sup>), Consumption/Biomass (Q/B y<sup>-1</sup>), Ecotrophic Efficiency (EE), Trophic Level (TL) Omnivory Index (OI) Keystoness index (KS), Overall Effect (OE)

	Group name	B	P/B	Q/B	EE	TL	OI	KS	OE
1	S dolphin	0.042	0.080	16.850	0.000	4.71	0.25	- 0.25	0.57
2	CB dolphin	0.007	0.080	20.120	0.000	4.47	0.31	- 0.82	0.15
3	R dolphin	0.006	0.080	18.760	0.000	5.40	0.31	- 0.55	0.28
4	S whale	0.018	0.050	6.230	0.000	5.16	1.29	- 0.73	0.19
5	F whale	0.011	0.040	4.140	0.000	3.73	0.19	- 2.70	0.00
6	Log turtle	0.007	0.270	3.500	0.469	3.37	0.27	- 1.76	0.02
7	Seabirds	0.000	4.600	60.830	0.174	3.85	1.13	- 2.70	0.00
8	L pel F	0.025	0.513	4.624	0.890	4.79	0.18	- 0.72	0.19
9	SL_SR_B	0.009	0.583	3.080	0.142	4.70	0.30	- 1.13	0.07
10	SH-SHB_SR_BP	0.014	0.600	3.400	0.143	4.38	0.27	- 1.19	0.06
11	SH_SR_B	0.035	0.755	3.569	0.552	4.24	0.21	- 1.23	0.06
12	SL_Sharks_BP	0.054	0.656	6.057	0.529	4.17	0.47	- 0.86	0.14
13	SHB-SL_DemF_gen	0.156	0.595	2.844	0.863	3.98	0.47	- 0.51	0.31
14	SH-SHB_DemF_gen	0.345	0.970	4.431	0.703	3.80	0.54	- 0.51	0.31
15	SH-SHB_DemF_pisc	0.135	1.318	6.793	0.571	4.12	0.26	- 0.46	0.35
16	SL_BathypelF_pisc	0.299	2.040	8.187	0.868	4.09	0.14	- 0.39	0.41
17	SL_DemF_Decapcrust	0.175	1.016	4.351	0.868	3.83	0.37	- 0.67	0.21
18	SHB-USL_F_BP crust	0.287	1.306	5.117	0.946	3.58	0.34	- 0.53	0.30
19	SH-SHB_DemF_B crust	0.537	0.899	6.462	0.929	3.39	0.19	- 0.42	0.39
20	SH-SHB_DemF_Binv	0.305	0.952	4.887	0.962	3.21	0.26	- 0.92	0.12
21	SHB_F_plank	0.445	1.323	7.058	0.961	3.19	0.02	- 0.72	0.19
22	S pel F	1.438	1.798	7.120	0.978	3.20	0.05	- 0.22	0.63
23	M pel F	0.490	1.294	6.167	0.801	3.77	0.38	- 0.35	0.45
24	Macrourids	0.526	0.671	4.493	0.895	3.53	0.29	- 0.73	0.19
25	Mesopel F	1.237	2.665	9.711	0.915	3.27	0.25	- 0.27	0.56
26	R mullet	0.142	1.327	6.375	0.907	3.23	0.17	- 0.91	0.12
27	Hake	0.078	1.448	8.614	0.858	4.36	0.10	- 0.65	0.23
28	Anglers	0.023	0.817	4.055	0.736	4.59	0.14	- 0.39	0.41
29	SL_Squids_BP	0.087	2.852	12.447	0.871	4.66	0.21	- 0.13	0.75
30	SHB_Squids_BP	0.122	2.850	15.046	0.942	4.08	0.24	- 0.39	0.41
31	SH_Ceph_B	0.220	3.646	14.338	0.968	3.56	0.45	- 0.35	0.45
32	SL_Ceph_B	0.044	2.638	10.797	0.982	3.87	0.42	- 0.82	0.15
33	SHB_BobSquids_BP	0.064	4.143	24.100	0.900	3.62	0.03	- 0.82	0.15
34	Shrimps_BP	1.503	2.429	12.475	0.985	3.19	0.34	- 0.34	0.48
35	SL_Decap_Scav	0.863	1.485	8.197	0.950	3.07	0.40	- 0.41	0.40
36	SH-SHB_Crabs	0.900	2.849	12.584	0.965	3.02	0.21	- 0.39	0.42
37	DWR Shrimp	0.203	2.147	8.867	0.808	3.21	0.37	- 0.54	0.29
38	RG Shrimp	0.165	1.184	7.318	0.783	3.60	0.24	- 0.74	0.18
39	BR Shrimp	0.305	0.726	7.318	0.871	3.15	0.35	- 0.74	0.18
40	Polychaets	<b>1.376*</b>	5.140	20.708	0.950	2.01	0.01	- 0.32	0.50
41	Macrobentinv	4.230	5.310	22.540	0.725	2.15	0.17	- 0.09	0.91
42	Gel plank	<b>0.031*</b>	14.600	50.480	0.900	2.83	0.32	- 0.88	0.13
43	Suprabentcrust	<b>1.2854**</b>	7.730	36.510	0.990	2.15	0.16	- 0.41	0.41



