Marine Environmental Research 211 (2025) 107398

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Bottom trawling affects trophic niche diversity of red mullet in muddy bottoms of the Mediterranean continental shelf

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ARTICLE INFO

Keywords:
Trawl exclusion
Trophic ecology
Fishing impact
Food web
Trophic level

ABSTRACT

Bottom trawling causes detrimental effects on marine ecosystems, and significantly alter benthic communities, potentially affecting the diet and trophic role of benthic feeders. The ban on bottom trawling is a common spatial fishing restriction that has been implemented in tropical and temperate regions to restore overexploited marine resources and ecosystems. In northern Sicily (central Mediterranean Sea) two trawl ban areas, the Gulf of Castellammare and the Gulf of Patti, were established in 1990. In both gulfs, the red mullet *Mullus barbatus*, a commercially important demersal fish and benthic feeder main target of bottom trawlers, has since experienced an impressive increase in biomass. We investigated the stomach contents, prey selectivity, and trophic position (using carbon and nitrogen stable isotope analysis) of red mullet in the two untrawled gulfs and compared the results with two trawled gulfs. Our results show that bottom trawling affects the diet and trophic position of red mullet following the trophic erosion process. In untrawled areas, the species feeds in a less disturbed and well-structured benthic community at a higher trophic position, while in trawled areas it benefits from the more opportunistic epibenthic fauna associated with trawling-induced resuspension of organic matter.

1. Introduction

The call for a ban on bottom trawling in certain overexploited regions through the designation of fishery restricted areas (FRAs) is gaining support, largely due to the detrimental effects of bottom-towed gear on marine ecosystems (Badalamenti et al., 2012; Pipitone et al., 2023). The intense practice of bottom trawling on soft seafloor has been shown to have negative impacts on benthic assemblages, resulting in the alteration to their abundance, biomass, diversity, production, and size structure (Agnetta et al., 2024; Greenstreet and Hall, 1996; de Juan et al., 2007; McCauley et al., 2015; Romano et al., 2016; Sweeting et al., 2009; Sinopoli et al., 2022).

The physical damage to the seafloor caused by bottom-towed gear and the associated sediment resuspension amplifies these impacts, releasing buried organic matter that modifies nutrient dynamics (Jennings and Kaiser, 1998; Trush et al., 2002; Consoli et al., 2017;

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https://doi.org/10.1016/j.marenvres.2025.107398
Received 19 May 2025; Received in revised form 7 July 2025; Accepted 24 July 2025

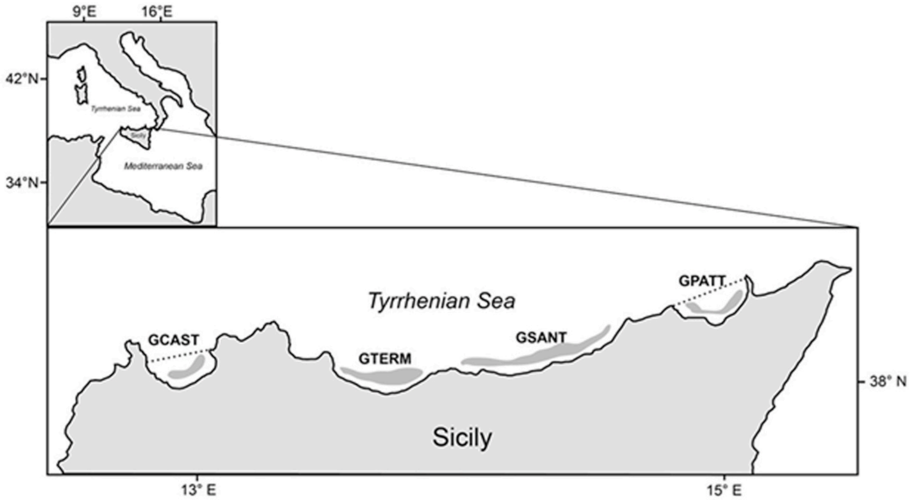

Fig. 1. Study area with the four investigated gulfs along the northern Sicilian coast. GCAST = Gulf of Castellammare, GTERM = Gulf of Termini Imerese, GSANT = Gulf of Sant'Agata, GPATT = Gulf of Patti. Dotted lines indicate the trawl ban boundaries in the two untrawled gulfs. Shaded areas indicate the muddy bottoms at 40–80 m depth.

Pusceddu et al., 2005). Some opportunistic and resilient taxa such as deep worms, small crustaceans and shrimps show minimal growth and increased abundance under these conditions. However, many invertebrates particularly tubicolous worms, experience population declines, leading to altered benthic community structures (Hiddink et al., 2008; Beauchard et al., 2023). Such alteration in benthic composition may in turn correspond to modifications in the quantity and quality of prey for demersal fishes (Kaiser and Spencer, 1994; Quillien et al., 2016). Although the response of different fish species depends on their ability to find prey and on the susceptibility of prey to fishing disturbance, the general effect of a reduction in benthic biomass due to bottom trawling is a general depressed foraging base for benthivorous fishes due to reduced prey availability (Johnson et al., 2015; Agnetta et al., 2024). By severely affecting the structure of invertebrate and fish populations and the availability of food sources, bottom trawling can also promote a reshuffling of energy in the entire food web (Agnetta et al., 2022; Piroddi et al., 2015) and determine a decrease in mean trophic positions (Agnetta et al., 2024; Badalamenti et al., 2002; Bianchi and Morri, 2000; Fanelli et al., 2010; Pauly et al., 1998; Shannon et al., 2014).

Marine protected areas have proven to be an effective spatial tool for the management of fisheries and a mainstay of the ecosystem-based approach (Coll et al., 2013), capable of assuring protection to marine biodiversity and essential habitats as well as rebuilding and sustainably using fishery resources (Claudet et al; Feinberg et al., 2012; Halpern, 2003; Sala et al., 2021; Sumaila and Charles, 2002). Several types of marine protected areas exist with different levels of restrictions, ranging from no-take areas to partially protected areas with bans on specific fishing gears (Auster and Shackell, 1997; Pipitone et al., 2014; Batista and Cabral, 2016; Horta e Costa et al., 2016; Riginella et al., 2022). Bottom trawling bans are among the most common forms of partial protection and are widely implemented in tropical and temperate regions (Murawski et al., 2005; Mak et al., 2021; Pipitone et al., 2023).

In northern Sicily two trawl ban areas, the Gulf of Castellammare and the Gulf of Patti, were established in 1990 (Pipitone et al., 2000a). In both gulfs, the red mullet *Mullus barbatus* L., 1758, one of the main commercially relevant demersal fish in the Mediterranean and a primary target of bottom trawlers (Stergiou, 1990), underwent an impressive biomass increase (Agnetta et al., 2019 and references therein; Pipitone et al., 2023) showing a higher trophic position when compared to trawled areas (Agnetta et al., 2024; Badalamenti et al., 2000, 2002). Moreover, higher abundance and slightly modified isotopic structure were also detected in the benthic macrofauna of both gulfs (Romano et al., 2016).

These findings suggest that protection from trawling has modified the structure of the benthic community, which in turn may have altered the diet and trophic position of red mullet (Agnetta et al., 2024). Despite recent advances, there is still a lack of mechanistic understanding of how trawling-induced changes in benthic communities affect fish condition and population parameters such as trophic position through diet shifts. To date, only a few studies have analysed the relationships between prey resources and fish populations in relation with fishery activity (but see Johnson et al., 2015), and there are few simultaneous examinations of the effects of bottom trawling on prey availability, fish stomach contents and trophic position especially when comparing areas with different levels of fishing disturbance, mainly due to the difficulty of monitoring enforced FRAs over large temporal scales.

In this study, we investigate how bottom trawling affects the diet and trophic position of the red mullet in four Sicilian gulfs with different protection levels. We tested two hypotheses: (1) the diet of the red mullet differs between trawled *vs.* untrawled areas, due to changes in prey availability; (2) a suboptimal diet in trawled areas leads to a lower trophic position. By integrating stomach content analysis, stable isotope data and assessment of prey availability, we present a comprehensive evaluation of the impact of benthic habitat disturbance on trophic dynamics in a commercially significant demersal fish.

2. Materials and methods

2.1. Study area

The study was conducted in four gulfs along the northern coast of Sicily (Fig. 1): the gulfs of Castellammare (GCAST, 38°03′N 12°54′E), Termini Imerese (GTERM, 38°00′N 13°44′E), Sant'Agata (GSANT, 38°03′N 14°23′E) and Patti (GPATT, 38°10′N 15°06′E). GCAST and GPATT are designated no-trawl areas where bottom trawling has been prohibited year-round since 1990 (Regional Act no. 25/1990), while artisanal and recreational fishing are permitted (Pipitone et al., 2000a). Conversely, GTERM and GSANT permit trawl and artisanal fisheries but, like many other Mediterranean areas, are overfished (Colloca et al., 2013; Fiorentino and Vitale, 2021a,b). The primary fishing restriction in these two gulfs is the ban on trawling within three nautical miles from the coast or within the 50 m isobath where this is closer to the shoreline, established by European legislation for the Mediterranean (Council Regulation (EC) no. 1967/2006).

2.2. Stomach content analysis (SCA)

The diet of red mullet was studied using specimens collected during a bottom trawl survey carried out in spring 2005 (Pipitone et al., 2023). Sampling took place in the four gulfs over muddy bottoms at depths of 40–80 m. Fish were frozen at −20 °C on board after capture. In the laboratory, the total length (TL) of each fish was measured to the nearest mm.

