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Addressing Cetacean–Fishery Interactions to Inform a Deep-Sea Ecosystem-Based Management in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea)

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Abstract: Understanding of cetaceans’ trophic role and the quantification of their impacts on the food web is a critical task, especially when data on their prey are linked to deep-sea ecosystems, which are often exposed to excessive exploitation of fishery resources due to poor management. This aspect represents one of the major issues in marine resource management, and trade-offs are needed to simultaneously support the conservation of cetaceans and their irreplaceable ecological role, together with sustainable fishing yield. In that regard, food web models can represent useful tools to support decision-making processes according to an ecosystem-based management (EBM) approach. This study provides a focus on the feeding activity occurrence and the trophic interactions between odontocetes and the fishery in the marine food web of the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea), by zooming in on cetaceans’ prey of commercial interest. In particular, the quantification of trophic impacts is estimated using a food web mass-balance model that integrates information on the bathymetric displacement of both cetaceans’ prey and fishing activity. The results are discussed from a management perspective to guide future research and knowledge enhancement activities as well as support the implementation of an EBM approach.

Keywords: feeding habits; Gulf of Taranto; odontocetes; resources competition; trophic impacts

1. Introduction

Cetaceans are key marine organisms due to the countless ecosystem services they deliver, such as food provisioning, biodiversity enhancement, climate regulation and many others including diverse cultural benefits [1–3]. Thanks to their ecological role and contribution to human well-being, they are priority animals for conservation. The implementation of management measures for cetacean protection requires the best available knowledge related to their ecology, as well as on how this can be affected by direct and indirect human-derived pressures [4,5]. The characterization of the trophic interactions supported by cetaceans and the related mechanisms of energy transfer within the marine food web is key to inform ecosystem-based management (EBM) [6,7]. Prey–predator relationships go beyond the single interaction of consumption between two species. Rather, changes in certain prey and predator abundance can trigger cascade effects on other species and the entire ecosystem’s functioning [8]. Cetaceans are recognized as important top-down controllers in the marine environment with the capability to activate trophic cascade

processes [9,10]. In addition, beyond being top predators, cetaceans have been defined as ecosystem engineers for their additional role in transferring nutrients through faecal plumes along the water column down to the greatest marine depths [11], and for being a remarkable source of organic matter once dead and sunk as carcasses into the abyss [12].

However, understanding of cetaceans' trophic role and the quantification of its impacts on the food web is still critical. In fact, dietary information is usually obtained by means of stomach content analysis of stranded individuals or stable isotope analysis [13], and only recently through metabarcoding combined with biologging analysis [14]. In particular, the stomach content analysis is still the most adopted one, even though it brings biases and a certain degree of uncertainty since it only leads to the acquisition of site-specific data [15,16]. Moreover, the level of uncertainty increases when data on prey are linked to deep-sea ecosystems, which are home to a large amount of unknown biodiversity [17,18]. Indeed, cetacean feeding behavior has been associated with deep-sea environments, which fall below 200 m in depth [19–21]. Thus, the poor knowledge of deep-sea biodiversity may hamper the ability to characterize cetacean prey diversity.

The trophic behavior of cetaceans, especially toothed whales (odontocetes), has often been explored to assess the potential competition between them and fishing activity [22,23]. Indeed, sharing the same marine resources can lead to conflicts between cetaceans and fisheries [24]. For instance, if several odontocetes recognize the depredation of fishing nets as a feeding opportunity, the excessive exploitation of fishery resources due to poor management of the sector can have a major impact on the marine food web and be a primary cause of odontocetes' decline [25,26]. Furthermore, overfishing consequences are driving fishing activities towards deep-sea environments [27–29] with possible amplification of their impact on cetaceans. This aspect represents one of the major issues in marine resource management, and trade-offs are needed to simultaneously support the conservation of cetaceans and their irreplaceable ecological role, together with sustainable fishing yield [30,31].

Better knowledge on the indirect impact of the fishing activity of cetaceans due to their prey's depletion is key to informing EBM of fisheries. Thus, ecological indicators able to assess what species and ecological domains are affected by cetaceans' predation and fishing pressures are needed. In this framework, food web models can represent useful tools to assess the trophic dynamics and impacts of top predators [15] as well as to support decision-making processes addressed towards fishery management [32]. The capability to analyze the trophic relationships according to a holistic approach leads to better understanding of the possible consequences of alterations to ecological mechanisms and the potential for effective conflicts between cetaceans and the fishery to guide EBM [33].

The Gulf of Taranto covers a wide portion of the Northern Ionian Sea (Central Mediterranean Sea) and for over 10,000 km², it is characterized by depths ranging from 200 to over 1000 m. In the last decade, numerous studies have described the gulf as a hot spot of cetacean biodiversity distributed from the coastal shelf to deep waters [34]. In particular, the odontocetes have been described as top-down controllers of the entire food web of the gulf and promoters of trophic cascades up to the middle trophic levels [35,36]. Recently, several pressures affecting cetaceans in the Gulf of Taranto have been assessed and fishery activity has been found to be one of the major sources of indirect impact due to prey depletion and habitat degradation [5].

This study provides a focus on the feeding activity occurrence and the trophic interactions between odontocetes and the fishery in the marine food web of the Gulf of Taranto, by zooming in on cetaceans' prey of commercial interest. In particular, the quantification of trophic impacts is estimated using an already implemented food web mass-balance model for the Gulf of Taranto [35] that integrates information on the bathymetric displacement of both cetaceans' prey and fishing activity. Moreover, consumption fluxes and trophic impacts exerted by cetaceans and fisheries were analyzed by aggregating the species (or species groups) described in the trophic model into ecological domains (or compartments), in order to explicitly consider spatial management needs. The results are discussed from a

management perspective to guide future research and knowledge enhancement activities, as well as support the implementation of EBM in the Gulf of Taranto.

2. Materials and Methods

2.1. Study Area

The Gulf of Taranto, located in the Northern Ionian Sea, extends from Santa Maria di Leuca to Punta Alice covering a surface of 14,000 km² (Figure 1). The eastern side of the basin offers a wide continental shelf that slowly descends toward the continental slope, while a steep shelf ends in the slope depths on the western coast [37]. The area contains the “Taranto valley”, an underwater canyon with NW-SE development that reaches 2200 m in depth, an ecological shelter for many species, inaccessible to trawling that hosts important biocenosis such as crinoid facies [38]. The basin also includes valuable habitats from a conservation perspective such as the Santa Maria di Leuca cold-water coral province and the Amendolara shoal [39–43]. The occurrence of many of these habitats is the result of the circulation of gulf waters, which sees the mixing of warm surface and cold deep-water masses as well as vertical flows aided by the seabed shape [44,45]. Both the complex bottom topography and the mix of environmental conditions make this area suitable for the presence of thriving cetacean populations [46,47]. In particular, the common bottlenose dolphin *Tursiops truncatus* usually occurs within the continental shelf [46–48], while the striped dolphin (*Stenella coeruleoalba*), the short-beaked common dolphin (*Delphinus delphis*), Risso’s dolphin (*Grampus griseus*), the Cuvier’s beaked whale (*Ziphius cavirostris*), the sperm whale (*Physeter macrocephalus*) and the fin whale (*Balaenoptera physalus*) are mainly distributed in offshore waters on the continental slope [46–57]. Most of these species act as top-down controls on the entire food web [35], activating trophic cascades up to the middle trophic levels [36]. Moreover, this area has been suggested as a critical habitat for the common bottlenose, the striped and Risso’s dolphins [46,47,49].

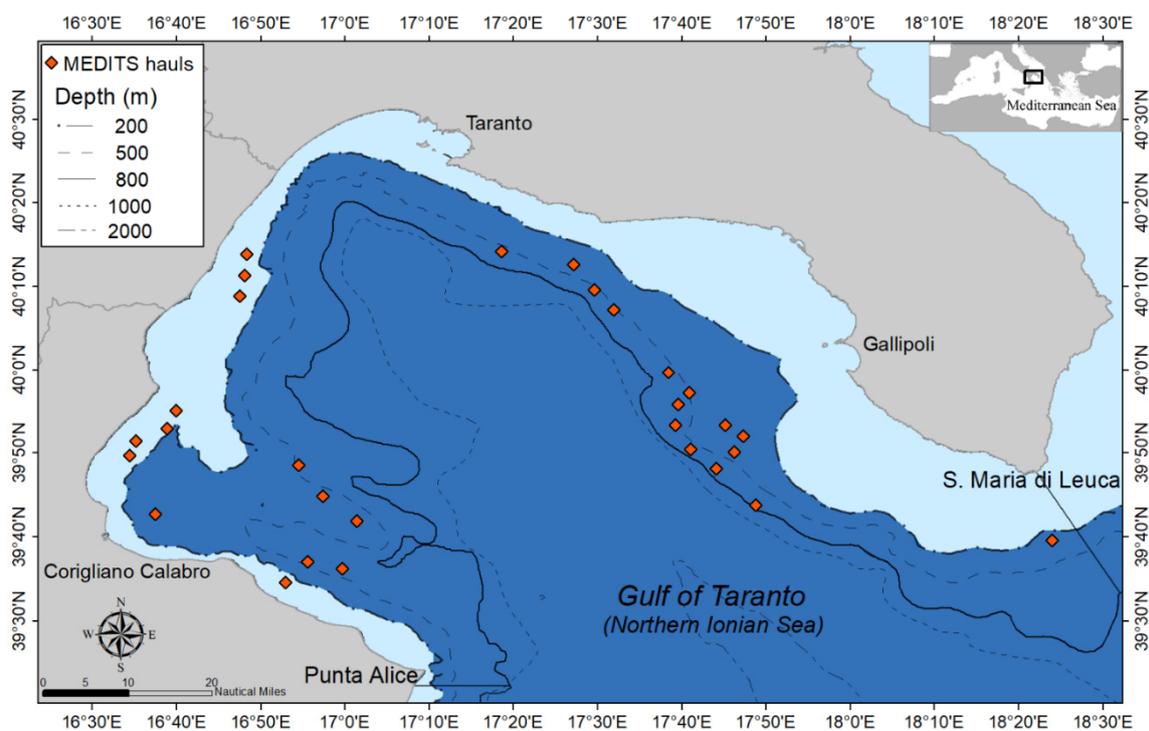


Figure 1. Map of the Gulf of Taranto with the MEDITS experimental trawl hauls and the modelled area included in the black line (800 m of depth). The depth of 200 m separates shelf (light) and slope areas (dark).