**Table 2** continued

	Group name	B	P/B	Q/B	EE	TL	OI	KS	OE
44	Macrozooplank	<b>1.504**</b>	18.000	66.000	0.990	2.65	0.32	0.00	1.03
45	Meso_Microzooplank	<b>4.313**</b>	22.090	94.100	0.990	2.12	0.11	- 0.10	0.89
46	Bacterioplank	6.000	25.870	89.780	0.261	2.00		- 1.05	0.10
47	Seagrasses and algae	<b>1.685***</b>	5.240		0.600	1.00		- 1.18	0.07
48	Phytoplank	6.500	185.730		0.231	1.00		- 0.25	0.67
49	Disc	1.000			0.651	1.00			
50	M Snow	1.000			0.477	1.00			
51	Det	1.000			0.178	1.00			

In bold, biomasses estimated fixing the EE value at 0.95\*, 0.99\*\* and 0.60\*\*\*

values used in the form of a pedigree index varied between 0 (low quality) and 1 (high quality).

The fractional Trophic Levels (TLs; Odum and Heald 1975) of the FGs were estimated and the cetacean’s TLs were compared.

The Omnivory Index (OI) was calculated for each FG as the variance of the trophic level of a consumer’s prey groups (Pauly et al. 1993). When the OI value is zero, the consumer in question is specialized (i.e., it feeds on a single trophic level).

The Niche Overlap index ( $O_{jk}$ ) was obtained by the Ecopath routine for the 5 FGs of cetaceans using the equation proposed by Pianka (1973):

$$O_{jk} = \frac{\sum_{i=1}^n (P_{ji} * P_{ki})}{\sqrt{\left(\sum_{i=1}^n (P_{ji}^2 * P_{ki}^2)\right)}} \quad (2)$$

where  $P_{ji}$  and  $P_{ki}$  are the proportions of the resource  $i$  used by species  $j$  and  $k$ , respectively. The index is symmetrical and assumes values between 0 and 1. A value of 0 suggests that the two species do not share resources, 1 indicates complete overlap, and intermediate values show partial overlap in resource utilization.

The Keystoness index (KSi) and Overall relative Impact were calculated through the Mixed Trophic Impact (MTI) analysis (Ulanowicz and Puccia 1990), which quantifies direct and indirect trophic interactions among functional groups. The net MTI ( $m_{ij}$ ) was used to estimate the overall impact ( $\epsilon_i$ ) of the functional group  $i$  over all other groups ( $j$ ) of the food web:

$$\epsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2} \quad (3)$$

where in  $m_{ij}$  the impact on the group itself is not considered, and  $\epsilon_i$  normalized is calculated as a relative value with respect to the maximum in the food web elements (Libralato et al. 2006). KSi is calculated as:

$$KS_i = \log[\epsilon_i(1 - p_i)] \quad (4)$$

where  $p_i$  is the relative biomass of the group, excluding detritus biomass. In addition, the positive and negative impacts of each cetacean species on all food web elements were used to determine impacts at the level of discrete TLs by weighting each functional group impact ( $m_{ij}$  with  $i$  = cetaceans and  $j$  all other functional groups) by the proportion of flows of group  $j$  belonging to integer TLs. The negative and positive impacts were expressed as percentage values of the total (%). This representation proved useful to provide a schematic description of the cascading effects due to the predation of cetaceans on the food web.

The Predation mortality rate ( $y^{-1}$ ) and the consumption flows ( $t \text{ km}^{-2} \text{ y}^{-1}$ ) for each cetacean species were estimated.

### Fishing impacts on the food web

The fishing impacts on the food webs were assessed by a set of indicators. The species composition of the catches ( $t \text{ km}^{-2} \text{ y}^{-1}$ ) were analysed by each gear. The

mean Trophic Level of catches (mTLc) was estimated for each gear and the total fleet using the following equation:

$$\overline{TL} = \frac{\sum_i (TL_i) \cdot (Y_i)}{\sum_i Y_i} \quad (5)$$

where  $Y_i$  refers to the landings of species (or group)  $i$ . The index represents the mean trophic level given by the species exploited by the fishery. A low value or temporal decrease in the mTLc could represent alterations in the structure of the food web with a potential overexploitation of a species occurring in the basal trophic level of the food web (Pauly and Watson 2005).

The exploitation rate (E rate) of each functional group represents the proportion of fishing mortality on the total mortality.

Similarly to cetaceans, the negative and positive impacts of each gear on the FGs were used to estimate impacts by integer TLs expressed as percentage values.