To achieve a representative sample size for the stomach content analysis, a minimum of 25 non-empty stomachs were selected from each gulf, across three size classes: 81–120 mm TL (class I), 121–170 mm TL (class II), >170 mm TL (class III). Stomachs were dissected, and their contents were preserved in 70 % ethanol. Prey items were identified to the lowest possible taxonomic level, counted, and weighed (wet weight, accuracy: 0.0001 g). Fragmented prey were quantified by counting identifiable anatomical parts such as number of eyes, mouthparts, telsons, or otoliths traceable to single specimens. These reconstructed specimen counts were then used to estimate abundance and were weighted to obtain biomass.

2.3. Stable isotope analysis (SIA)

Red mullet for SIA was obtained from the same trawl survey as for SCA and within the same depth range and size classes. A sample of dorsal white muscle was extracted from 20 red mullet individuals from each gulf and size class, for a total of 240 fish.

Surface mesozooplankton samples were collected as a food source proxy using a WP2 net (200 μm mesh size) towed parallel to the shoreline of the four gulfs in spring 2005. To minimize variability in carbon isotope data, inorganic carbonate was removed from half of mesozooplankton samples by acidification with 1 M HCl for 3 h, followed by rinsing and re-grinding, however no lipid extraction was performed. There were 3 replicates per each gulf. Stable isotope data for red mullet preys and for sedimentary organic matter were sourced from Badalamenti et al. (2007), Fanelli (2007) and Romano et al. (2016).

SIA was performed using a Thermo Delta Plus XP continuous-flow isotope-ratio mass spectrometer coupled to a Thermo EA 1112 elemental CHN analyser. Experimental precision, based on the standard deviation of replicates of the internal standard for both $\delta^{13}C$ and $\delta^{15}N$, was 0.2 ‰. Isotope ratios were expressed relative to Vienna PeeDee Belemnite (VPDB) standard for carbon and to atmospheric N_2 for nitrogen. Ratios were calculated as follows (Peterson and Fry, 1987):

$$\partial X = \left[\left(\frac{R_{sample}}{R_{standard}} - 1\right)\right] * 1000$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.4. Data analysis

2.4.1. Stomach contents

The importance of each prey item was quantified using indices described by Hyslop (1980): percent gravimetric composition (%W), and Index of Relative Importance (IRI = (%N + %W) * %F) (Pinkas et al., 1971), where %N is the percent number and %F the percent frequency of occurrence of prey items in the stomachs. To standardize comparisons across the four gulfs, the IRI was expressed as a percentage (%IRI = (IRI/∑IRI) * 100).

A three-way permutational MANOVA (PERMANOVA) (Anderson, 2001) was conducted to assess dietary differences between trawled and untrawled gulfs and among different size classes of red mullet. The analysis was based on a resemblance matrix of prey biomass data (modified Gower similarity resemblance, 4th root transformed), to evaluate the influence of trawling on diet. The factors considered were Protection (fixed, 2 levels: Tr, trawled; uTr, untrawled), Gulf (random, 2 levels), nested within Protection, and Size (fixed, 3 levels: class I, class II, class III), crossed with Protection and Gulf. The PERMANOVA test and pairwise comparisons were performed under the permutation of residuals under a reduced model method with 9999 permutations.

Table 1
Functional groups (FG) used for the prey identified in the stomach contents analysis and for stable isotope analysis, named after taxonomic group and trophic guild. For the details of species belonging to the different functional groups see Table SM1.

Taxonomic group	Trophic guild	FG acronym
Bivalvia	suspension feeder	Bsf
Crustacea	deposit feeder	Cdf
Crustacea	omnivore	Co
Crustacea	suspension feeder	Csf
Holothuroidea	deposit feeder	Hdf
Gastropoda	deposit feeder	Gdf
Mollusca others (Caudofoveata, Scaphopoda)	deposit feeder	Mdf
Polychaeta	carnivore	Pc
Polychaeta	deposit feeder	Pdf
Sipuncula	deposit feeder	Sdf
Teleostei (*Callionymus maculatus*)	carnivore	Tc1
Teleostei (*Lesueurigobius suerii*)	carnivore	Tc2
Teleostei	carnivore	Tc
Mesozooplankton	omnivore	Zoo
Sedimentary organic matter		SOM

A principal coordinate analysis (PCoA) (Anderson and Willis, 2003) was performed using the same resemblance matrix to visualize dietary variation within factors Protection and Size. Prey items with the strongest Pearson correlation to protection and size classes were over-imposed on the PCoA plot.

Trophic diversity in the four gulfs was quantified using the Shannon-Weaver index (Shannon and Weaver, 1949) as follows: $H' = \sum p_i \ln(p_i)$, where p_i is the proportion of each prey in the diet of each fish. This index can be considered a good indicator of trophic niche width (Marshall and Elliott, 1997).

To compare the number and weight of the different prey items, two permutational univariate analyses of variance (PERANOVA) were performed. These analyses followed the same experimental design adopted for the multivariate analysis, but in this case, it was used a Euclidean distance resemblance matrix of 4th root transformed data.

Food preferences of red mullet were assessed in each gulf using Ivlev's electivity index (Ivlev, 1961):

$$E = (ri - pi) / (ri + pi)$$

where ri is the relative wet weight of prey item i in the stomach and p_i is its relative wet weight in the benthic community. Values range from +1 (active selection) to −1 (avoidance), with 0 indicating no selection. For calculation, a matrix was prepared with the organisms occurring in the benthic samples (drawn from Romano et al., 2016) and the prey items found in stomach contents, each placed within comparable taxonomic categories, mainly at family or higher level.

Finally, to facilitate comparisons between diets in trawled and untrawled gulfs, prey items were categorised into functional groups according to similar taxonomy and trophic guild (i.e., suspension feeders, deposit feeders, omnivores and carnivores) as per Sinopoli et al. (2012). The final grouping is provided in Table 1, SM1.

2.4.2. Stable isotopes

The most significant prey identified through SCA were analysed for SIA as expected to greatly contribute to the diet of red mullet. To have a high dietary resolution (Phillips et al., 2014), preys were grouped *a priori* according to the same functional groups used in SCA (Table 1) and successively refined according to isotopic similarity (Table SM1).

For each study area, an isospace plot of mean $\delta^{13}C$ and $\delta^{15}N$ values was created to qualitatively assess the inclusion of potential prey in the diet of each red mullet across different size classes (Fry, 2013; Phillips

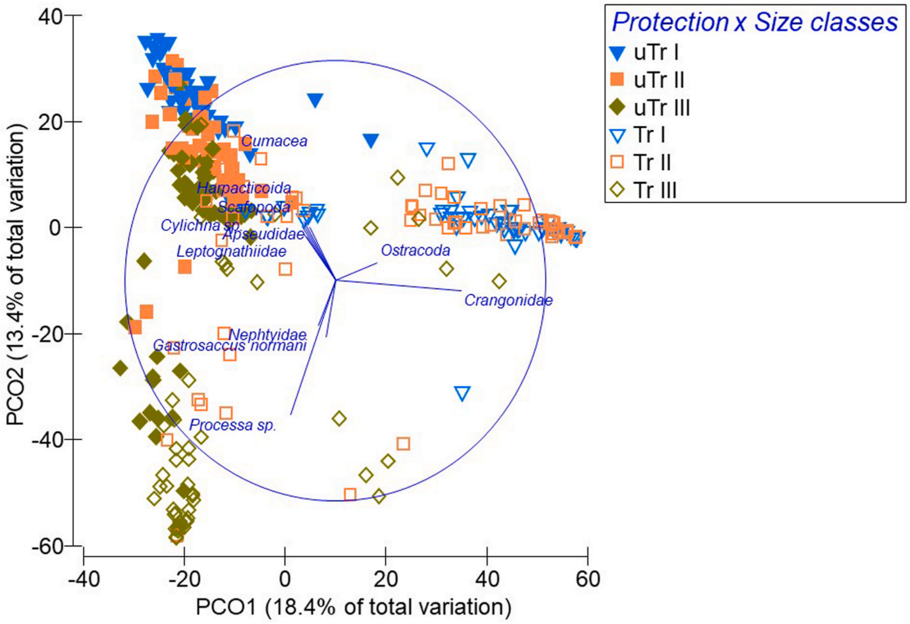

Fig. 2. Principal Coordinates Analysis (PCoA) ordination performed on all stomachs of red mullet in the untrawled (uTr) and trawled (Tr) gulfs in the three size classes. The blue vectors indicate the value of Pearson correlations and the two-dimensional location of the main prey. Class I: 81–120 mm TL, Class II: 121–170 mm TL, Class III: >170 mm TL. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2014). Specifically, a five-endmember polygon was depicted around the predator isotopic values (adjusted for trophic enrichment factor, TEF) to identify potential dietary contributors common to the gulfs. Prey functional groups located within or near the polygon were considered likely contributors to the diet. However, prey groups with isotopic overlap were excluded from the subsequent application of Bayesian mixing model (BMM) due to methodological constraints (Fry, 2013; Phillips et al., 2014). The BMM was conducted using the MixSIAR package in R (Stock et al., 2018) to estimate the proportional contribution of plausible food sources to the diet of red mullet (Parnell et al., 2010, 2013). A single model with a multiplicative error formulation (Stock et al., 2018) was run incorporating two fixed factors: Gulf and Size, and assuming *a priori* a generalist uniform distribution. Uncertainty (standard deviation) in both the isotopic data and TEF values was integrated into the model. The TEFs applied, 1.5 for δ^{13}C and 3.2 for δ^{15}N, are well established for dorsal muscle of groundfish species including *Mullus barbatus*, and are supported by Sweeting et al. (2007a, 2007b).