Unfortunately, the coastal area of the Gulf of Taranto is also characterized by high urbanization and multi-species fishing activities, representing a source of environmental

disturbance and contamination mainly on the shelf break and slope [58]. Fishing exploitation occurs from the coastal waters up to 800 m depth, focused on several commercial species such as the red mullet (*Mullus barbatus*) on the continental shelf, the European hake (*Merluccius merluccius*) and the deep water rose shrimp (*Parapenaeus longirostris*) over a wide bathymetric range as well as the deep-water red shrimps (*Aristeus antennatus* and *Aristaeomorpha foliacea*) on the slope [43,59]. The trawl fleet is characterized by vessels with a length-over-all (LOA) of 12–18 m and it mainly exploits the shelf break and slope grounds [43,58]. Trawlers represent about 21% in number, 64% in gross tonnage and 56% in engine power of the whole Northern Ionian Sea fleet [59]. 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. Considering the effect of trawling, and to a lesser extent of other types of fishing gear, the General Fishery Commission for the Mediterranean (GFCM FAO) created a new Fishery Restricted Area (FRA) on the Santa Maria di Leuca cold-water corals (SML CWC), recommending the prohibition of towed gear [40,41,44,45,60]. Moreover, chemical pollution, marine traffic, noise pollution, climate change and habitat fragmentation are all threats to biodiversity in the area, especially for cetaceans [5].

2.2. Data Collection on Behavioral Activities of Cetaceans

Behavioral activity data were collected during standardized vessel-based surveys carried out from 2009 to 2020 on board a 12 m catamaran. The focal group method with instantaneous scan sampling of the predominant behavior was applied [61]. A group was defined as dolphins within an approximately 100 m radius of each other [62] that were observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity [63]. The focal group was defined as an aggregation of dolphins engaged in the same activity within 100 m of the boat. This prevents possible bias in the identification of a behavioral activity during sightings with a group size greater than 100 dolphins.

The focal group was scanned every 3 min for at least 15 min, recording the predominant activity state during the entire session, which is the activity state in which more than 50% of the dolphins within the group were involved at the time of sampling [64,65]. Activity classes identified during surveys were classified according to [63] as feeding, resting, socializing and travelling (Table 1). To avoid possible interference in dolphin behavior due to the presence of the vessel, the sampling was interrupted when specimens were observed at less than about 50 m [66]. Moreover, observers had to maintain a safe distance not less than 5 m from dolphins, lowering speed or interrupting navigation to prevent collisions or possible injuries [67]. In addition, date, sea-weather condition, geographic coordinates at the beginning of sighting and when the vessel approaches the group of dolphins, depth (m), time of first contact, and group size (number of individuals) were recorded.

Table 1. Description of behavioral features of odontocetes used to identify the activity class.

Activity Class	Description of Observed Behaviors
Feeding	Dolphin(s) involved in chases or captures of prey items close to the surface, and/or showing erratic movements at the surface, multidirectional diving and rapid circle swimming.
Resting	Dolphins observed in a tight group (<1 body length between individuals) stay close to the surface, emerging at regular intervals and swimming very slowly.
Socializing	Physical interactions ranging from chasing to body contact, such as rubbing and touching or copulation among dolphins. Aerial behaviors such as breaching and leaping were frequently observed.
Travelling	Dolphins persistently swimming in the same direction at sustained speed and making noticeable headway.

Sighting positions were located using ArcGis 10.1 and the bathymetric distribution of feeding activities engaged in by the odontocetes was analyzed.

2.3. Data Analysis and Ecological Indicators

A total of 51 functional groups (FGs) were represented in the Gulf of Taranto (GoT) food web model during the period 2010–2014, with 5 cetaceans represented: the striped dolphin, common bottlenose dolphin, Risso’s dolphin, the sperm whale and the fin whale (Table 2). In addition, fishery operations in the modelled area were represented by 5 types of fishing gear: bottom otter trawls (Trawl), set long lines (Long line), passive nets (Nets), other gear (drifting long lines, driftnets, pots, traps and beach seines) (Others) and purse seines (Purse seine). More details on the modelling approach, taxa characteristics and data of the FGs are reported in [35]. In the present analysis, FGs were aggregated into ecological domains using the bathymetric distribution of species calculated by the centre of gravity (COG, [68,69]) obtained by the sampling hauls of the “Mediterranean International Trawl Survey” project (MEDITS, Figure 1) [70], and integrative ecological information obtained from the SeaLifeBase database [71]. In particular, 8 domains were defined: Planktonic groups (Plank), Pelagics of shelf (PEL-SH), Pelagics of slope (PEL-SL), Demersals of shelf (DEM-SH), Demersals of slope (DEM-SL), Benthopelagic groups of shelf (BP-SH), Benthopelagic groups of slope (BP-SL) and Discards (Table 2).

Table 2. Functional groups with codes and the relative domains in the Gulf of Taranto food web model. Domains are coded as Planktonic (Plank), Benthic (BENT), Pelagic groups of shelf (PEL-SH), Pelagic groups of slope (PEL-SL), Demersal groups of shelf (DEM-SH), Demersal groups of slope (DEM-SL), Benthopelagic groups of Shelf (BP-SH), Benthopelagic groups of Slope (BP-SL). The centre of gravity (COG, m) and variance (Var) in meters are reported when available.

No.	Functional Group	FG Code	Domain	COG (m) Var
1	Striped dolphin	S dolph	PEL-SL	-
2	Common bottlenose dolphin	CB dolph	PEL-SH	-
3	Risso’s dolphin	R dolph	PEL-SL	-
4	Sperm whale	S whale	PEL-SL	-
5	Fin Whale	F whale	PEL-SL	-
6	Loggerhead Turtle	Log turtle	PEL-SH	-
7	Seabirds	Seabirds	-	-
8	Large pelagic fishes	L pel F	PEL-SL	-
9	Slope Sharks and Rays benthic feeders	SL_SR_B	DEM-SL	523 (113)
10	Shelf-Shelf Break Sharks and Rays benthopelagic feeders	SH-SHB_SR_BP	BP-SH	171 (56)
11	Shelf Sharks and Rays benthic feeders	SH_SR_B	DEM-SH	29 (55)
12	Slope Sharks benthopelagic feeders	SL_Sharks_BP	BP-SL	614 (113)
13	Shelf Break-Slope Demersal fishes generalist feeders	SHB-SL_DemF_gen	DEM-SL	359 (164)
14	Shelf-Shelf Break Demersal fishes generalist feeders	SH-SHB_DemF_gen	DEM-SH	69 (59)
15	Shelf-Shelf Break Demersal fish piscivorous	SHB_DemF_pisc	DEM-SH	89 (66)
16	Slope Bathypelagic fishes piscivorous	SL_BathypelF_pisc	BP-SL	520 (104)
17	Slope Demersal fishes decapods feeders	SL_DemF_Decap	DEM-SL	412 (119)
18	Shelf Break-Slope Fishes benthopelagic crustacean feeders	SHB_F_BP crust	DEM-SL	229 (100)
19	Shelf-Shelf Break Demersal fishes benthic crustacean feeders	SH_DemF_B crust	DEM-SH	77 (47)
20	Shelf-Shelf Break Demersal fishes benthic invertebrate feeders	SH_DemF_Binv	DEM-SH	65 (54)
21	Shelf Break Fishes zooplanktivorous	SHB_F_plank	DEM-SH	90 (60)
22	Small pelagic fishes	S pel F	PEL-SH	46 (31)
23	Medium pelagic fishes	M pel F	PEL-SH	92 (76)
24	Macrourids benthic invertebrate feeders	Macrourids	DEM-SL	531 (120)
25	Mesopelagic fishes	Mesopel F	BP-SL	445 (129)
26	Red mullet	R Mullet	DEM-SH	38 (49)
27	Hake	Hake	DEM-SH	131 (176)
28	Anglers	Anglers	DEM-SL	232 (196)
29	Slope Squids benthopelagic feeders	SL_Squids_BP	BP-SL	545 (127)
30	Shelf Break-Slope Squids benthopelagic feeders	SHB_Squids_BP	BP-SH	121 (85)
31	Shelf-Shelf Break Cephalopods benthic feeders	SH_Ceph_B	DEM-SH	77 (64)

Table 2. Cont.