#### *Assessment of cetacean-fishery interactions*

A series of comparative analysis was applied to identify different pressures of cetaceans and fishing activities on the FGs of the GoT food web and to quantify their interactions. These analyses were based on the mortality rates ( $\text{year}^{-1}$ ), consumption flows ( $\text{t km}^{-2} \text{year}^{-1}$ ) and negative impacts estimated by MTI and all indices are expressed as percentage values. The impact of mortalities is represented by the Predation mortality (PM) and Fishing mortality (F) rates of each cetacean and gear, respectively. Similarly, the consumption flows ( $\text{t km}^{-2} \text{y}^{-1}$ ) of cetaceans and the catch flows of fishing gears ( $\text{t km}^{-2} \text{y}^{-1}$ ) were compared.

An assessment of the overlap between cetacean diets and catch composition was estimated by means of an overlap index (Fishery Overlap index, FOi) on the basis of the Pianka approach (1973). A similar index was applied by Trites et al. (1997) and Bearzi et al. (2010) to cetacean-fishery interactions, assuming that the fishing gears act as “predators” and using their catches similarly to the diet of a consumer. The diet and catch composition were expressed as percentages and the index was calculated as:

$$FO_{ijk} = \frac{\sum_{i=1}^n (P_{ji} * C_{ki})}{\sqrt{\left(\sum_{i=1}^n (P_{ji}^2 * C_{ki}^2)\right)}} \quad (6)$$

where  $P_{ji}$  and  $C_{ki}$  are the proportions of the resource  $i$  consumed by odontocetes species  $j$  and fishing gear  $k$ , respectively. The index is ranged between 0 (no overlap) and 1 (full overlap between prey and the catches). The FOi was adopted here because it is much simpler and more intuitive than other indicators reported in the literature (see Kaschner and Pauly 2005). Moreover, the FOi was estimated on the catches and the landings for both the overall fleet and the single gear.

## Results

### Food web traits and the role of cetaceans in the GoT food web

The Pedigree Index of the GoT model was 0.75, indicating the good quality of the model. The mean TL of the GoT food web (excluding the non-living groups) is equal to 3.52 with the highest values estimated for the Risso’s dolphin (5.40), the sperm whale (5.16), the L pel F (4.79), the striped dolphin (4.71), the SL\_SR\_B (4.70), the SL\_Squids\_BP (4.66) and the Anglers (4.59) (Table 2). The common bottlenose dolphin showed the lowest TL (4.47) of the odontocetes. The TL estimated for the fin whale was equal to 3.73.

The striped dolphin showed the lowest Omnivory Index (OI) value (0.25), the Risso’s dolphin and the common bottlenose dolphin showed the same OI (0.31) and the sperm whale was the species with the highest OI (1.29) in the GoT food web (Table 2). The OI estimated for the fin whale was equal to 0.19.

The overlap index of the trophic niches ( $O_{jk}$ ) among the odontocetes showed the highest value for the S whale-R dolph pair (0.84), followed by the S whale-S dolph pair (0.60). The  $O_{jk}$  value estimated for the S dolph-R dolph pair (0.31) was higher than the value estimated for the S dolph-CB dolph pair (0.18). Moreover, the same  $O_{jk}$  value equal to 0.04 was estimated for both the CB dolph-R dolph and CB dolph-S whale pairs, which were the lowest trophic niche overlaps.

The highest values of Keystoness index (KSi) were estimated for the zooplanktonic groups, the macrobenthic invertebrates, the SL\_Squids\_BP, the S pel F, the striped dolphin, the phytoplankton and the Mesopel F (Fig. 2a, Table 2). The high relative biomass and overall relative impact observed for the zooplanktonic groups, the macrobenthic invertebrates and the phytoplankton identified them as structural/dominant groups of the GoT food web (Fig. 2b). Differently, the SL\_Squids\_BP and the striped dolphin were characterized by a low relative biomass and high overall effect. Therefore, they were identified as keystone predators in the food web. The F whale showed the lowest KSi in the food web.

The mean predation mortality rate (PM) estimated for the cetaceans represented 3.6% of the total PM within the food web. Among the cetaceans, the striped dolphin showed the highest PM percentage (56.5%), followed by the Risso's dolphin (20.3%), the sperm whale (12.4%), the common bottlenose dolphin (10.6%) and the fin whale (< 0.02%) (Online Resources 2, Table S4).