To estimate the trophic position (TP) of red mullet, δ^{15}N values were used in the following equation:

$$TP = \left[\left(\delta^{15}N - \delta^{15}Nref\right) / \ (3.2)\right] + 2$$

where δ^{15}N is the mean isotopic value for red mullet, and δ^{15}Nref represents the mean isotopic value of the baseline species for each gulf. The TEF of 3.2 ‰ was applied following Sweeting et al. (2007b), assuming a baseline trophic level of 2.

The baseline used here included the average δ^{15}N values of three deposit-feeder crustaceans: the decapods *Alpheus glaber* and *Goneplax rhomboides* and the tanaid *Apseudes spinosus* (Romano et al., 2016). These species were selected for their abundance in muddy-bottom communities, their representation in the diet of benthic feeders, and their suitability as a baseline for demersal fish (Fanelli et al., 2009; Agnetta et al., 2024). To evaluate the effect of factors Protection and Size on TP, a scatterplot of TP values against size for each gulf was generated and fitted with alinear regression model. Additionally, a PERANOVA was conducted on the same design applied for SCA to assess the significance of these factors.

3. Results

3.1. Stomach content analysis

Analysis of the stomach contents of 327 red mullet specimens revealed a total of 3581 prey items belonging to 68 taxa (see Table SM2). Crustaceans, molluscs, polychaetes, and teleosts were the most represented prey items. In GCAST, harpacticoid copepods had the highest %IRI (25.4). The decapods *Alpheus glaber* and *Goneplax rhomboides* contributed significantly, with %IRI values of 8.7 and 13.3, respectively. Other notable prey included scaphopods (7.2 %IRI), bivalves (5.9 %IRI), and the polychaete *Sternaspis scutata* (12.9 %IRI). In GPATT the mysid *Leptomysis gracilis* had the highest %IRI (38.6), followed by the decapods *A. glaber* (17.0 %IRI) and *Solenocera membranacea* (12.3 %IRI). In GTERM, the decapods *Processa* sp. was the dominant item (30.3 %IRI) with other high contributions from the crustaceans Crangonidae (15.2 % IRI) and *L. gracilis* (15.2 %IRI) and the bivalve *Abra alba* (18.3 %IRI). The teleost *Callionymus maculatus* contributed a small but notable %IRI (4.2). In GSANT the crustaceans *Processa* sp. (34.4 %IRI), Crangonidae unid. (38.0 %IRI) and *Gastrosaccus normani* (16.1 %IRI) were the prey with the highest IRI values.

Principal Coordinates Analysis (PCoA) explained a cumulative variance of the first four axes of 45.37 % and revealed three distinct clusters based on prey composition in the stomachs (Fig. 2). In the upper left corner of the graph, fish of all size classes from untrawled gulfs clustered together, strongly associated with such prey as cumaceans, harpacticoid copepods, scaphopods, *Cylichna* sp., Leptognathiidae and Apseudidae. Size class III fish from trawled gulfs formed a separate cluster in the lower left corner, together with a few fish of the same size from untrawled gulfs. This group was correlated with prey such as *Processa* sp., Nephtyidae, and *Gastrosaccus normani*. On the right side of the graph, size classes I and II fish from trawled gulfs clustered together, mainly associated with Ostracoda and Crangonidae. In the upper left corner of the graph, fish of all size classes from untrawled gulfs clustered together, strongly associated with prey such as cumaceans, harpacticoid copepods, scaphopods, *Cylichna* sp., Leptognathiidae and Apseudidae. Size class III fish from trawled gulfs formed a separate cluster in the lower left corner, together with a few fish of the same size from

Table 2
Results of PERMANOVA based on a three-factor design (Protection (Pr): trawled, Tr, untrawled, uTr; Size (Si): I, II, III) carried out on stomach content data as prey weight. *** = $p < 0.001$.

Source	df	MS	Pseudo-F	P (perm)	perms	Pairwise
Pr	11	143000	4,3514	***	9999	**Protection x Size**
Si	3	78707	5,7844	***	9997	I; uTr ≠ Tr
Gulfs (Pr)	2	27302	10,448	***	9997	II; uTr ≠ Tr
Pr x Si	3	35987	2,6447	***	9999	III; uTr ≠ Tr
Gulfs(Pr)x Si	6	14105	5398	***	9998	uTr: I = II = III
Res	409	2613,1				Tr: I = II ≠ III
Total	424					

untrawled gulfs. This group was correlated with such prey as *Processa* sp., Nephtyidae, and *Gastrosaccus normani*. On the right side of the graph, size classes I and II fish from trawled gulfs clustered together, mainly associated with Ostracoda and Crangonidae.

The PERMANOVA based on prey weight showed a significant interaction between factors Protection and Size (Table 2). Post-hoc comparisons showed clear differences in diet between trawled and untrawled areas across all size classes. There was no significant difference between red mullet sizes in untrawled areas, while in trawled areas sizes I and II were similar and differed from size III.

Additionally, the PERMANOVA indicated significant variability among the four gulfs, emphasizing the influence of local factors on diet composition.

The univariate PERANOVA showed a significant difference in prey number for factor Protection, with a higher mean prey abundance per stomach in the untrawled gulfs (Table 3a; Fig. 3a) and high variability

Table 3
Results of PERANOVA based on a three-factor design (Protection (Pr): trawled, Tr, untrawled, uTr; Size (Si): I, II, III) carried out on a) total number of prey; b) total weight of prey. ** = $p < 0.01$; *** = $p < 0.001$; n.s. = not significant.

Variables	Source	df	MS	Pseudo-F	P(perm)	perms	Pairwise
a) **Prey number**	Pr	1	394,83	12,701	***	6	**Protection**
	Si	2	7,8098	0,45032	n.s.	9967	
	Gulfs (Pr)	2	31,611	9,8285	***	9948	
	Pr x Si	2	35,271	2,0338	ns	9960	uTr > Tr
	Gulfs (Pr) x Si	4	17,883	5,5601	***	9946	
	Residual	300	3,2163				
		311					
b) **Prey weight**	Pr	1	0,095	17,922	n.s.	6	**Protection x Size Class**
	Si	2	0,076	10,626	**	9954	I; uTr = Tr
	Gulfs (Pr)	2	0,005	2,4884	n.s.	9948	II; uTr = Tr
	Pr x Si	2	0,037	5,2594	**	9973	III; uTr = Tr
	Gulfs (Pr) x Si	4	0,007	3,3685	**	9943	uTr:
	Residual	289	0,002				I = II = III
	Total	300					Tr:
							I = II ≠ III

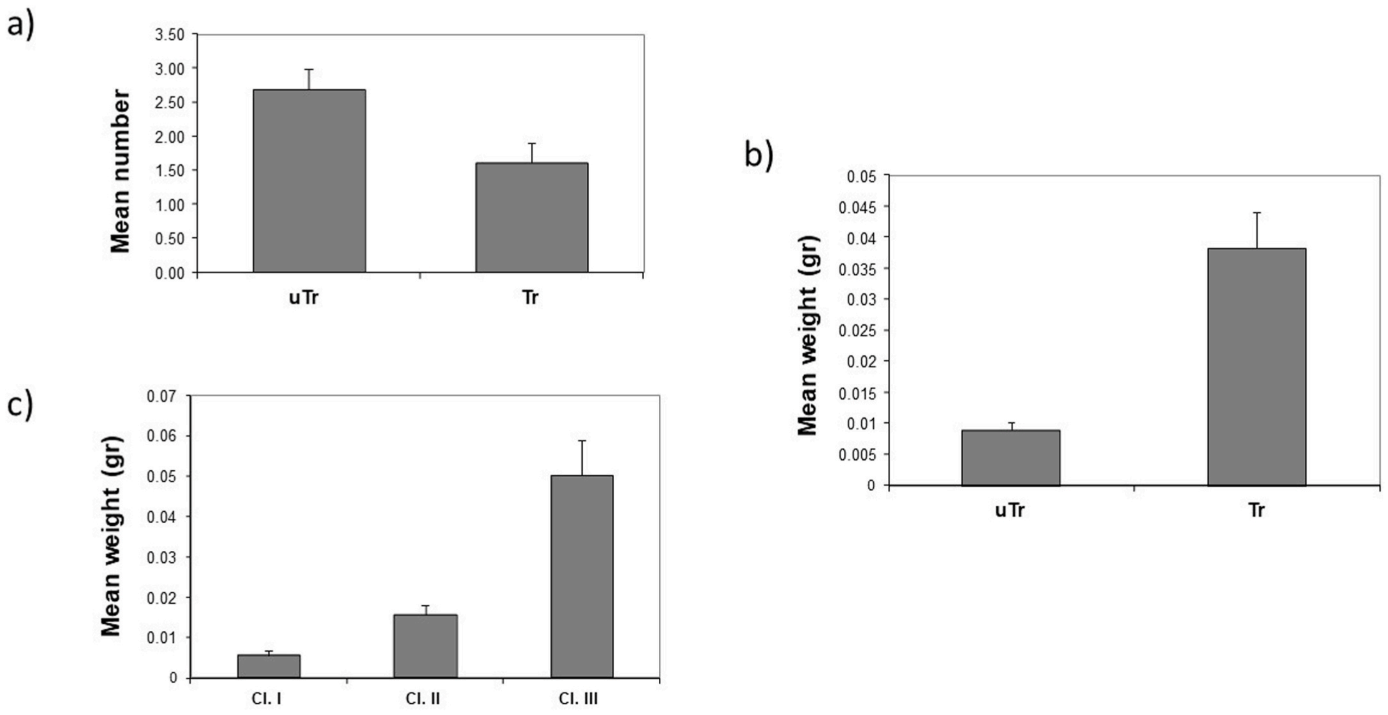

Fig. 3. Prey found in stomach contents. a) Mean number of prey in untrawled (uTr) and trawled (Tr) gulfs. b) Mean weight of prey in untrawled (uTr) and trawled (Tr) gulfs. c) Mean weight of prey in the three size classes. Cl. I: 81–120 mm TL, Cl. II: 121–170 mm TL, Cl. III: >170 mm TL. Vertical bars are standard deviation.