No.	Functional Group	FG Code	Domain	COG (m) Var
32	Slope Octopus and Bobtail Squids benthic feeders	SL_Ceph_B	DEM-SL	430 (133)
33	Shelf Break-Slope Bobtail Squids benthopelagic feeders	SHB_BobSquids_BP	BP-SL	232 (98)
34	Benthopelagic Shrimps	Shrimps_BP	BP-SL	446 (97)
35	Slope Decapods	SL_Decap_Scav	DEM-SL	403 (118)
36	Shelf and Shelf Break Crabs	SHB_Crabs	DEM-SH	60 (61)
37	Deep-water rose shrimp	DWR Shrimp	DEM-SL	252 (96)
38	Red giant shrimp	RG Shrimp	DEM-SL	436 (152)
39	Blue and red shrimp	RB Shrimp	DEM-SL	545 (126)
40	Polychaets	Polychaets	BENT	-
41	Macrobenthicinvertebrates	Macrobentinv	BENT	-
42	Gelatinous plankton	Gel plank	PLANK	-
43	Suprabenthic crustaceans	Supbentcrust	BENT	-
44	Macrozooplankton	Macrozooplank	PLANK	-
45	Meso and Microzooplankton	Meso_Microzooplank	PLANK	-
46	Bacterioplankton	Bacterioplank	PLANK	-
47	Seagrasses and Macrophytobenthos	Seagrasses and algae	BENT	-
48	Phytoplankton	Phytoplank	PLANK	-
49	Discards	Disc	DISC	-
50	Marine snow	M Snow	DET	-
51	Bottom Detritus	Det	DET	-

Concerning cetaceans' trophic traits, feeding habits were described by means of quantitative information (expressed as % weight) derived from stomach content analysis carried out in several Mediterranean areas, such as the North Aegean Sea [72], Western Mediterranean areas [73,74], Ionian Sea [75], Ligurian Sea [76,77], and Greek seas [78]. These different pieces of information were aggregated providing an average diet for each cetacean species [35]. Moreover, in the present study, some qualitative information obtained by means of food remains and observations carried out during feeding activities of odontocetes in the Gulf of Taranto were integrated to increase the quality of diet information. In particular, parts of *Histioteuthis bonnellii* were collected on the water surface during a sighting of sperm whales [79] and chases of individuals of *Coryphaena hippurus* by common bottlenose dolphins were observed (personal communication). In order to validate the use of odontocetes' diets in the Gulf of Taranto model obtained from close areas, an analysis of the odontocetes' prey occurrence in the Gulf of Taranto was carried out using the diet information collected in the literature and information on the taxa sampled by MEDITS in the study area during the period 2009–2019. For each prey listed in the diets, the biomass index (kg km^{-2}) was calculated on 30 experimental hauls distributed in the Gulf of Taranto. A total of 9 diets of odontocetes were acquired. The following species belonging to the Myctophidae family, detected in the diets and MEDITS sampling data, were aggregated as single food items in the analysis: *Benthosema glaciale*, *Ceratospelus maderensis*, *Diaphus holti*, *Electrona rissoi*, *Hygophum benoitti*, *H. hygomii*, *Hygophum* spp., *Lampanyctus crocodilus*, *Lobianca dofleini*, *L. gemellari*, *Myctophum punctatum*, *Myctophum* spp., *Symbolophorus veranyi*.

Ecological indicators were selected by the Ecopath model to characterize the trophic interactions between cetaceans and the fishery. Thus, the mixed trophic impacts (MTI), the keystone index (KSi) and the consumption flows ($\text{t km}^{-2} \text{ year}^{-1}$) were calculated for each FG.

The KSi was calculated through mixed trophic impact analysis (MTI) [80], by quantifying the relative impact of biomass change within a component (impacting group) on each of the other components (impacted groups) in the food web, including the fishing gear. Positive/negative MTI values indicate an increase/decrease in biomass of the group j due to a slight increase in biomass of the impacting group i. Thus, negative impacts can be associated with prevailing top-down effects and positive ones to bottom-up effects [81].

The overall effect (ε_i) of a group i represents all the direct or indirect MTI values of group i on all the other groups in the food web:

$$\varepsilon_i = \sqrt{\sum_{j=1}^n m_{ij}^2}$$

where the impact on the group itself (m_{ij} with $i = j$) is not considered, and ε_i is calculated as a relative value with respect to the maximum [81]. The parameter p_i is the relative biomass of the group in the food web, excluding detritus biomass:

$$p_i = B_i / \sum_k B_k$$

Thus, two expressions of KSi provided by the Ecopath routine were calculated in this study [81]:

$$KSi = \log[\varepsilon_i(1 - p_i)] (L_KSi)$$

where p_i is the relative biomass of the group, excluding detritus biomass [82].

$$Ksi = ICL \times BC0 (V_KSi)$$

where ICL (impact component) is estimated by means of the overall effect (ε_i) and BC0 (the biomass component) is estimated from (p_i), where BC0 is the biomass in a descending order ranking. The former KSi assigns high values to functional groups with low biomass but high overall effect on the trophic network, while the latter enhances the greater relevance of species of high trophic levels.

The MTI analysis was carried out on the displacement of the trophic impacts of the cetaceans and the fishery to identify which groups and domains are most involved. In particular, the analysis was carried out by means of the aggregation of the groups into 8 domains. In addition, the direct and indirect trophic impacts exerted by the cetaceans and the fishery were classified by identifying the contribution on the shelf and slope domains. In particular, the direct impacts on the consumed groups were identified by their diet information being prey, while the indirect impacts corresponded to the impacts on the groups not consumed by the cetaceans. Moreover, a positive direct impact of a predator on a prey represents a beneficial interaction for the prey, which allows the impacting group to be classified as beneficial predators [80]. The prey positively impacted by each odontocete were identified in the analysis [83]. The displacements of fishing pressures among domains were analyzed using the total catches and the MTI split by fishing gear.

The consumption flows ($t \text{ km}^{-2} \text{ year}^{-1}$) from the prey towards the cetaceans and fishing gear (as catches, $t \text{ km}^{-2} \text{ year}^{-1}$) were analyzed by means of the aggregation of the groups into domains.

3. Results

3.1. Spatial Distribution and Traits of Odontocetes' Feeding Activities

Out of 1377 total sightings collected during 2009–2020 in the Gulf of Taranto, 256 (19%) were classified as feeding (Figure 2). Most of the sightings of feeding activity involved the striped dolphin (75%), followed by the common bottlenose dolphin (18%), Risso's dolphin, and the sperm whale (>5%). Most of these sightings of feeding activity were displaced over 200 m of depth, except for *T. truncatus*, which was observed in the feeding state at a median depth of 50 m (interquartile range IR = 100) (Figure 2). The striped dolphin was observed in feeding activities on the surface in waters with a median bottom depth of 464 m (IR = 270). Although Risso's dolphin and the sperm whale were observed while feeding fewer than 10 times, they showed the highest median depths of 820 m (IR = 365) and 600 m (IR = 490), respectively.

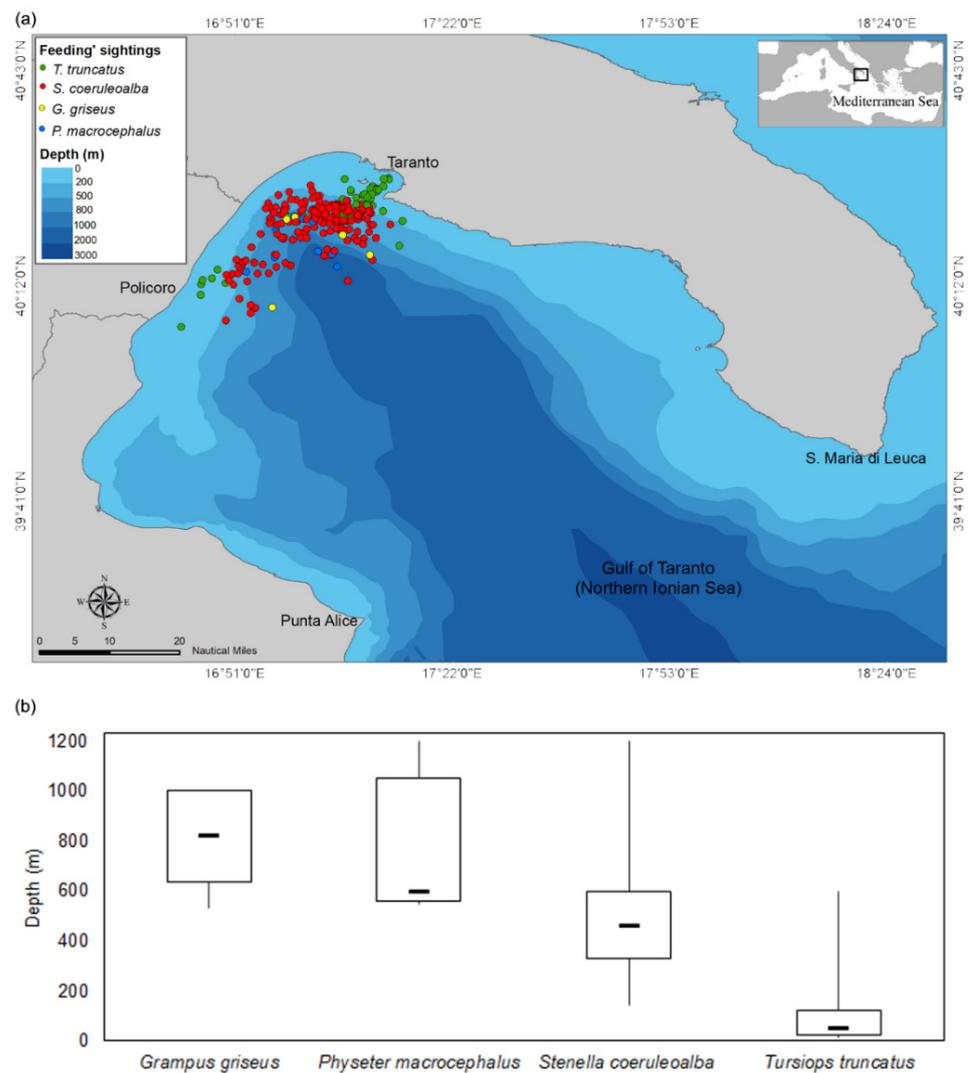


Figure 2. (a) Spatial distribution of the sightings of feeding activity. (b) Boxplot of bathymetric values recorded in the study area during the period 2009–2020. The boxplots show the median (midline), quartiles (box limits) and minimum and maximum values (whiskers).