The consumption flows of the odontocetes within the GoT food web represented less than 1% of the total consumption. Considering the cetaceans, the striped dolphin showed the highest percentage of consumption equal to 65%, followed by the common bottlenose dolphin (13%), the Risso's dolphin (10%), the sperm whale (8%) and the fin whale (4%) (Online Resources 2, Table S4). The main prey consumed by striped dolphin were Mesopel F (37%), SHB\_Squids\_BP and SL\_Squids\_BP (a total of 23%) and SL\_BathypelF\_pisc (11%). The common bottlenose dolphin showed consumption mainly based on the S pel F (23%) and demersal fishes, such as SHB\_DemF\_crust feed (23%), SH\_DemF\_gen (14%). The Risso's dolphin showed specialist feeding habits on the cephalopod groups, with the highest consumption on the SL\_Squids\_BP (66%) and the SHB\_Squids\_BP (21%). The sperm whale showed the highest consumption on the SL\_Squids\_BP (54%), the Mesopel F (21%) and the SHB\_Squids\_BP (11%). Finally, the consumption of the fin whale was mainly on the Macrozooplank group (88%).

Overall, the impacts of the cetaceans on all living FGs in the GoT food web were 64.5% negative and 35.5% positive (Fig. 3a, Online Resources 2, Table S5). The striped dolphin showed the highest percentage of negative and positive impacts (32.7%

and 14.1%, respectively). In addition, the striped dolphin showed the highest percentages of negative impacts in the TLs IV and V (15.2% and 12.3%, respectively), while the highest percentage of positive impacts were estimated in TL III (6.5%). Excluding the common bottlenose dolphin, the negative impacts of the other odontocetes were higher than the positive impacts on the FGs of TL V and IV. Instead, the opposite condition was detected for the impacts on TL III. The impact of the F whale on the food web was very low ( $MTI < -0.005$ ). This latter result as well as those from KSi, PM, and consumption flows indicated a negligible role in the investigated food web in comparison with that played by the odontocetes. Thus, the following comparative analysis on the cetaceans and fishery impacts and the estimation of the Fishery Overlap index were carried out only considering the odontocetes.

#### Fishing impacts on the GoT food web

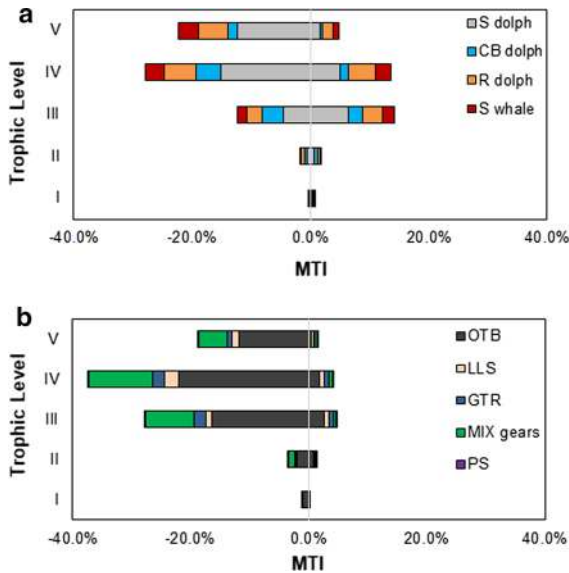
The total catches during the period 2010–2014 were equal to  $1.845 \text{ t km}^{-2} \text{ y}^{-1}$  mainly represented by the DWR Shrimp (14.7%), the BR Shrimp (7%), the octopus and cuttlefish within the SH\_Ceph\_B group (6.8%), the Shrimps BP (6.1%), the SHB\_DemF\_B crust (5.8%), Mesopel F (5.8%), the RG Shrimp (5.4%) and the R mullet (5.4%) (Online Resources 2, Table S6). The Mesopel F group was totally represented by discarded species, similarly to the group of Shrimps BP. Differently, the SH-SHB\_DemF\_B crust group showed the occurrence of commercial species, such as tub gurnard (*Trigla lucerna*) and annular seabream (*Diplodus annularis*) exploited mainly by the GTR. Other important catches with commercial values regarded the M pel F (4.7%) and the Hake (3.8%). The OTB gear represented 82% of the total catches followed by the GTR (10%), the MIX (3.1%), the LLS (2.9%) and the PS gears (1.8%).

The mTLc of the overall fleet was 3.46, with the highest and the lowest values estimated for the LLS (4.00) and the PS (3.40), respectively.

The Exploitation rate (E) values estimated for each FG showed the highest over-exploitation conditions for the Anglers (0.74), the DWR Shrimp and the Hake (0.62), and the L pel F (0.61) (Online Resources 2, Table S6). In addition, the commercial species RG and BR Shrimps and R mullet showed the lowest over-exploitation (E values ranged from 0.50–0.60), as well as



**Fig. 2** **a** Keystoness index analysis of the FGs in the GoT food web; **b** FGs are classified by means of Overall relative impact and Relative biomass as keystone groups/species (very low biomass proportion and high overall effect) or dominant groups/species (high biomass proportion and high overall effect). The main FGs are indicated by the FG codes reported in the Table 1. The white circles indicate the cetacean's species (in bold)



**Fig. 3** The Mixed Trophic Impact (MTI) estimated for the cetaceans (a) and the fishing gears (b). The MTI values of the living FGs impacted by the cetaceans and the fishing gears are aggregated by discrete trophic levels. The values are split into positive and negative impacts (expressed as percentages). The cetaceans and fishing gears are coded as the striped dolphin (S dolph), the common bottlenose dolphin (CB dolph), the Risso's dolphin (R dolph) the sperm whale (S whale) and for Trawl (OTB), set long lines (LLS), nets (GTR), other gears (MIX) and purse seine (PS)

the sharks and rays of the SH\_SR\_B group (0.54) impacted as by-catch.