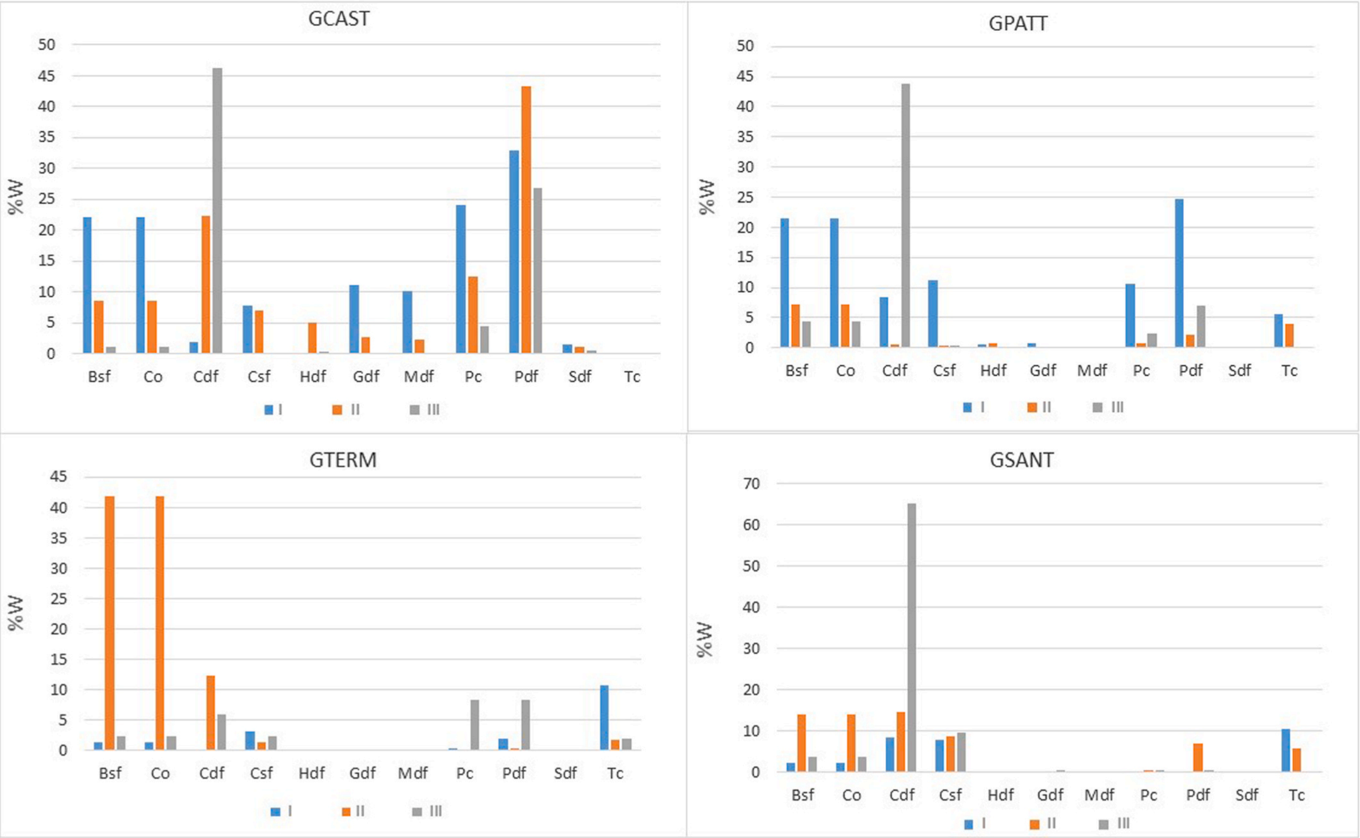

Fig. 4. %W values calculated on the functional categories of prey in the four gulfs. Cl.I: 81–120 mm TL, CL. II: 121–170 mm TL, Cl. III: >170 mm TL. Bsf = Bivalvia suspension feeder; Co = Crustacea omnivore; Cdf = Crustacea deposit feeder; Csf = Crustacea suspension feeder; Hdf = Holothuroidea deposit feeder; Gdf = Gastropoda deposit feeder; Mdf = other Mollusca depositfeeder; Pc = Polychaeta carnivore; Pdf = Polychaeta deposit feeder; Sdf = Sipuncula deposit feeder; Tc = Teleostei carnivore. GCAST: Gulf of Castellammare; GPATT: Gulf of Patti; GTERM: Gulf of Termini Imerese; GSANT: Gulf of Sant'Agata.

for factor Gulf. No significant differences were found with respect to factor Size, nor were significant interactions between factors considered. The PERANOVA on prey weight showed a significant interaction between factors Protection and Size however the post-hoc tests were non-significant (Table 3b; Fig. 3b). There was a significant difference for factor Size but the post-hoc tests were non-significant, although the average prey weight per stomach increased with fish size (Table 3b; Fig. 3c).

Trophic diversity as measured by the Shannon-Weaver index, was higher in GCAST and GPATT (1.28 and 1.48, respectively), indicating a broader dietary niche if compared to the lower values found in GTERM and GSANT (0.97 and 0.68). However, this index measured on the stomach contents is an individual-level diet breadth and therefore, in addition to being influenced by the availability of prey, it is influenced by the selectivity of the predator.

As regards the %W contribution of functional groups to the diet of red mullet, omnivorous and deposit-feeder crustaceans (Co, Cdf) gave the largest contribution in all gulfs and for the three size classes, although there was a variability in the contribution of crustaceans across gulfs and red mullet size (Fig. 4). In GCAST more functional categories than in other gulfs contributed to the diet of the red mullet, but carnivorous polychaetes (Pc) and deposit-feeder polychaetes (Pdf) were more abundant in the diet from untrawled gulfs.

3.1.1. *Feeding preference*

A total of 89 taxa were identified across benthic samples and stomach contents, with 38 taxa common to both that were used to calculate the electivity index (Table SM3). The number of positively selected prey items varied by gulfs and size classes, being generally higher in GCAST (21, 22, 11 for size class I, II and III, respectively) and GPATT (22, 11, 11), compared to GTERM (10, 12, 6) and GSANT (10, 11, 12). In GCAST, red mullet from size classes I and II exhibited positive selection for all Mollusca, while in GPATT selection was limited to Bivalvia (class I, II) and Caudofoveata (class I, III). Cumacea were selected by size class I from GCAST and GPATT. Among Decapoda, Paguridae were selected by most size classes of predator in all gulfs except GCAST, while Brachyura was positively selected mostly anywhere except GPATT. Among Amphipoda, Oedicerotidae were positively selected almost everywhere except GTERM. Several polychaete families were selected exclusively in the untrawled gulfs, especially in GCAST, while only very few families were selected in GTERM and none in GSANT, highlighting distinct dietary patterns in these two gulfs.

3.1.2. *Stable isotope analysis*

Red mullet showed the highest mean δ^{15}N values in the two untrawled areas (GCAST: 10.62 ± 0.81 ‰, GPATT: 9.6 ± 0.6 ‰ vs.) while δ^{13}C values were similar across all areas, ranging from a maximum −17.6 in GCAST to a minimum −18.1 in GPATT (Fig. 5). A trend of ^{15}N enrichment was observed in size classes II and III in untrawled areas, suggesting that trophic position increases with size (Fig. 5). Potential food sources plotted on the left side of Fig. 5, including the teleost *L. suerii*(Tc2), omnivorous crustaceans (Co1), mesozooplankton (Zoo) and SOM, showed δ^{13}C values too depleted to provide significant dietary contribution to red mullet and were more likely part of the pelagic food