A total of 77 taxa were identified from the literature as food items in cetaceans’ diets of different geographic areas and 64 of these were collected during the MEDITS surveys in the Gulf of Taranto (Table A1). The biomass of these taxa (403.5 kg km^{-2}) represented 51.8% of the total sampled biomass. Among the potential prey, the highest biomasses were detected for *Engraulis encrasicolus* (23.5%), *Merluccius merluccius* (10.6%), *Phycis blennoides* (8.2%) and *Trachurus* spp. (7.9%). *Illex coindettii* was the most abundant cephalopod (4.7%), followed by *Octopus vulgaris* (2.4%) and *Todaropsis eblane* (approximately 2.0%). The biomass of bony fishes and cephalopods contributed about 82% and 15% of the total, respectively.

3.2. Trophic Interactions of Cetaceans in the Gulf of Taranto

The rank obtained by V_KSi indicates the relevant importance of the striped dolphin, Risso’s dolphin and the sperm whale as keystone predators in the food web classified in 2nd, 4th and 11th position in the rank, respectively (Table A2). The highest V_KSi value was estimated for bathyal benthopelagic squids (FG 29) and other top predators, such as the anglers and the large pelagic fishes (FGs 28 and 8). In contrast, in the L_KSi rank, the striped dolphin was the only keystone predator among odontocetes classified in 6th

position of rank, while the top positions were occupied by basal groups (FG 44, 41, 45), the benthopelagic cephalopods and small pelagic fishes.

S. coeruleoalba was a beneficial predator of seven groups, with the highest positive impact on the group of SH- SH_DemF_Binv (FG 20) composed of species such as *Mullus surmuletus*, *Diplodus* spp., and *Pagellus acarne* (Figure 3). Moreover, the striped dolphin showed its highest negative impacts on offshore pelagic and benthopelagic domains, particularly on groups of large pelagic fishes and bathyal benthopelagic squids (Figure 4, Table S1). Furthermore, other indirect positive impacts were found on the group of Macrourids (FG 24) and the bathyal benthic cephalopods (FG 32). The common bottlenose dolphin showed its highest negative direct impacts on shelf and slope demersal domains, mainly impacting groups of demersal fishes (FG 14, 19, 13) as well as hake and red mullet. This species proved to be a beneficial predator exclusively for the SHB_Crabs. Risso's dolphin showed its highest negative direct impacts on the groups of squids (FG 29 and 30). The species was found to be a beneficial predator for the bathyal benthic cephalopods and to have positive impacts on demersal domains in the shelf and slope. The sperm whale showed the highest negative direct impacts on the bathyal benthopelagic domain, particularly on the squids, while positive indirect impacts were detected on the bathyal demersal domain.

The striped dolphin was found to have the strongest direct impacts both on the slope and the shelf, with percentage values of 25% and 13%, respectively (Table A3). In contrast, the common bottlenose dolphin had strong direct impacts on the shelf groups with a percentage equal to 10%. The strongest indirect impacts were found for both the Risso's dolphin and sperm whale on the slope with percentage values of 9% and 6%, respectively. Excluding Risso's dolphin, all odontocetes showed negative impacts higher than positive impacts both on the groups of the shelf and slope. The striped dolphin had the highest negative impacts on the slope groups, while the Risso's dolphin exerted the highest positive impacts on the slope groups (10% of the total impacts).

The main prey consumed by the *S. coeruleoalba* belonged to the BP-SL domain, comprising a percentage value of 63.3% of its consumptions, followed by those of the DEM-SH domain (14.1% of its consumptions) and the BP-SH domain (11.9% of its consumption). *T. truncatus* fed especially on prey distributed within the demersal domain (63.5% of its consumption), which was formed by 52.5% of DEM-SH. A consistent proportion of its consumption (27%) was also provided by the prey of the PEL-SH domain. Risso's dolphin consumption was exclusively characterized by benthopelagic prey, primarily from the BP-SL domain (79.3% of its consumption) and then the BP-SH domain (20.6% of its consumption). The sperm whale also fed primarily in the benthopelagic domain, 82% of its consumption being BP-SL prey.

As a final consideration, over 65% of the biomass estimated as consumed by cetaceans during the year came from benthopelagic prey, followed by demersal (20.2%) and then by pelagic (8.7%). In addition, the consumption of slope prey (59.8%) was higher than that of shelf prey (36.3%).

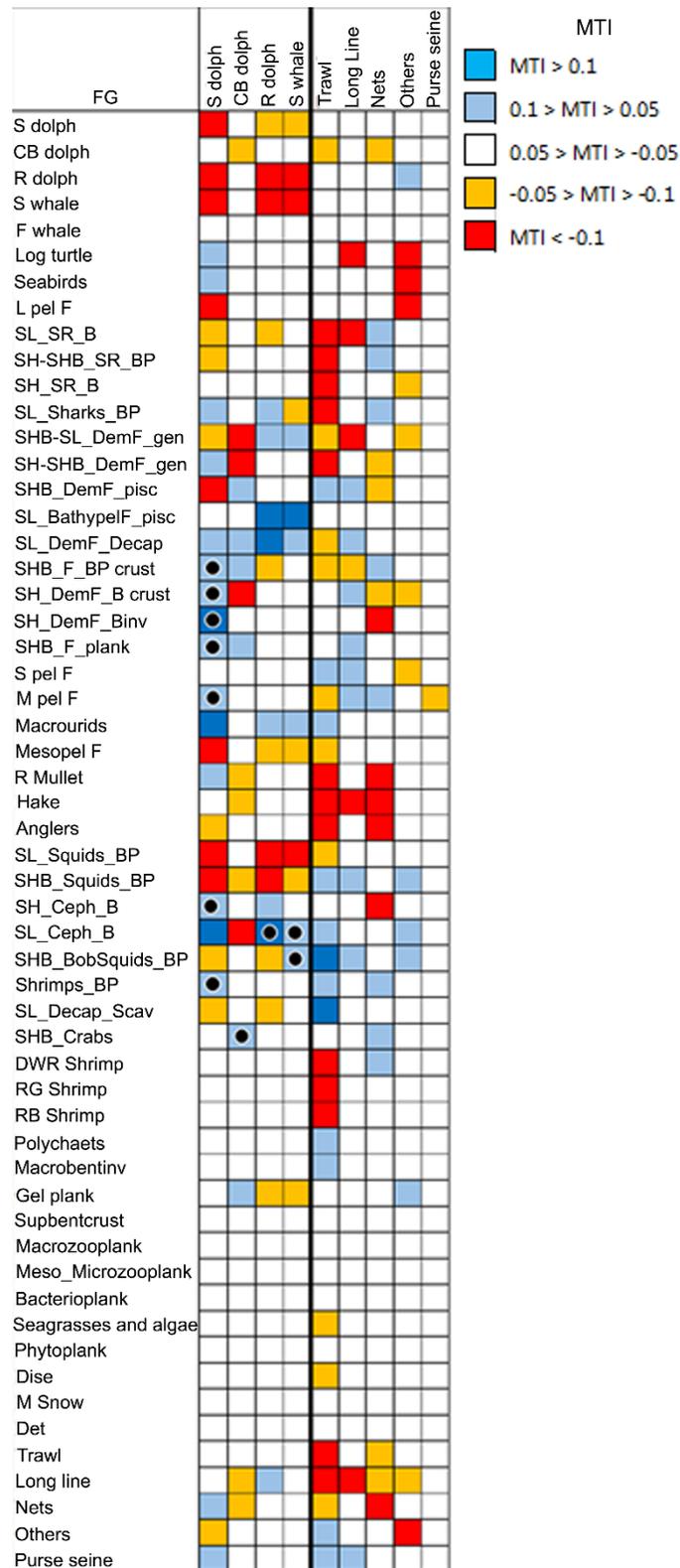


Figure 3. Mixed trophic impacts by odontocetes and fisheries estimated for all FGs and fishing gear during the period 2010–2014. The numbers at the head of the columns indicate the odontocete species and the fishing gear impacting on the FGs of the GoT food web. The black circle indicates the condition of beneficial predator (positive impact on a prey). FG codes are reported in Table 2.