The percentage value of the negative impacts on the GoT food web due to all fishing gears was equal to 88.2% (Fig. 3b; Online Resources 2, TableS7). These negative impacts were mainly for the OTB gear (53.2%) and the MIX gears (24.9%). The negative impacts of the OTB gear were focused on TLs IV, III and V (21.9%, 16.3% and 11.9%, respectively), while the MIX gear showed high percentages of impacts on the TLs IV and III (10.9% and 8.1%, respectively).

## Odontocetes and fishing interactions

The impact of the fishing mortality (F) on the FGs was higher than the predation mortality (PM) due to the odontocetes, with percentage values of 63.1% and 36.9%, respectively (Fig. 4a). In particular, the OTB gear showed the highest F percentage (45.9%), while the lowest was estimated for the PS gear (0.3%). The MP of striped dolphin (20.9%) was higher than that of the other odontocetes.

The consumption flows towards the odontocetes and fishing gears showed the highest percentage values for the striped dolphin and the OTB gear (40.1% and 38.6%, respectively) (Fig. 4b).

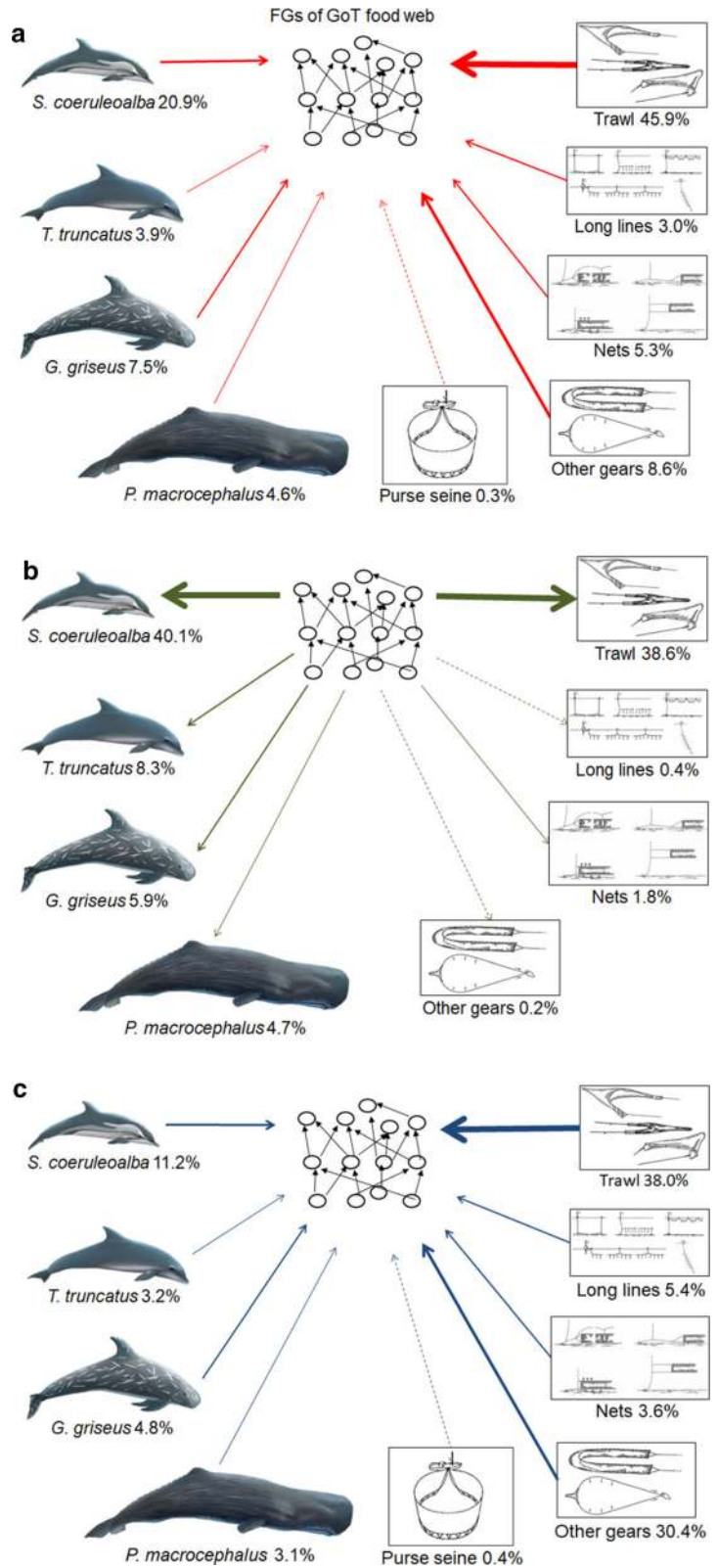
The highest negative impact estimated by MTI was observed for the OTB gear (38.0%) followed by that of the MIX (30.4%) and the striped dolphin FGs (11.2%) (Fig. 4c). The remaining odontocetes and gears were characterized by negative impacts less than 10%.