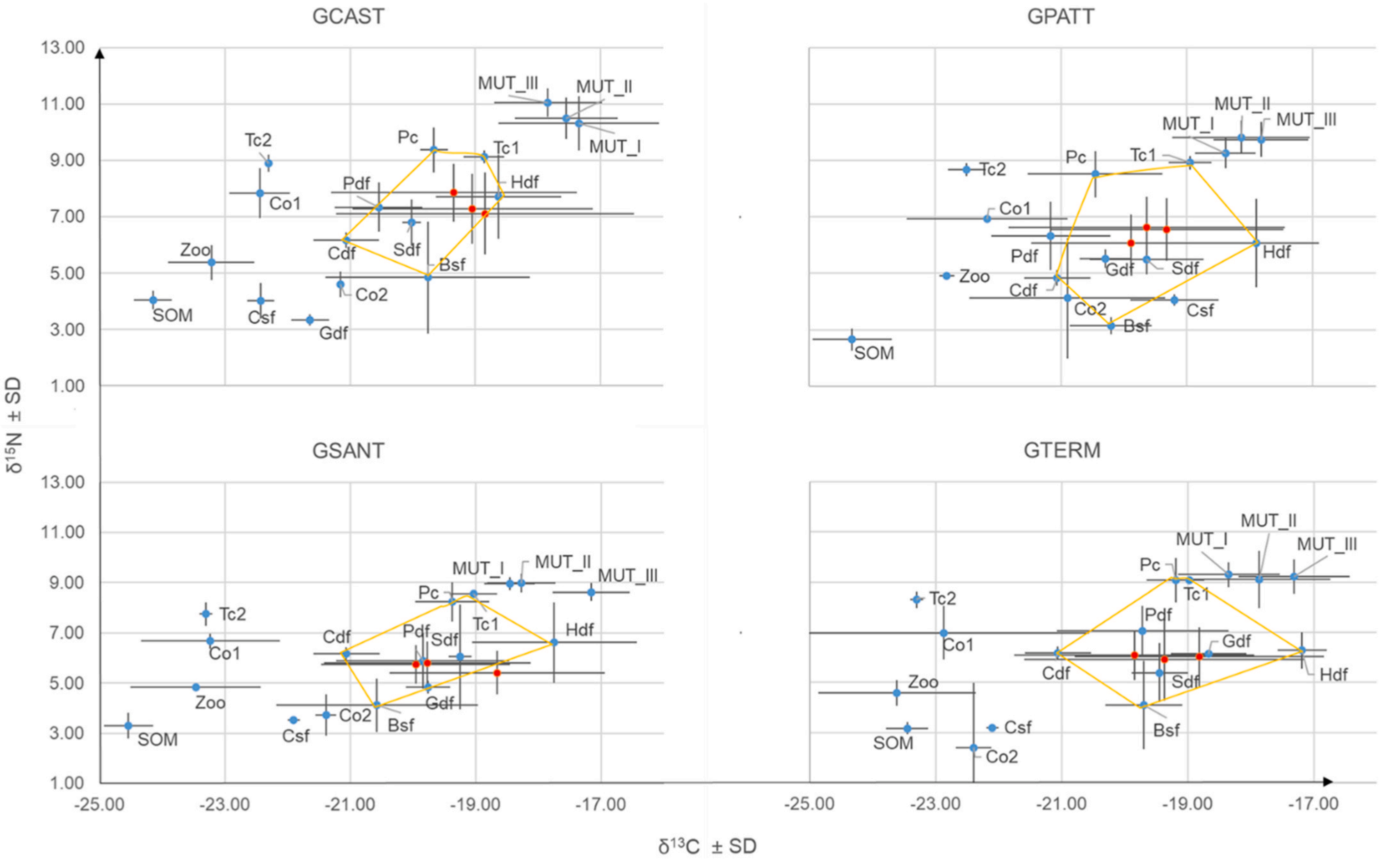

Fig. 5. Mean $\delta^{15}N$, $\delta^{13}C$ (‰) and standard deviation (SD) showing predator-prey relationships across untrawled (GCAST, GPATT) and trawled gulfs (GSANT, GTERM). Blue dots represent the three size classes of red mullet (MUT_ I, MUT_II, MUT_III) and their potential prey. Red dots indicate the isotopic values of the three size classes of red mullet corrected for trophic enrichment factor (TEF). The five polygons show the isotopic ranges of endmembers (prey sources) contributing to the red mullet diet. Bsf = Bivalvia suspension feeder; Co1 = Crustacea omnivore 1; Co2 = Crustacea omnivore 2; Cdf = Crustacea deposit feeder; Csf = Crustacea suspension feeder; Hdf = Holothuroidea deposit feeder; Gdf = Gastropoda deposit feeder; Mdf = other Mollusca deposit feeder; Pc = Polychaeta carnivore; Pdf = Polychaeta deposit feeder; Sdf = Sipuncula deposit feeder; Tc2 = Teleostei carnivore (*Lesueurigobius suerii*); Tc1 = Teleostei carnivore (*Callionymus maculatus*); SOM = sedimentary organic matter; Zoo = mesozooplankton omnivore. GCAST: Gulf of Castellammare; GPATT: Gulf of Patti; GTERM: Gulf of Termini Imerese; GSANT: Gulf of Sant'Agata. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

web. Conversely, macrobenthic groups plotted near red mullet on the right side of the plot are potential contributors to their diet.

Bayesian Mixing Models (MixSiar BMM) showed the contribution of five prey groups common to the four gulfs to the diet of red mullet of the three size classes across the four areas (Fig. 6, Table SM4). Carnivorous polychaetes (Pc) and detritus feeding crustaceans (Cdf) notably distinguished the diet between trawled and untrawled areas. Pc accounted for a mean dietary proportion of 35 % in untrawled areas compared to 11 % in trawled areas. On the contrary Cdf contributed approximately 15 % in trawled areas but only 0.05 % in untrawled areas (Fig. 7). In all areas, Bsf (bivalve suspension feeders) and Cdf were consistently replaced by holothurians and all polychaete groups as red mullet grew larger (from MUT_I to MUT_III). This shift was especially evident in untrawled gulfs, where the contribution of polychaetes increased significantly for size classes MUT_II and MUT_III (Fig. 6).

Although the PERANOVA showed variability among gulfs, TP differed between trawled and untrawled gulfs but not between Size classes (Table 4a). Large red mullet feed on average at a trophic position lower by 0.5 in trawled gulfs than in untrawled gulfs (Table 4b). The correlation between TP and fish size was positive in untrawled gulfs whereas it was null or slightly negative in trawled gulfs (Fig. 8).

4. Discussion

The red mullet *Mullus barbatus* is known to feed on benthic organisms such as decapod crustaceans, polychaetes, bivalves, gastropods and amphipods (Wirszubski, 1953; Gharbi and Ktari, 1979; Ben-Eliahu and Golani, 1990; Golani and Galil, 1991; Badalamenti et al., 1993; Vassilopoulou and Papacostantinou, 1993; Golani and Galil, 1991; Machias and Labropoulou, 2002). The present study supports previous results by adding new data on the red mullet feeding habits and, food preferences through a combined stomach contents and stable isotopes approach. The comparison of trawled and untrawled gulfs, suggests that bottom trawling reduced trophic diversity and simplified prey composition on the muddy-bottom community of the continental shelf. The effect of trawling on the diet of red mullet was more pronounced in larger fish. In untrawled gulfs more polychaetes, bivalves and epibenthic crustaceans (especially amphipods and decapods) were consumed, while in trawled areas the diet was dominated by Crangonidae, *Processa* sp. and Mysida. Similar results related to trawling pressure were reported for other benthic mesopredators in previous studies from the same area: trawling has been suggested to affect the diet of scaldfish, *Arnoglossus laterna* by increasing the consumption of the fish *Lesueurigobius suerii* and the shrimp *Alpheus glaber* (Fanelli et al., 2009). Likewise, *A. glaber* was eaten more frequently by pandora, *Pagellus erythrinus* in trawled areas, while in untrawled areas its place was taken by *Goneplax rhomboides*, a crab associated with more stable and structured habitats (Fanelli et al., 2010). This suggests that some benthic organisms, such as the aforementioned fish and shrimp are more abundant in trawled areas, where they probably benefit from trawling disturbance and contribute

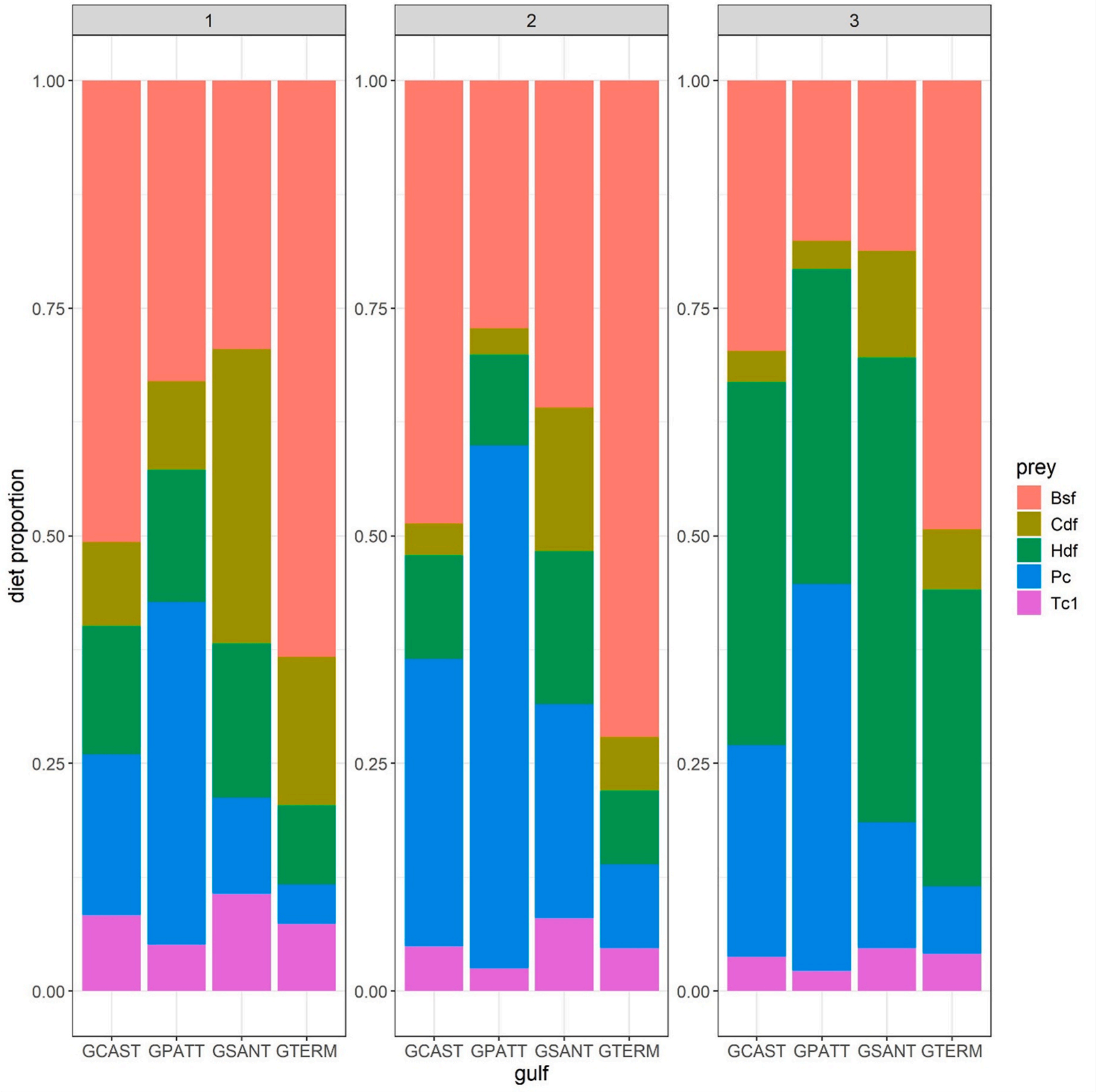

Fig. 6. Cumulative proportion of the main prey functional groups from MixSiar BMM for untrawled (GCAST, GPATT) and trawled gulfs (GSANT, GTERM) and the 3 size class (1,2,3) of the red mullet. Bsf = Bivalvia suspension feeder; Cdf = Crustacea deposit feeder; Hdf = Holothuroidea deposit feeder; Pc = Polychaeta carnivore; Tc1 = Teleostei carnivore (*Callionymus maculatus*). GCAST: Gulf of Castellammare; GPATT: Gulf of Patti; GTERM: Gulf of Termini Imerese; GSANT: Gulf of Sant'Agata. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

significantly to the diet of demersal fish.