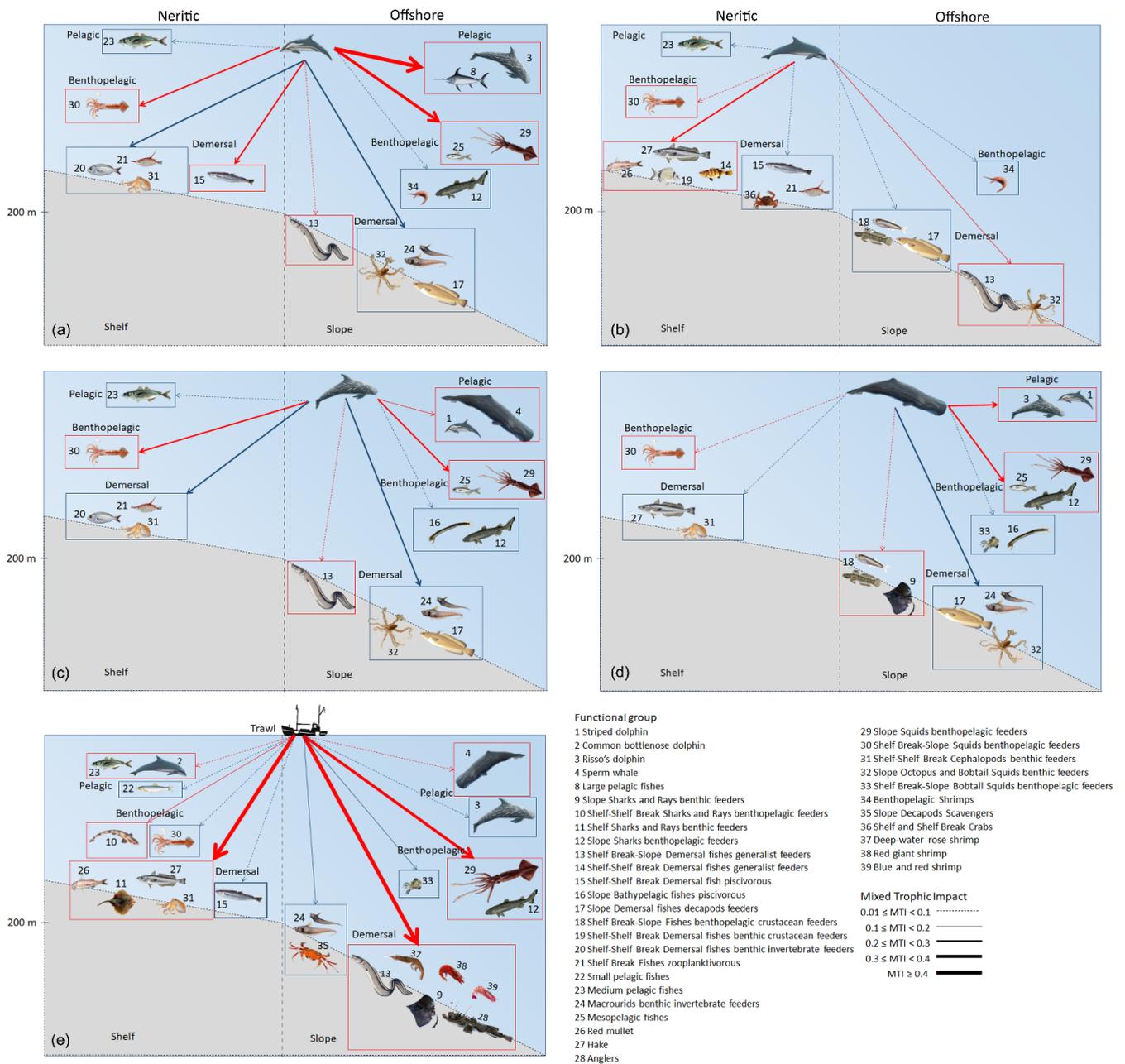


Figure 4. Positive (blue) and negative (red) trophic impacts made by (a) the striped dolphin, (b) common bottlenose dolphin, (c) Risso’s dolphin, (d) the sperm whale and (e) the trawl on the functional groups aggregated into pelagic, benthopelagic, and demersal domains within the food web of the Gulf of Taranto. The bathymetric separation between shelf and slope as well as neritic and offshore areas are indicated by the mark of 200 m of depth and the dashed line. FG code numbers are reported in the legend.

3.3. Fishing Impacts on the Food Web of the Gulf of Taranto

The trawl showed its highest negative impacts on the groups of the bathyal benthopelagic domain and demersal domain of the shelf and slope (Figure 4). Groups of anglers, commercial shrimps (FG 37, 38 and 39), the red mullet, hake and demersal fishes that are generalist feeders of shelf (FG 14, *Zeus faber*, *Scorpaena porcus*, etc.) showed the highest negative direct impacts (Figure 3, Table S1). Similarly, the highest indirect negative impact was exerted on sharks and rays (FG 9, 10, 11 and 12). Small positive impacts were observed on the groups of bathyal decapods scavengers and bobtail squids (FGs 35, 33). The Long line showed its highest negative direct impacts on hake and the group of de-

mersal fishes generalist feeders of slope (FG 13, *Conger conger*, *Polyprion americanus*, etc.). Nets showed their highest direct negative impact on the SH_Ceph_B, the SH_DemF_Binv, hake, red mullet and the anglers. The Others category of gear showed its highest direct negative impact on the large pelagic fishes, while the highest indirect negative impact was on loggerhead turtles.

Overall, the trawl exerted the highest negative impacts on the slope and shelf groups, with percentage values of 32% and 26% of the total impact, respectively (Table A2). Similarly, the Others category of gear accounted for 11% and 8% of the total negative impacts on the shelf and slope groups, respectively.

Amongst the investigated types of fishing gear, trawling was responsible for 82.1% of total catches, followed by Nets with a percentage value of 10% (Figure 5b, Table A4). Trawling exploited mainly DEM-SL and DEM-SH groups with percentage values of 46.2% and 30.1% of its catches, respectively. In addition, the BP-SL species represented 18.2% of the trawl catches. The Net catches represented 10% of the total and were almost totally composed of DEM-SH (93%) and PEL-SH species (3%).

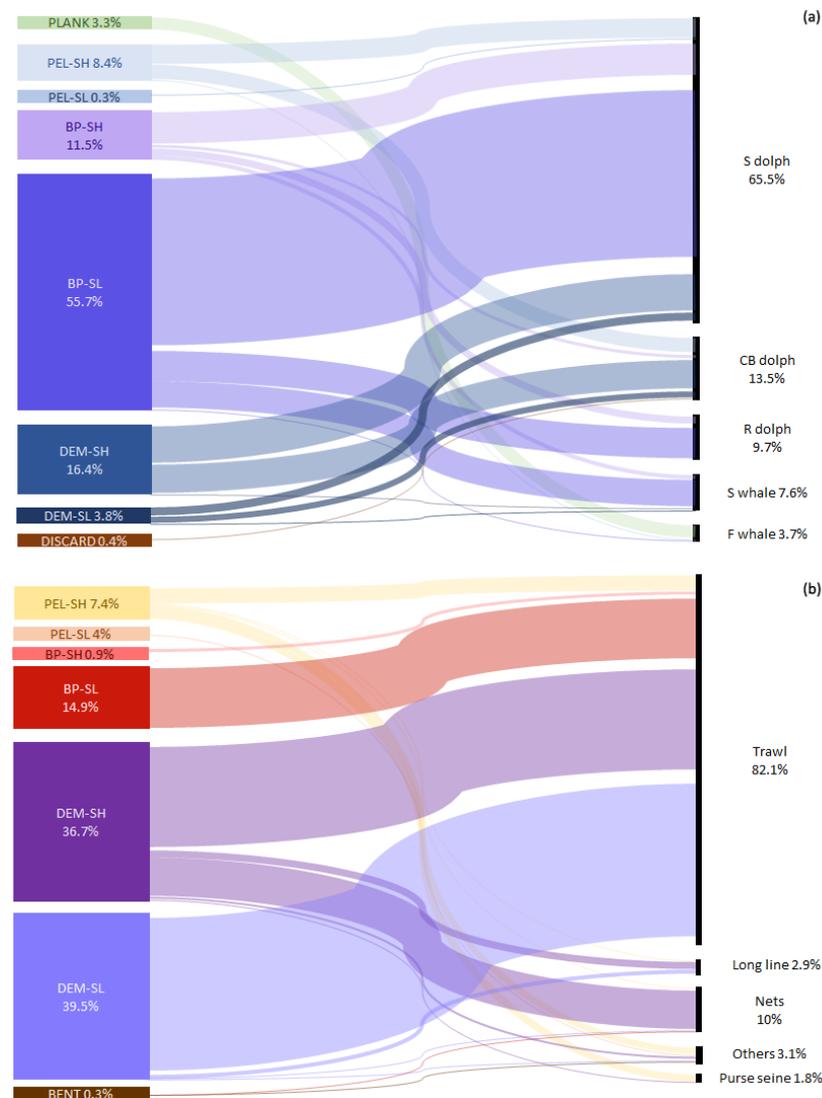


Figure 5. Sankey plots of (a) consumption flows towards cetaceans; (b) catches of types of fishing gear by FGs both aggregated into ecological domains: Planktonic (PLANK), Pelagics groups of shelf (PEL-SH), Pelagics groups of slope (PEL-SL), Demersal groups of shelf (DEM-SH), Demersal groups of slope (DEM-SL), Benthopelagic groups of shelf (BP-SH), Benthopelagic groups of slope (BP-SL), and Discards.

Most of the catches were characterized by demersal species of the shallowest and bathyal zones, representing 76.2% of the total catches. The BP-SL species represented 14.9% of the total catches, totally due to trawl fishing activity, while PEL-SH species were 7.4% and were exploited by trawl, other types of gear and purse seine.

A total of 21 FGs were common resources for both odontocetes and the fishery in the study area (Figure 6). The FGs mostly consumed by odontocetes were SHB_DemF_pisc, SL_BathypelF_pisc, S pel F, Mesopel F, SL_Squids_BP, SHB_Squids_BP, SL_Ceph_B, SHB_BobSquids_BP.