The Fishery Overlap index (FOi) estimated on the total catches (landing and discards) only showed relevant values for the common bottlenose dolphin (0.41) and the striped dolphin (0.33), while the sperm whale (0.15) and the Risso's dolphin ( $FOi < 0.05$ ) were characterized by low values (Table 3). In particular, the common bottlenose dolphin showed the highest overlap values with the MIX, PS and GTR catches (0.72, 0.70 and 0.44, respectively), while the striped dolphin showed relevant overlap value with the OTB catches (0.30). The FOi estimated exclusively on the total landings showed the only relevant difference for the striped dolphin (0.16 with overall fleet), for which this overlap was lower than the FOi value estimated on the total catches. Nevertheless, the difference was also confirmed by the low value estimated for the OTB landings (0.05).

## Discussion

The comparative analysis on the impacts of odontocetes species and fishery on the food web showed that those due to fishing exploitation are greater than those due to cetacean predation. Trawling was estimated to be the most negatively impacting fishing gear considering the mortality rates, consumption flows and negative mixed trophic impacts. On the other hand, the striped dolphin was the main impact on the food web due to its highest consumption flows. This can be

**Fig. 4** The comparative analysis of **a** the Predation Mortality-Fishing Mortality (red); **b** the consumption flows (green) and **c** the negative overall effects (blue) of the odontocetes and the fishing gears on the FGs of the GoT food web. The thickness of the arrows is proportional to the magnitude of the mortalities, consumption flows and trophic impacts



**Table 3** Niche overlap index estimated for the cetaceans (upper part). Fishery overlap index (FOi) was estimated to assess the competition between the odontocetes and fishery (lower part)

FG	S dolphin	CB dolphin	R dolphin	S whale	F whale	
<i>Niche overlap index</i>						
S dolphin	–					
CB dolphin	0.18	–				
R dolphin	0.31	0.04	–			
S whale	0.60	0.04	0.84	–		
F whale	0.07	0.02	0.00	0.03	–	
FG	Overall Fleet	OTB	LLS	GTR	MIX	PS
<i>Fishery overlap index (FOi)</i>						
Catches						
S dolphin	0.33	0.30	0.02	0.18	0.18	0.16
CB dolphin	0.41	0.26	0.28	0.44	0.72	0.70
R dolphin	0.04	0.04	0.00	0.00	0.00	0.01
S whale	0.15	0.16	0.01	0.02	0.01	0.01
Landings						
S dolphin	0.12	0.05	0.02	0.18	0.18	0.16
CB dolphin	0.43	0.22	0.28	0.43	0.70	0.69
R dolphin	0.01	0.01	0.00	0.00	0.00	0.01
S whale	0.02	0.01	0.01	0.02	0.00	0.01

The FOi were applied to the catches (landings plus discard) and the landings by the overall fleet and the single gears: trawl (OTB), set long lines (LLS), passive nets (GTR), other gears (MIX) and purse seines (PS)

explained by the large energy costs required from the food web to sustain the resident cetacean population that is larger for *S. coeruleoalba* than for the other odontocetes. In addition, the total consumption by odontocetes in the food web was higher than that harvested by fishing.

**Role and impacts of cetaceans in the GoT food web**

The trophic levels of the cetaceans distributed in the Gulf of Taranto were generally in line with those reported in several studies carried out at Mediterranean and global scale (Pauly et al. 1998; Kaschner et al. 2004). The striped dolphin in the Gulf of Taranto showed a TL that overlapped with the only existing comparable values estimated for *S. coeruleoalba* in the Northeast Atlantic applying both an EwE model and a stable isotope analysis in the Bay of Biscay (Lassalle et al. 2014). The common bottlenose dolphin showed a TL very similar to the values observed for the species in the North-eastern Ionian Sea (Piroddi et al. 2010), in the South Catalan Sea (Navarro et al. 2011) and in the Adriatic Sea (Coll et al. 2007). However, the TL value estimated in the Gulf of Taranto for *T. truncatus* was lower than that estimated for the other investigated