The red mullet caught in the untrawled gulfs consumed a larger variety of prey items than in the trawled gulfs, as indicated by the higher values of the diversity index calculated from stomach contents. This result is reinforced by the higher selectivity index values in untrawled gulfs where there is a higher availability of prey due to the protection. Moreover, a lower number of preys per stomach, but larger in size, was observed in red mullet from trawled areas. However, this pattern should be interpreted with caution, as the post-hoc tests for prey weight did not confirm significant pairwise differences. This effect of trawling on prey diversity has not fully been observed in previous studies on scaldfish and pandora, where slight differences in the dietary diversity were found when comparing stomach contents from trawled and untrawled areas, suggesting that the diet of red mullet is more affected by trawling than in the two others mentioned mesopredators (Fanelli et al., 2009, 2010). This finding suggests that species specific fish response determine the pattern observed comparing areas with different fishing disturbance.

Significant ontogenetic variations were found only in untrawled gulfs.Fish of size classes I and II had similar diets but the diet of size III fish shifted towards larger prey such as the crustaceans *Gastrosaccus normani and Processa* sp., while the contribution of polychaetes was less marked. The higher trophic diversity observed for red mullet in the untrawled gulfs probably explains these differences and is also consistent with the more complex benthic assemblage structure determined by the absence of trawling impact (Romano et al., 2016).

The Ivlev index showed that the number of selected prey items increased with the number of taxa available in the environment, confirming a generalist predation strategy in the red mullet (Badalamenti et al., 1993). Other studies from a surf zone along the Tyrrhenian coast of Sicily report on a similar relationship between local prey availability and prey composition in red mullet stomach contents (Esposito et al., 2014).

Results from the stable isotope analysis were largely consistent with those from stomach content analysis and provided further insight into the effect of the trawl ban on the trophic ecology of red mullet. Bayesian mixing models identified several functional groups contributing to the

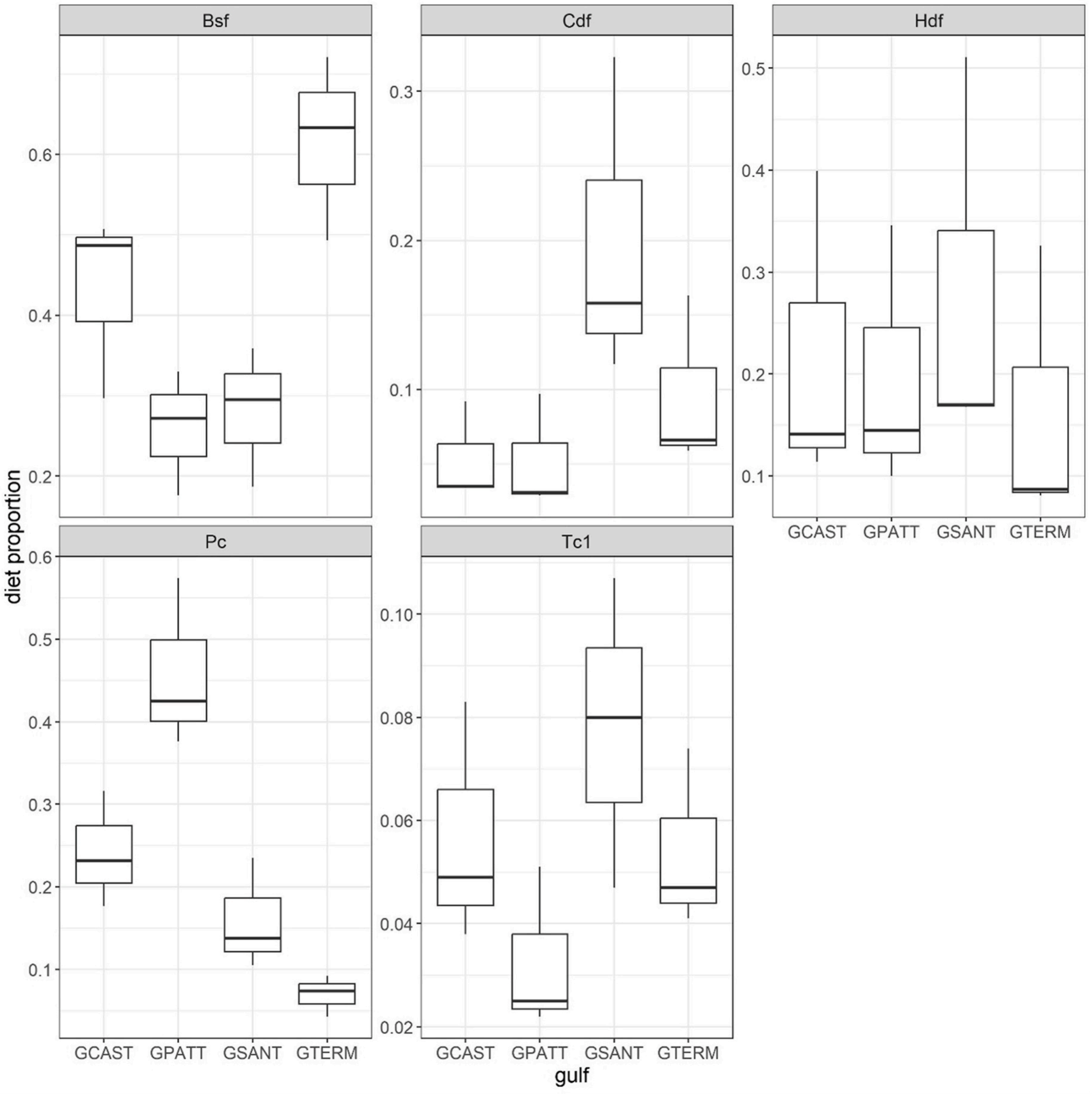

Fig. 7. Diet proportion of the main prey functional groups from the application of MixSiar BMM across untrawled (GCAST, GPATT) and trawled gulfs (GSANT, GTERM). Cdf = Crustacea deposit feeder; Hdf = Holothuroidea deposit feeder; Pc = Polychaeta carnivore; Tc1 = Teleostei carnivore (*Callionymus maculatus*). GCAST: Gulf of Castellammare; GPATT: Gulf of Patti; GTERM: Gulf of Termini Imerese; GSANT: Gulf of Sant'Agata.

dietary dissimilarity of red mullet between untrawled and trawled gulfs. The results of the models are quite consistent with those obtained from SCA. In fact, in both analyses, carnivorous polychaetes played a significant role as prey in the untrawled gulfs, while highly mobile suspension-feeding crustaceans contributed more to the red mullet diet in trawled gulfs. This result is in accordance with findings of other authors that recently reported high abundance of tube worms in low impact trawl areas and high abundance of shrimps, crustaceans and deep infauna worms in heavily trawled areas (Beauchard et al., 2023).

Previous stable-isotope research from the same study areas had investigated the effect of trawling on the trophic level of several demersal fish species. Badalamenti et al. (2008) reported limited trophodynamics effects of trawling for hake, *Merluccius merluccius*, and red mullet, and no effects for monk fish, *Lophius budegassa*, based only on stable isotopes data. Fanelli et al. (2009) and Sinopoli et al. (2012), reported no differences between trawled and untrawled gulfs for scaldfish, *Arnoglossus laterna* and hake, despite differences in diet composition. For hake this was attributed to greater predation on pelagic prey, which is unaffected by trawling (Sinopoli et al., 2012), while for scaldfish, which exploit benthic preys, it was attributed to low power of the analysis due to suboptimal sampling (Fanelli et al., 2009). On the other hand, a significantly higher trophic level has been found in pandora from untrawled areas, due to higher δ^{15}N values observed in all benthic species analysed therein, including pandora's preferred prey (Fanelli et al., 2010). The present study on red mullet supports an indirect mechanism related to a "fishing down the food web" (Pauly et al., 1998) effect such as the trophic position erosion (Agnetta et al., 2024).