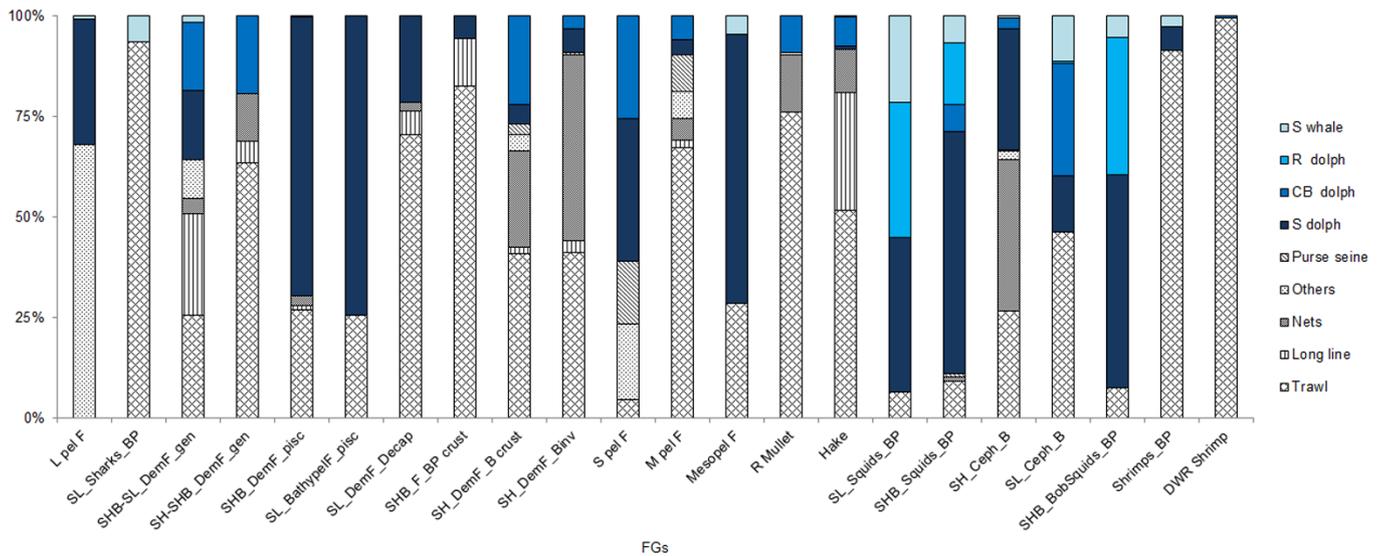


Figure 6. Comparison between odontocetes’ feeding and fishery catches (expressed in %) by FGs estimated by the food web model in GoT. Blue shading corresponds to the FGs of odontocetes and the pattern fill represents different types of fishing gear.

4. Discussion

This study reports a hypothesis on the trophic interactions between cetaceans and the fishery in the Gulf of Taranto, according to the available data and assumptions. The matching between taxa known to be preyed on by odontocetes (derived exclusively from the literature) and those sampled in the study area prove to be consistent, even though there are several aspects which need to be ascertained and defined, including the group of species in each FG, the relative COG, the capture of FG by different types of gear and the consumption of cetaceans in the Gulf of Taranto. The application of the model indicates that bony fishes and cephalopods are the main prey consumed by the odontocetes. A high level of cephalopod biodiversity is distributed throughout the entire study area [84–91]. Of no less importance, bathypelagic cephalopods (e.g., *A. lesueurii*, *G. armata*, *O. bartramii*), despite not being found in the sampling hauls, had already been recorded in the Northern Ionian Sea [39,59,92–94]. Some of them, such as *O. sicula*, can constitute the main prey item of marine mammals, thus playing an important role in their diet [94–96]. Most of the bony fishes known to be consumed by *S. coeruleoalba* and *T. truncatus* are widely distributed in the gulf and Ionian area [43,59]. Despite the lack of local diet information on cetaceans representing a critical gap to be better filled by future studies, the analysis highlights the availability of important food resources that fit the trophic needs of the resident odontocete populations, in line with observations reported in other locations, especially the Aegean Sea, even though these displayed different levels of abundance [72,78], and the Ligurian Sea [76,77]. This evidence supports the robustness of the here applied modelling approach.

4.1. Trophic Role Played by Cetaceans in the Gulf of Taranto

The model seems to indicate that all odontocetes act as top predators that consume a variety of prey, mostly represented by benthopelagic fauna distributed over 200 m of depth. The only exception is *T. truncatus*, which inhabits shallow grounds feeding mainly on demersal species.

The keystone analysis highlights the importance of the striped dolphin as a keystone predator through both Libralato's and Valls' KSi that rank, similar to previous results obtained by [35]. The comparison between two KSi derived from the model applied stresses that other odontocetes emerge as keystone predators when keystone-ness is estimated by assigning a higher weight to the species of high trophic levels [97]. Therefore, Libralato's KSi detects which top predators play a more relevant role in a food web structure driven by basal groups (e.g., zooplankton, phytoplankton and macrobenthic invertebrates) and their bottom-up control. The substantial importance of basal groups is favored by the oligotrophic conditions in the Ionian Sea [98,99].

Interestingly, the striped dolphin proved to be the most important apex predator, located in 6th position of the rank together with other keystone predators belonging to the meso-predators, such as the bathyal benthopelagic squids (FG 29) and benthic cephalopods (FG 31). Thus, this dolphin is involved in the main pathway of trophic regulations in the investigated food web, likely due to its high abundance in the study area [46,47,53,100] and the direct predation on mesopelagic fishes, which are key players as wasp-waist species in the Gulf of Taranto [35,36]. On the other hand, Valls' KSi stresses the central role of other offshore odontocetes (i.e., *G. griseus* and *P. macrocephalus*) as stronger keystone predators than other consumers in the Gulf of Taranto food web. This importance as top-down controllers is due to their high consumption rates on a large variety of trophic levels, as well as their behavioral feeding strategies [101]. In particular, behavioral strategies could represent key elements in the activation of behavior-mediated trophic cascades with respect to more common processes of direct predation as an additional driver of prey biomass decline [102,103]. Such evidence is supported by mixed trophic impacts analysis, which focuses on the direct and indirect impacts of the odontocetes on other groups. It is known that the strength of top-down control is enough to switch on trophic cascades in the study area [35,36]. Such control seems to be driven by direct impacts being higher than the indirect ones, except for Risso's dolphins. In fact, this species shows more specialized feeding on some species of cephalopods than other odontocetes [72]. The exclusive controls of benthopelagic cephalopods, which are important keystone meso-predators in the investigated food web, are likely to induce an amplification of indirect impacts on other groups.

Only the striped dolphin seems to play a remarkably beneficial role as a predator. Indeed, it exerts a positive impact on prey belonging to the demersal fish and benthopelagic shrimp groups, likely due to a removal of predators or competitors. For instance, the high predation rate on mesopelagic fishes, which compete with benthopelagic shrimps for the zooplankton, can favor these latter. Notably, high positive impacts are exerted on the demersal groups of fishes characterized by commercial species (e.g., *Mullus surmuletus*, *Diplodus* spp., *Pagellus acarne*), which are also distributed on the coastal shelf.

The analysis of the consumption flows amidst ecological compartments highlights the use of bathyal benthopelagic resources distributed on the continental slope by *S. coeruleoalba*, *G. griseus* and *P. macrocephalus*, while *T. truncatus* exploits the demersal and benthopelagic prey associated with the shelf. The striped dolphin, with its larger population, proves to be the most important consumer of these resources in the area [47,49,104].

This is a first explorative study addressed towards the characterization of the diet of a variety of cetacean species populations in the Gulf of Taranto, which finds a rich and varied supply of food resources, especially in the deep sea. The fact that it is an important area for the life history traits of species of priority for conservation is one of the main criteria applied for site selection of different area-based management tools (ABMTs), both legally binding and not (i.e., Special Areas of Conservation—SACs, Ecologically and Biologically

Significant Areas—EBSAs, Important Marine Mammals Areas—IMMAs, Critical Cetacean Habitats—CCHs) [5]. The need to designate an ABMT in the Gulf of Taranto to conserve the cetaceans and the vulnerable habitats that allow them to thrive in the area (e.g., CWC habitat) has already been assessed [5,43,105]. Here we confirm such urgency also in light of the key role these animals probably play at multiple trophic levels. In fact, the reported results suggest a possible domino effect starting from any impact exerted on cetaceans that would propagate on multiple species, leading to a disruption of the trophic balance and important alterations of the ecosystems present in the area [5]. Indeed, protecting the cetaceans of the Gulf of Taranto implies preserving the supply of the benefits they provide and that support the functioning of the present ecosystems, including the deep-sea ones. Among the various benefits provided, we find that cetaceans control the trophic balance between deep-sea fish communities. We underline the need to designate an ABMT to conserve the cetaceans in the gulf, as it would be potentially a driving force capable of promoting the conservation of the entire marine environment.

4.2. Cetacean–Fishery Interactions

In the investigated area, the significant events of cetacean by-catches are not reported. Feeding activities of the striped dolphin, Risso’s dolphin and the sperm whale are mainly concentrated in the northern area of the Gulf of Taranto in correspondence with slope bottoms. The area covered by the head of the “Taranto Valley” canyon has been shown to favor the avoidance of odontocetes–fishery competition, not representing a suitable site for hosting trawl fishing grounds [5]. In contrast, the common bottlenose dolphin carries out its feeding activities in the shallowest grounds more exposed to fishing pressure, where a higher competition with odontocetes could arise through the adoption of several types of fishing gear [22]. Further studies on the spatial overlap between odontocetes’ feeding areas and fishing grounds should be performed on the entire gulf to clarify the effective overlap status.