odontocetes in the area. This difference is probably due to the more opportunistic behaviour of this flexible predator possibly allowing it to exploit the discard from trawling (Broadhurst 1998). In contrast, the striped dolphin is characterized by more specialist feeding, mostly based on mesopelagic fishes as observed in the Eastern Mediterranean areas (Dede et al. 2016). The Risso’s dolphin and sperm whale showed the highest TLs in the Gulf of Taranto trophic-web due to their preferential predation on the medium and large squids, which occupy the TLs > 3. The TL values estimated for these latter top predators in the study area were higher than corresponding values estimated in other Mediterranean areas. In this regard, the relative importance of the cephalopods in their diets and the geographical variability in the abundance distribution of their main prey could explain the observed differences (Kaschner et al. 2004). The fin whale showed a TL equal to 3.73 in the Gulf of Taranto which is in the range of values estimated in the NW Mediterranean Sea (TL = 3.63, Corrales et al. 2015) and in the Eastern Ionian Sea (TL = 4.17, Moutopoulos et al. 2013).

In agreement with reports for other Mediterranean areas (Blanco et al. 2006; Bearzi et al. 2011b), a high

niche overlap was observed in the Gulf of Taranto between the sperm whale and Risso's dolphin, both being characterized by feeding based on the bathyal squids. In this regard, while the former species usually hunts on deeper slopes ( $> 1000$  m of depth), the latter mainly exploits resources on the upper slope (Carlucci et al. 2018a). Therefore, as reported for *P. macrocephalus* and *G. griseus* in the North Western Mediterranean Sea (Praca and Gannier 2008), their coexistence in the Gulf of Taranto seems to be enhanced by the cephalopod diversity distributed along the depth gradient (Capezzuto et al. 2010; Carlucci et al. 2018a). In addition, whilst the Risso's dolphin seems to be resident in the study area (Carlucci et al. 2018d, 2020; Maglietta et al. 2018), the sperm whale has been proved to be characterized by a migration pattern in the Mediterranean Sea (Frantzis et al. 2011). A partial niche overlap was observed between *S. coeruleoalba* with *P. macrocephalus* and *G. griseus*. In fact, although the striped dolphin shares different bathyal squids as food items with both the sperm whale and Risso's dolphin, it preferentially exploits the mesopelagic fishes (Dede et al. 2016). Finally, the slight niche overlap between *T. truncatus* and the other odontocetes in the Gulf of Taranto is due to its spatial segregation in the shallower portion of the investigated area exploited for its feeding (Carlucci et al. 2016, 2018c). The fin whale showed negligible niche overlapping with the odontocetes in the area because its feeding is based on the macro-zooplankton group.

The striped dolphin was found to be among the most important keystone species (and groups) in the investigated food web. According to the analysis of Overall relative impact, Relative biomass and the MTI analysis, *S. coeruleoalba* resulted a keystone predator playing top-down controls together with the SL\_Squids\_BP. Differently, the most important keystone groups in the food web were found to be the Macrozooplankton and Macrobenthic invertebrates characterized by bottom-up controls. This observation confirms the results obtained by Ricci et al. (2019) identifying the striped dolphin as the most important keystone species among the odontocetes. In addition, the striped dolphin exerted its main impacts on the mesopelagic fishes and groups belonging to TL IV and III characterized by high values of Keystoness. Therefore, it seems to affect species involved in the "wasp-waist" control and vertical energy exchanges

from bathyal zones to the sea surface in the investigated food web (Hunt and McKinnell 2006; Baum and Worm 2009; Griffiths et al. 2013).

#### Fishing impacts on the GoT food web

The small-scale fishery (gillnets, trammel nets, set long lines, traps) is characterized by vessels limiting operation to the coastal grounds, while the bottom otter trawls mainly exploit the shelf break and slope (Russo et al. 2017). The mean trophic level of the catches (mTLc = 3.46) estimated for the overall fleet in the area was higher than that modelled with a similar approach in the North-Central Adriatic Sea and the Greek Ionian Sea (mTLc = 3.07 and 3.33, respectively) (Coll et al. 2007; Moutopoulos et al. 2013) but similar values were observed in the North Aegean Sea (mTLc = 3.47) (Tsagarakis et al. 2010). These results seem to confirm the spatial pattern observed throughout the Mediterranean Sea, where highly exploited northern-central areas showed higher mTLc values than those estimated in the eastern areas (Peristeraki et al. 2019). An overfishing condition was estimated for the main commercial species (hake, red mullet, anglers and deep-water shrimps) by the EwE model in the Gulf of Taranto which was confirmed by independent stock assessment analyses performed for the Northern Ionian Sea (STECF 2016). In addition, the low exploitation rate estimated for the small pelagic fishes was consistent with the stock assessment performed for anchovies and sardines in the study area (STECF 2013). The negative fishing impacts showed a condition of non-selected impacts within the investigated food web on the species grouped at trophic levels III, IV and V, with a consequent loss of secondary production. Potential risks of ecosystem overfishing could be occurring in the food web of the Gulf of Taranto due to unsustainable fishing exploitation impacting the target and non-target species together with the entire food web (Libralato et al. 2008; Jennings et al. 2016).