Changes in the trophic position of predators can have major consequences on the food web length of demersal communities (Post and Takimoto, 2007). Our data, along with previous studies on the benthic trophic structure in the same study areas, suggest a more complex and better structured food web in untrawled areas, particularly in GCAST (Romano et al., 2016). Badalamenti et al. (2002, 2008) showed that the trophic position of a small-size benthic fish such as red mullet (maximum recorded TL 38 cm, common TL around 23 cm: Froese and Pauly, 2024), which preys mainly on carnivorous polychaetes, is close to that of larger piscivorous predators (Badalamenti et al., 2000). It should be noted that these studies used mesozooplankton as baseline and this

Table 4

a) Results of the three-way PERANOVA for the trophic position. ** = $p < 0.05$; n.s. = not significant. GCAST = Gulf of Castellammare; GTERM = Gulf of Termini Imerese; GSANT = Gulf of Sant'Agata, GPATT = Gulf of Patti. b) Mean trophic position (TP) and standard deviation (SD) of red mullet in each gulf and size class.

a) Variables	Source	df	MS	Pseudo-F	P(MC)	Perms	Pair-wise
Trophic Position	Protection	1	53.671	29.887	**	3	Utr > Tr
	Size Class	2	0.10022	11.352	n.s.	9952	
	Gulfs (Protection)	2	0.17958	44.093	**	9943	
	Protection x Size Class	2	0.29992	33.973	n.s.	9947	
	Gulfs (Protection) xSize Class	4	8.83E-02	21.676	n.s.	9958	
	Res	228	4.07E-02				
	Total	239					

b) Gulf x size class	Mean TP	SD	n
GCAST tot	3.39	0.25	60
GCAST I	3.30	0.30	20
GCAST II	3.35	0.23	20
GCAST III	3.53	0.16	20
GPATT tot	3.49	0.19	60
GPATT I	3.38	0.17	20
GPATT II	3.56	0.18	20
GPATT III	3.54	0.19	20
GSANT tot	3.16	0.12	60
GSANT I	3.19	0.08	20
GSANT II	3.20	0.12	20
GSANT III	3.09	0.11	20
GTERM tot	3.12	0.25	60
GTERM I	3.14	0.16	20
GTERM II	3.09	0.35	20
GTERM III	3.14	0.21	20

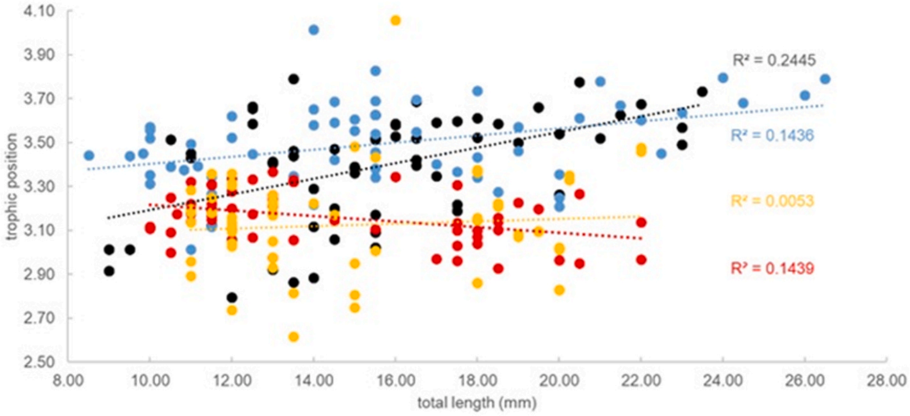

Fig. 8. Relationships between total length and trophic position of red mullet in each gulf (black = GCAST, blue = GPATT, red = GSANT, orange = GTERM). R^2 is the coefficient of determination. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

choice may have inflated the estimated trophic position. The present study strengthens this result by showing a higher trophic level for red mullet in untrawled areas.

This scenario highlights a paradigm in the untrawled gulfs, especially in GCAST. Despite lower benthic biomass - partially compensated by a higher production/biomass ratio - (Romano et al., 2016), the red mullet biomass has increased nearly 7-fold since the trawling ban (Pipitone et al., 2023). Additionally, its trophic position is higher following the trophic erosion process (Agnetta et al., 2024), and its diet is more diverse than in trawled gulfs (this study). Since complex food webs require substantial energy to sustain biomass at higher trophic levels (Post and Takimoto, 2007), the ability of the benthic system in GCAST to support a high biomass of demersal feeders suggest an unexpectedly high carrying capacity. This is particularly relevant for oligotrophic systems such as those in the southern Tyrrhenian Sea, where reduced fishing mortality in managed areas (i.e. FRAs) could further enhance fish biomass production. In contrast, in trawled areas resuspended sediments appear to be a fundamental resource for opportunistic consumers through the modification and simplification of the benthic food web (Quillien et al., 2016). The resuspension of this energy source in the water column depletes the substrate of organic matter, making it available to suspension feeders (Pusceddu et al., 2014; Eigaard et al., 2017). However, it remains unclear whether this energy could support a high biomass of demersal fish, as they are removed from the community by trawling.

5. Conclusion

This study shows that bottom trawling significantly changes the structure of benthic communities, which has clear consequences for the feeding habits and trophic position of *Mullus barbatus*. In untrawled areas, red mullet feed on more diverse and stable benthic assemblages, resulting in a higher trophic level than in trawled areas, where the diet shifts towards species favoured by sediment resuspension. Through the integration of stomach content analysis, prey availability data and stable isotopes, we reveal a robust correlation between the condition of the benthic habitat and the trophic dynamics of this significant demersal species.

Our findings suggest that banning trawling can help to maintain complex benthic food webs that can support higher fish biomass and trophic levels, even in relatively oligotrophic systems such as the southern Tyrrhenian Sea. However, the source of the high energy budget sustaining such systems remains unclear and requires further investigation. Additionally, it is uncertain whether energy made available through sediment resuspension in trawled areas can support comparable fish production given the continuous removal of demersal biomass by fishing.

Overall, this work emphasises the importance of spatial management measures, such as restricted fishery areas, to preserve benthic habitat integrity, enhance ecosystem functioning and support sustainable fisheries.

CRediT authorship contribution statement

Mauro Sinopoli: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Franco Andaloro:** Writing – review & editing. **Davide Agnetta:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Resources. **Davide Campo:** Writing – review & editing, Investigation, Data curation. **Luca Castriota:** Writing – review & editing, Investigation, Data curation. **Giovanni D'Anna:** Writing – review & editing, Methodology, Data curation. **Valentina Esposito:** Writing – review & editing, Investigation, Data curation. **Emanuela Fanelli:** Writing – review & editing, Methodology, Investigation, Data curation. **Chiara Romano:** Writing – review & editing, Methodology, Investigation, Data curation. **Gianfranco Scotti:** Writing – review & editing, Methodology, Data curation. **Salvatrice Vizzini:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Fabio Badalamenti:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carlo Pipitone:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107398.

Data availability

Data will be made available on request.

References

Agnetta, D., Badalamenti, F., Sweeting, C.J., D'Anna, G., Libralato, S., Pipitone, C., 2024. Erosion of fish trophic position: an indirect effect of fishing on food webs elucidated by stable isotopes. Phil. Trans. R. Soc. B. https://doi.org/10.1098/rstb.2023-0167.

Agnetta, D., Badalamenti, F., Colloca, F., Cossarini, G., Fiorentino, F., Garofalo, G., et al., 2022. Interactive effects of fishing effort reduction and climate change in a central Mediterranean fishing area: insights from bio-economic indices derived from a dynamic food-web model. Front. Mar. Sci. 9, 909164.

Agnetta, D., Badalamenti, F., D'Anna, G., Sinopoli, M., Andaloro, F., Vizzini, S., Pipitone, C., 2019. Sizing up the role of predators on Mullus barbatus populations in Mediterranean trawl and no-trawl areas. Fish. Res. 213, 196–203.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–524.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Auster, P.J., Shackell, N.L., 1997. Fishery reserves. Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse, pp. 159–166.

Badalamenti, F., D'Anna, G., Fazio, G., Gristina, M. e Lipari R., 1993. Relazioni trofiche fra quattro specie ittiche catturate su differenti substrati nel Golfo di Castellammare (Sicilia N/O). Biologia Marina, Suppl. al notiziario SIBM 1, 145–150.

Badalamenti, F., D'Anna, G., Pipitone, C., 2007. Ricostituzione delle risorse di pesca in un'area precedentemente soggetta ad intenso sfruttamento: dinamiche a larga scala del popolamento ittico e della struttura trofica della comunità marina. Relazione finale del progetto n. 63. Ministero dell'Istruzione dell'Università e della Ricerca 247. https://doi.org/10.5281/zenodo.1199558.

Badalamenti, F., Pinnegar, J.K., Polunin, N.V.C., D'Anna, G., 2000. Estimates of trophic level in the red mullet Mullus barbatus : comparison between gut-contents and stable-isotope data. Fishing down the Mediterranean food webs? CIESM workshop series 12, 19–21.

Badalamenti, F., D'Anna, G., Pinnegar, J.K., Polunin, N.V.C., 2002. Size-related trophodynamic changes in three target fish species recovering from intensive trawling. Marine Biology 141, 561–570. https://doi.org/10.1007/S00227-002-0844-3.

Badalamenti, F., Pipitone, C., Fiorentino, F., D'Anna, G., 2012. - the trawling ban in Hong Kong's inshore waters – a round of applause and a plea to learn from others' mistakes. Mar. Pollut. Bull. 64, 1513–1514.

Badalamenti, F., Sweeting, C.J., Polunin, N.V.C., Pinnegar, J., D'Anna, G., Pipitone, C., 2008. Limited trophodynamics effects of trawling on three Mediterranean fishes. Marine Biology 154 (5), 765–773.

Batista, M.I., Cabral, H.N., 2016. An overview of Marine Protected Areas in SW Europe: factors contributing to their management effectiveness. Ocean Coast Manag. 132, 15–23. https://doi.org/10.1016/j.ocecoaman.2016.07.005.

Beauchard, O., Bradshaw, C., Bolam, S., Tiano, J., Garcia, C., De Borger, E., Laffargue, P., Blomqvist, M., Tsikopoulou, I., Papadopoulou, N.K., Smith, C.J., Claes, J., Soetaert, K., Sciberras, M., 2023. Trawling-induced change in benthic effect trait composition - a multiple case study. Front. Mar. Sci. 10, 1303909. https://doi.org/10.3389/fmars.2023.1303909.