According to the mixed trophic impacts analysis, different patterns of impacts seem to be exerted by trawling and the odontocetes on prey and other groups. The striped dolphin, Risso’s dolphin and the sperm whale have negative impacts on benthopelagic and pelagic components, while positive impacts seem to be generally exerted on demersal assemblages in shallower and deep grounds. In contrast, trawling has mostly negative impacts focused on the demersal communities, and to a much lesser extent on the bathyal benthopelagic species, which are part of the discards and by-catch coming from deep grounds [106]. This condition is due to the non-selective nature of the trawl, which removes demersal and benthic species, while benthopelagic species are not targeted and could be mainly affected by weak indirect interactions. Thus, it is important to stress the lack of relevant direct fishing impacts on the benthopelagic fauna, which is the main feeding resource for offshore odontocetes. This condition highlights the absence, or very low levels, of competition between these three odontocetes species and the fishery in the Gulf, as observed by Carlucci et al. [35]. Among these odontocetes, only the striped dolphin could be affected by potential fishing impacts, especially if overexploitation conditions and an increase in discard species in the catches should occur [107]. Indeed, a higher overlap between the trophic niches of *S. coeruleoalba* and trawling has been estimated when the discard is included in the fishing catches [35]. Regarding the common bottlenose dolphin, the main conflict is due to the sharing of the shelf grounds’ demersal prey with trawl and passive nets, as detected at the Mediterranean scale [108–111]. Although *T. truncatus* exhibits a high plasticity in its feeding behavior, exploiting the discarded species and showing a tolerance to the presence of fishing vessels [25], high acoustic disturbances could negatively affect its behavioral strategies [112]. Studies on altered behavior of this species to compensate prey depletion and the masking noise due to the fishing vessel traffic should be carried out in the study area.

Fishing pressure does not seem to directly affect the odontocetes of the Gulf of Taranto, nor does the overlap between the species caught and their prey seem so relevant. Therefore,

more attention should be addressed towards indirect impacts potentially generated by less evident trophic mechanisms, as possible effects on the bathyal benthopelagic species. Indeed, these species play an important role in the benthic–pelagic coupling mechanisms, by controlling the energy transfer from the pelagic to the benthic domain, and from deep grounds to the water column up to the surface [113]. This coupling is key to marine ecosystem functioning, and its equilibrium is also shaped by species–fisheries interactions [114]. Many of these species are forage fishes consumed by larger predators. In the food web of the Gulf of Taranto the mesopelagic fishes and benthopelagic shrimps have been identified as potential wasp-waist groups [35,69]. Therefore, they could be involved in these mechanisms, exerting top-down and bottom-up controls on the zooplankton and meso-consumers (e.g., benthopelagic cephalopods, demersal piscivorous), and on apex consumers (odontocetes and demersal sharks). Further studies should be carried out on the benthopelagic fauna in the Gulf of Taranto food web, in order to clarify its functional role and to eventually address targeted management measures in the area to preserve the trophic web. These future investigations should integrate knowledge on other pressures that could affect the benthopelagic species because, as observed in the results, the fishing impact seems to be less relevant to these species [5]. Furthermore, the effects of climate change on fish resources, including the deep-sea ones, should be addressed as a priority in fisheries management, as these can seriously alter trophic balances and hinder the recovery of eventually overfished areas [115].

The hypothesis proposed in this study indicates that an EBM approach to fisheries is needed to preserve the diversity of habitats and species, including cetaceans, in the Gulf of Taranto. The designation of an ABMT targeting cetaceans will be not enough and a more holistic approach to conservation is necessary [116]. Among the core principles of EBM, the need to recognize connections in the marine environment is paramount [117,118] and implies addressing nutrient fluxes and conservation of species interactions through management measures. Nonetheless, the incorporation of connectivity aspects in marine management and planning is barely implemented despite that they are critical [119]. This study outlines that there is a potential negative effect of fishing in the demersal domain along the depth gradient and basal trophic levels in the gulf, with partial direct and indirect impacts on cetaceans and their food web. The latter spans a relevant number of species characterized by critical functional roles, which could affect complex ecological processes strongly linked to the ecological connectivity in the area [118]. Therefore, the trophic interactions hypothesized in this study and their implications for the ecology of the gulf should feed the future management of the fishery, considering trade-offs with conservation priorities in the area and incorporating the vertical dimension of the marine environment within conservation strategies [21,120]. In addition, an EBM approach would support fisheries, since favoring cetacean conservation would deliver benefits to the sector per se. Indeed, we have observed the striped dolphin playing a positive role on diverse species of commercial interest.

About 75% of the Gulf of Taranto is covered by deep-sea environments. Here we have tried to use ecological proxies to prove their relevance in supporting the food web of the gulf and the well-being of odontocetes in the area. The relevance of the natural capital of this portion of deep sea is currently unknown, but it is reasonably foreseeable that it outweighs the profits from fishing. Thus, a deep-sea EBM strategy is highly recommended to favor sustainable fishery practices in the area, thus avoiding the degradation of the existing ecosystems and the consequent loss of the ecosystem services they provide. Furthermore, the added value of adopting an EBM approach is that it avoids the sectorial approach by addressing multi-sectorial impacts [121]. The Gulf of Taranto is an area crowded with maritime activities and affected by multiple human pressures that reach the deep sea (e.g., oil and gas exploration and extraction, marine litter, underwater noise) and that, if combined with the fishery, might exert enhanced negative effects on the environment [29,122]. To manage the fishery and the multi-use context that is present in the gulf an ad hoc strategy

for the deep sea, which hosts species and habitats with completely different life traits and resilience capacities compared to the shallow ones [123], is recommended.

Among other things, we acknowledge the need to increase the monitoring effort to assess cetacean prey depletion and deep-sea habitat degradation processes in the Gulf of Taranto due to fishing, and the need to increase understandings of the combined effects of the fishery with other pressures, including climate change, through scenario analysis to inform future fishery management. Moreover, the collection of integrative samples (e.g., skins pieces, etc.) could be useful to perform stable isotope analysis to improve the quality of the food web model.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/jmse9080872/s1>, Table S1: Matrix of the Mixed Trophic Impact (MTI) estimated for the FGs and the fishing gears.

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Appendix A

Table A1. Prey consumed by odontocetes (Pm = *P. macrocephalus*; Gg = *G. griseus*; Sc = *S. coeruleoalba*; Tt = *T. truncatus*) obtained from the literature (Ref.): [72–78,97,124,125]. The prey biomass values (B kg km⁻²; %) refer to those sampled in the Gulf of Taranto by means of MEDITS experimental hauls during the period 1995–2018.

Prey List	Cetaceans	Ref.	B (kg km ⁻²)	%
<i>Argonauta argo</i>	Gg	[72,73]	0.003	>0.01%
<i>Eledone chirrosa</i>	Gg	[73]	15.52	1.80%
<i>Octopus macropus</i>	Gg	[73]	0.36	0.04%
<i>Octopus salutti</i>	Gg	[73]	3.41	0.40%
<i>Histioteuthis bonnellii</i>	Gg, Pm	[72,73,77,78,97]	3.47	0.40%
<i>Ommastrephes bartramii</i>	Gg, Pm	[73,78,97]	-	-
<i>Histioteuthis reversa</i>	Gg, Pm, Sc	[72,73,76,78,97]	1.15	0.13%
<i>Ancistroteuthis lichtensteinii</i>	Gg, Sc	[72,73,76]	0.21	0.02%
<i>Brachioteuthis riisei</i>	Gg, Sc	[72,73]	0.004	>0.01%
<i>Heteroteuthis dispar</i>	Gg, Sc	[72,73,76]	0.03	0.00%
<i>Todarodes sagittatus</i>	Gg, Sc, Pm	[72,73,76,78]	10.16	1.18%
<i>Todaropsis eblane</i>	Gg, Sc	[72,73,76]	10.64	1.24%
<i>Chiroteuthis veranii</i>	Gg, Sc, Pm	[72,73,78,97]	0.03	0.00%
<i>Onychoteuthis banksii</i>	Gg, Sc, Pm	[72,73,76,78]	0.01	0.00%
<i>Sepiola</i> sp.	Gg, Sc	[73,76]	0.03	0.00%
<i>Ancistrocheirus lesueurii</i>	Pm	[78,97]	-	-
<i>Chtenopteryx sicula</i>	Pm	[78]	>0.001	>0.01%
<i>Elasmobranch</i>	Pm	[97,124]	28.72	3.34%
<i>Galiteuthis armata</i>	Pm	[77,78]	-	-
<i>Octopoteuthis</i> sp.	Pm	[77,78]	0.04	0.01%
<i>Other cephalopds family</i>	Pm	[78,124]	-	-

Table A1. Cont.