The MTI analysis showed the different selective predation on the trophic levels operated by the odontocetes with respect to the fishery. In fact, while a negative and non-selective impact on the exploited species was observed due to the fishing gears, the odontocetes proved to select their prey species and a provide positive impact in the assemblage. In particular, while the fishing gears are primarily size



selective, targeting mostly large and economically valuable fish (Heino and Dieckmann 2008), the odontocetes seem to follow a co-evolution process with their prey, developing a specialization in their resources (Trites et al. 2006; Genovart et al. 2010), providing control of the meso-consumers and ensuring trophic stability in the ecosystem (Heithaus et al. 2008; Roman et al. 2014).

#### Odontocetes and fishing interactions

Similarly to the estimations obtained from analogous indicators (Trites et al. 1997; Morissette et al. 2010, 2012), the FOi estimated in the Gulf of Taranto showed a low overlap between the odontocetes prey species and the resources exploited in the area. Several factors could explain the reduced competition for resources, especially among the striped dolphin, Risso's dolphin and sperm whale with all the fishing gears. Firstly, the preferential prey of these odontocetes, such as the mesopelagic fishes for the striped dolphin, are not commercial target species. In addition, the large bathyal squids hunted by the Risso's dolphin and sperm whale are distributed in zones scarcely accessible to fishing exploitation. The common bottlenose dolphin showed competition with the purse seine, the other gears and nets similarly to the observations performed with the overlap index in the Eastern Ionian Sea (Bearzi et al. 2010). In particular, the lower overlapping between *T. truncatus* and the fishery could be due to the wider spatial and depth distribution of the trawl fishing effort in the area. Differently, in the Eastern Ionian Sea the trawl exploits shallower fishing grounds with a high probability of interactions with the common bottlenose dolphin's prey. This result seems to confirm the interactions in terms of both fishing gear alteration and fish damage reported in 2002 for the common bottlenose dolphin in the Apulia region (Lauriano et al. 2009). However, the assessment performed by Lauriano et al. (2009) considered *T. truncatus* and *S. coeruleoalba* as a unique species category in both the Ionian and Adriatic areas of the Apulia, with a consequent overestimation of the interactions. Moreover, the results obtained in the Gulf of Taranto could indicate a different intensity level of competition and, consequently, could also highlight in different perspective the real gear damage and the economic losses due to the common bottlenose dolphin (Bearzi et al.

2010). In fact, the reduction of the nominal fishing effort process starting from the end of the 1990s on the small scale fishery in the Northern Ionian Sea could suggest a progressive lowering of the probability of interactions between the common bottlenose dolphin and nets (Piroddi et al. 2015; Russo et al. 2017). The striped dolphin only showed a high interaction with trawling when the FOi considers the overlapping between *S. coeruleoalba* feeding prey and the species discarded by this fishing gear. This result highlights that the conflicting competition between cetaceans and the fishery in the Gulf of Taranto is due to the non-selective use of this highly discarding fishing gear.

#### Conclusions

The assessment of the overlap between the prey of *S. coeruleoalba*, *G. griseus* and *P. macrocephalus* and the exploited resources has shown a general absence of any conflict between fishery activities and all the investigated odontocetes. This is probably a fortunate condition linked to the bio-geographic conformation of the study area, characterized by the presence of numerous canyons which limit access to fishing and prevent possible conflicts with cetaceans. The exception is the common bottlenose dolphin and the small-scale fisheries using nets. However, although damage to nets caused by *T. truncatus* cannot be excluded, the presence of the cetaceans in the area widely counter balances any economic effective loss due to their ecological roles maintaining the functional integrity of the food web which supports different ecosystem services and benefits (Pace et al. 2015). In fact, the occurrence of these cetacean species locally represents an important attraction for responsible ecotourism and citizen science (Carlucci et al. 2017). Moreover, this study highlights the importance of the striped dolphin as key predator in the Northern Ionian Sea and its ecological relevance concerns the mechanisms of the trophic regulations in the food web.

Starting from this modelling approach, future studies simulating the effects of the adoption of a large Marine Protected Area or different small fishery restricted areas in the Northern Ionian Sea could be developed to improve the knowledge required for both ecosystem-based managements of the fisheries and management plans targeting cetaceans. The study area is characterized by the persistent occurrence of

cetacean species and an intense human use of both coastal and offshore areas, highlighting the need for involvement of local, national and EU management systems in the setting up of a comprehensive strategy for maintaining potentially harmful anthropogenic activities within acceptable levels.

**Acknowledgements** This work contributes to the activities of the project FAIRSEA (Fisheries in the Adriatic Region—a Shared Ecosystem Approach) funded by the 2014–2020 Interreg V-A Italy—Croatia CBC Programme (Standard Project ID 10046951).

**Funding** Open access funding provided by Università degli Studi di Bari Aldo Moro within the CRUI-CARE Agreement.

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