Prey List	Cetaceans	Ref.	B (kg km ⁻²)	%
<i>Myctophidae</i>	Pm, Sc	[72,76,97,125]	11.97	1.39%
<i>Octopus vulgaris</i>	Pm, Tt	[72,74,78]	20.30	2.36%
<i>Abralia veranyi</i>	Sc	[72]	0.67	0.08%
<i>Abraliopsis morisii</i>	Sc	[72]	>0.001	>0.01%
<i>Acantheephyra pelagica</i>	Sc	[75,76]	0.01	0.00%
<i>Alloteuthis media</i>	Sc	[75,76]	1.59	0.18%
<i>Chauliodus sloani</i>	Sc	[76,86]	1.88	0.22%
<i>Gadicolus argentus argentus</i>	Sc	[125]	8.54	0.99%
<i>Illex coindetii</i>	Sc	[72,75,76]	32.71	3.80%
<i>Maurolicus muelleri</i>	Sc	[76]	0.04	0.00%
<i>Micromesistius potassou</i>	Sc	[76]	44.99	5.23%
<i>Neorossia caroli</i>	Sc	[76]	0.13	0.01%
<i>Pasiphaea multidentata</i>	Sc	[76]	1.82	0.21%
<i>Pyroteuthis margaritifer</i>	Sc	[72]	>0.001	>0.01%
<i>Scaergus unicirrhus</i>	Sc	[76]	1.34	0.16%
<i>Sepietta oweniana</i>	Sc	[76]	0.79	0.09%
<i>Sergia robusta</i>	Sc	[76]	0.09	0.01%
<i>Stomias boa</i>	Sc	[72,76]	0.64	0.07%
<i>Belone belone</i>	Sc, Tt	[72,76]	-	-
<i>Boops boops</i>	Sc, Tt	[72,76]	25.58	2.97%
<i>Conger conger</i>	Sc, Tt	[72,76]	14.59	1.69%
<i>Engraulis encrasicolus</i>	Sc, Tt	[74,76]	193.32	22.46%
<i>Gobius niger</i>	Sc, Tt	[72]	0.14	0.02%
<i>Lithognathus mormyrus</i>	Sc, Tt	[72]	-	-
<i>Loligo vulgaris</i>	Sc, Tt	[72,74]	4.32	0.50%
<i>Merluccius merluccius</i>	Sc, Tt	[72,74,76]	106.54	12.38%
<i>Ophidion barbatum</i>	Sc, Tt	[72,74]	1.73	0.20%
<i>Pagellus acarne</i>	Sc, Tt	[72]	7.48	0.87%
<i>Pteroctopus tetracirrhus</i>	Sc, Tt	[72]	1.60	0.19%
<i>Sardinella aurita</i>	Sc, Tt	[72]	4.94	0.57%
<i>Sepia officinalis</i>	Sc, Tt	[72]	0.67	0.08%
<i>Serranus cabrilla</i>	Sc, Tt	[72]	0.67	0.08%
<i>Sphyræna sphyraena</i>	Sc, Tt	[72]	0.57	0.07%
<i>Trachurus mediterraneus</i>	Sc, Tt	[72]	22.50	2.61%
<i>Alpheus glaber</i>	Tt	[74]	0.003	>0.01%
<i>Centracanthus cirrus</i>	Tt	[72]	0.04	0.00%
<i>Cepola rubescens</i>	Tt	[74]	2.92	0.34%
<i>Citharus linguatula</i>	Tt	[72]	0.02	0.00%
<i>Diplodus sp.</i>	Tt	[72]	1.36	0.16%
<i>Eledone moscata</i>	Tt	[74]	4.78	0.56%
<i>Lesueurigobius spp.</i>	Tt	[72]	0.31	0.04%
<i>Liza ramada</i>	Tt	[72]	-	-
<i>Loligo forbesi</i>	Tt	[72,74]	0.08	0.01%
<i>Oblada melanura</i>	Tt	[72]	-	-
<i>Pagellus erythrinus</i>	Tt	[72,74]	9.26	1.08%
<i>Pagrus pagrus</i>	Tt	[72]	0.44	0.05%
<i>Phycis blennoides</i>	Tt	[74]	66.69	7.75%
<i>Rondelotia minor</i>	Tt	[74]	0.33	0.04%
<i>Sardina pilchardus</i>	Tt	[74]	53.22	6.18%
<i>Scomber spp.</i>	Tt	[72]	12.64	1.47%
<i>Sepia spp.</i>	Tt	[74]	0.24	0.03%
<i>Solenocera membranacea</i>	Tt	[74]	2.78	0.32%
<i>Spicara spp.</i>	Tt	[72]	24.80	2.88%
<i>Spondilosoma cantharus</i>	Tt	[72]	0.08	0.01%
<i>Symphodus sp.</i>	Tt	[72]	-	-
<i>Trachurus spp.</i>	Tt	[74]	94.90	11.02%
Total			860.85	100%

Table A2. The functional groups in the food web model ranked in descending order according to their keystone, by means of Libralato [91] (L_Ksi) and Valls [92] (V_Ksi) indices.

Group Name	L_Ksi	Group Name	V_Ksi
Macrozooplank	0.0132	SL_Squids_BP	1.362
Macrobentinv	-0.0528	S dolph	1.309
SL_Squids_BP	-0.131	Anglers	1.217
Meso_Microzooplank	-0.142	R dolph	1.129
S pel F	-0.179	SHB_Squids_BP	1.092
S dolph	-0.248	SH_Ceph_B	1.021
Phytoplank	-0.272	SHB_DemF_pisc	1.001
Mesopel F	-0.278	L pel F	0.931
Polychaets	-0.289	SL_BathypelF_pisc	0.929
SH_Ceph_B	-0.343	SHB-SL_DemF_gen	0.899
SHB_Crabs	-0.345	S whale	0.89
M pel F	-0.351	Hake	0.881
Shrimps_BP	-0.359	Macrozooplank	0.875
Anglers	-0.386	M pel F	0.858
SHB_Squids_BP	-0.387	DWR Shrimp	0.849
SL_BathypelF_pisc	-0.396	CB dolph	0.839
SL_Decap_Scav	-0.409	RG Shrimp	0.827
SH_DemF_B crust	-0.418	SHB_F_BP crust	0.818
SHB_DemF_pisc	-0.462	S pel F	0.791
Bacterioplank	-0.468	Polychaets	0.766
SH-SHB_DemF_gen	-0.516	RB Shrimp	0.746
SHB_F_BP crust	-0.527	SHB_Crabs	0.744
SHB-SL_DemF_gen	-0.534	SH-SHB_DemF_gen	0.743
DWR Shrimp	-0.534	Mesopel F	0.736
RB Shrimp	-0.537	SH_DemF_B crust	0.734
R dolph	-0.543	SL_DemF_Decap	0.727
Supbentcrust	-0.569	R Mullet	0.721
RG Shrimp	-0.59	SL_Decap_Scav	0.714
Hake	-0.625	SL_Ceph_B	0.708
L pel F	-0.661	Gel plank	0.706
SL_DemF_Decap	-0.673	SHB_BobSquids_BP	0.693
S whale	-0.723	SL_Sharks_BP	0.663
R Mullet	-0.728	Macrobentinv	0.599
Macrourids	-0.731	Shrimps_BP	0.561
SHB_F_plank	-0.746	SHB_F_plank	0.489
CB dolph	-0.824	Macrourids	0.451
SHB_BobSquids_BP	-0.827	SH-SHB_SR_BP	0.436
SL_Ceph_B	-0.837	Meso_Microzooplank	0.4
SL_Sharks_BP	-0.869	SH_DemF_Binv	0.391
Gel plank	-0.874	SH_SR_B	0.326
SH_DemF_Binv	-0.914	SL_SR_B	0.242
Seagrasses and algae	-1.161	Supbentcrust	0.23
SH-SHB_SR_BP	-1.187	Phytoplank	0.0984
SH_SR_B	-1.242	Bacterioplank	-0.392
SL_SR_B	-1.402	Seagrasses and algae	-0.441
Log turtle	-2.19	Log turtle	-0.536
F whale	-2.69	F whale	-1.056
Seabirds	-2.971	Seabirds	-1.29

Table A3. Mixed Trophic Impact (MTI) of the odontocetes and the types of fishing gear exerted on the shelf (SH) and slope (SL) domains. The impacts were divided between positive (pos) and negative (neg) and between direct (dir) and indirect (ind).

MTI Absolute Values								
Fishing Gear	SH pos	SH neg	SL pos	SL neg	SH dir	SH ind	SL dir	SL ind
Trawl	0.122	-2.074	0.305	-2.550	-1.208	-0.745	-1.323	-0.923
Long line	0.123	-0.277	0.063	-0.197	-0.135	-0.019	-0.099	-0.035
Nets	0.087	-0.410	0.116	-0.009	-0.358	0.036	0.003	0.104
Others	0.065	-0.887	0.046	-0.644	-0.034	-0.789	-0.640	0.042
Purse seine	0.010	-0.028	0.008	-0.005	-0.025	0.007	-0.002	0.006
MTI Relative Values								
Fishing Gear	SH pos	SH neg	SL pos	SL neg	SH dir	SH ind	SL dir	SL ind
Trawl	2%	26%	4%	32%	18%	11%	20%	14%
Long line	2%	3%	1%	2%	2%	0%	2%	1%
Nets	1%	5%	1%	0%	5%	1%	0%	2%
Others	1%	11%	1%	8%	1%	12%	10%	1%
Purse seine	0%	0%	0%	0%	0%	0%	0%	0%
FG								
S dolph	8%	13%	7%	20%	13%	4%	25%	2%
CB dolph	2%	7%	2%	3%	10%	3%	6%	4%
R dolph	1%	2%	10%	9%	2%	1%	7%	9%
S whale	1%	1%	6%	6%	0%	0%	7%	6%

Table A4. Cetaceans’ consumption (t km⁻² year⁻¹) and different types of fishing gear’s catches (t km⁻² year⁻¹) on marine domains in the Gulf of Taranto area.

Cetaceans’ Consumption					
Cetacean	S Dolph	CB Dolph	R Dolph	S Whale	F Whale
PLANK	0.000	0.000	0.000	0.000	0.034
PEL-SH	0.049	0.038	0.000	0.000	0.001
PEL-SL	0.004	0.000	0.000	0.000	0.000
BP-SH	0.081	0.009	0.021	0.009	0.000
BP-SL	0.433	0.000	0.080	0.066	0.003
DEM-SH	0.096	0.074	0.000	0.001	0.000
DEM-SL	0.021	0.015	0.000	0.003	0.000
DISCARD	0.000	0.004	0.000	0.000	0.000
Types of Fishing Gear’s Catches					
Fishing Gear	Trawl	Long Line	Nets	Others	Purse Seine
PLANK	0.000	0.000	0.000	0.000	0.000
PEL-SH	0.070	0.002	0.006	0.031	0.029
PEL-SL	0.000	0.000	0.000	0.008	0.000
BP-SH	0.013	0.000	0.001	0.000	0.001
BP-SL	0.275	0.000	0.000	0.000	0.000
DEM-SH	0.456	0.033	0.172	0.011	0.004
DEM-SL	0.700	0.020	0.003	0.004	0.000
BENT	0.000	0.000	0.003	0.002	0.000

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