Ben-Eliahu, M.N., Golani, D., 1990. Polichaetes (Annelida) in the gut contents of Goatfishes (mullidae), whit new Polychaetae Records for the mediterranean coast of Istrael and the gulf of Elat (red sea). Marine Ecology, Pubblicazioni della stazione zoological di Napoli 11, 193–205.

Bianchi, C.N., Morri, C., 2000. Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. Mar. Pollut. Bull. 40 (5), 367–376.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., Garcia-Charton, J.A., Perez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., et al., 2008. Marine reserves: size and age do matter. Ecol. Lett. 11, 481–489. https://doi.org/10.1111/j.1461-0248.2008.01166.x, 650.

Coll, M., Cury, P., Azzurro, E., Bariche, M., Bayadas, G., Bellido, J.M., Chaboud, C., Claudet, J., El-Sayed, A., Gascuel, D., Knittweis, L., Pipitone, C., Samuel-Rhoads, Y., Taleb, S., Tudela, S., Valls, A., 2013. - the scientific strategy needed to promote a regional ecosystem-based approach to fisheries in the Mediterranean and Black Seas. Rev. Fish Biol. Fish. 23, 415–434.

Colloca, Francesco, Cardinale, Massimiliano, Maynou, Francesc, Giannoulaki, Marianna, Scarcella, Giuseppe, Jenko, Klavdija, Bellido, Jose Maria, Fiorentino, Fabio, 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish Fish. 14 (1), 89–109.

Consoli, P., Esposito, V., Falautano, M., Battaglia, P., Castriota, L., Romeo, T., et al., 2017. The impact of fisheries on vulnerable habitats: the case of trawling on circa-littoral grounds in the Strait of Sicily (central Mediterranean Sea). Mar. Biol. Res. 13 (10), 1084–1094.

de Juan, S., Thrush, S.F., Demestre, M., 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Mar. Ecol. Prog. Ser. 334, 117–129.

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., et al., 2017. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 74 (3), 847–865.

Esposito, V., Andaloro, F., Bianca, D., Natalotto, A., Romeo, T., Scotti, G., Castriota, L., 2014. Diet and prey selectivity of the red mullet, Mullus barbatus (Pisces: mullidae), from the southern Tyrrhenian Sea: the role of the surf zone as a feeding ground. Mar. Biol. Res. 10 (2), 167–178.

Fanelli, E., Trophic relationships in demersal communities of western Mediterranean: case studies from coastal and deep-sea ecosystems. PhD Thesis, Dipartimento di ecologia e sviluppo sostenibile, Università di Viterbo "La Tuscia": 312 pp.

Fanelli, E., Badalamenti, F., D'Anna, G., Pipitone, C., Romano, C., 2010. Trophodynamic effects of trawling on the feeding ecology of pandora, Pagellus erythrinus, off the northern Sicily coast (Mediterranean Sea). Mar. Freshw. Res. 61 (4), 408–417.

Fanelli, E., Badalamenti, F., D'Anna, G., Pipitone, C., 2009. Diet and trophic level of scaldfish Arnoglossus laterna in the southern Tyrrhenian Sea (western Mediterranean): contrasting trawled versus untrawled areas. J. Mar. Biol. Assoc. U. K. 89 (4), 817–828.

Feinberg, P.B., Caselle, J.E., Claudet, J., Clemence, M., Gaines, S.D., Antonio García-Charton, J., Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., et al., 2012. The science of European marine reserves: Status, efficacy, and future needs. 647 Marine Policy 36, 1012–1021. https://doi.org/10.1016/j.marpol.2012.02.021.

Fiorentino, F., Vitale, S., 2021a. How can we reduce the overexploitation of the Mediterranean resources? Front. Mar. Sci. 8, 674633. https://doi.org/10.3389/fmars.2021.674633.

Fiorentino, F., Vitale, S., 2021b. How can we reduce the overexploitation of the Mediterranean resources? Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.674633.

Fry, B., 2013. Minmax solutions for underdetermined isotope mixing problems: Reply to Semmens et al.(2013). Mar. Ecol. Prog. Ser. 490, 291–294.

Gharbi, H. e, Ktari, M.H., 1979. Règime Alimentaire des Rougets (Mullus barbatus L., 1758 et Mullus surmuletus L., 1758) du Golfe de Tunis. Bulletin Station Ocèanographique de Salammbo 6, 41–52.

Golani, D., Galil, B., 1991. Trophic relationship of colonizing and indigenous goatfish (Mullidae) in the eastern Mediterranean with special emphasis on decapod crustaceans. Hydrobiologia 21, 27–33.

Greenstreet, S.P., Hall, S.J., 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. J. Anim. Ecol. 577–598.

Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecol. Appl. 13, 117–137. https://doi.org/10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2.

Hiddink, Jan Geert, Rijnsdorp, Adriaan D., Gerjan, Piet, 2008. Can bottom trawling disturbance increase food production for a commercial fish species? Can. J. Fish. Aquat. Sci. 65 (7), 1393–1401.

Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A., Gonçalves, E.J., 2016. A regulation-based classification system for Marine Protected Areas (MPAs). Mar. Pol. 72, 192–198. https://doi.org/10.1016/j.marpol.2016.06.021.

Hyslop, E.P., 1980. Stomach contents analysis, a review of methods and their application. J. Fish. Biol. 17, 411–429.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, Connecticut.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. In: Advances in Marine Biology, vol. 34. Academic Press, pp. 201–352.

Johnson, Andrew Frederick, Giulia, Gorelli, Rees, Jenkins Stuart, Jan Geert, Hiddink, Hilmar, Hinz, 2015. Effects of bottom trawling on fish foraging and feeding. Proc. R. Soc. A B., 28220142336

Kaiser, M.J., Spencer, B.E., 1994. Fish scavenging behaviour in recently trawled areas. Marine ecology progress series. Oldendorf 112 (1), 41–49.

Machias, A., Labropoulou, M., 2002. Intra-specif variation in resourse use by red mullet, *Mullus barbatus*. Estuar. Coast Shelf Sci. l55 (4), 565–578.

Mak, Y.K.Y., Tao, L.S.R., Ho, V.C.M., Dudgeon, D., Cheung, W.W.L., Leung, K.M.Y., 2021. Initial recovery of demersal fish communities in coastal waters of Hong Kong, South China, following a trawl ban. Rev. Fish Biol. Fish. 31, 989–1007.

Marshall, S., Elliott, M., 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter-and intraspecific feeding relationships in estuarine fish. J. Fish. Biol. 51 (3), 526–545.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. Science 347 (6219), 1255641.

Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. - Effort distribution and catch patterns adjacent to temperate MPAs. ICES J. Mar. Sci. 62, 1150–1167.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS One 5 (3), e9672.

Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., et al., 2013. Bayesian stable isotope mixing models. Environmetrics 24 (6), 387–399.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. Science 279 (5352), 860–863.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Systemat. 18 (1), 293–320.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., et al., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92 (10), 823–835.

Pinkas, L., Oliphant, M.S., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Fish. Bull. 152, 1–105.

Pipitone, C., Badalamenti, F., D'Anna, G., Patti, B., 2000. Fish biomass increase after four-year trawl ban in the gulf of Castellammare (NW sicily, Mediterranean Sea). Fish. Res. 48 (1), 23–30.

Pipitone, C., Agnetta, D., Zenone, A., Giacalone, V.M., Badalamenti, F., Fiorentino, F., et al., 2023. When the trawl ban is a good Option: Opportunities to restore fish biomass and size structure in a mediterranean fisheries restricted area. Sustainability 15 (3), 2425.

Pipitone, C., Badalamenti, F., Fernández, T.V., D'Anna, G., 2014. Spatial management of fisheries in the Mediterranean Sea: problematic issues and a few success stories. Adv. Mar. Biol. 69, 371–402.

Piroddi, C., Coll, M., Steenbeek, J., Moy, D.M., Christensen, V., 2015. Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity. Mar. Ecol. Prog. Ser. 533, 47–65.

Post, D.M., Takimoto, G., 2007. Proximate structural mechanisms for variation in food chain length. Oikos 116, 775–782, 2007.

Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proc. Natl. Acad. Sci. 111 (24), 8861–8866.

Pusceddu, A., Grémare, A., Escoubeyrou, K., Amouroux, J.M., Fiordelmondo, C., Danovaro, R., 2005. Impact of natural (storm) and anthropogenic (trawling) sediment resuspension on particulate organic matter in coastal environments. Cont. Shelf Res. 25 (19–20), 2506–2520.

Quillien, N., Nordström, M.C., Schaal, G., Bonsdorff, E., Grall, J., 2016. Opportunistic basal resource simplifies food web structure and functioning of a highly dynamic marine environment. J. Exp. Mar. Biol. Ecol. 477, 92–102.

Riginella, E., Nalon, M., Sinopoli, M., Mazzoldi, C., 2022. Gain or loss for the inshore trawling ban within three miles? Preliminary data. Fishes 7 (6), 320.

Romano, C., Fanelli, E., D'Anna, G., Pipitone, C., Vizzini, S., Mazzola, A., Badalamenti, F., 2016. Spatial variability of soft-bottom macrobenthic communities in northern Sicily (Western Mediterranean): contrasting trawled vs. untrawled areas. Mar. Environ. Res. 122, 113–125.

Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M., Gaines, S.D., Garilao, C., Goodell, W., Halpern, B.S., Hinson, A., Kaschner, K., Kesner-Reyes, K., Leprieur, F., McGowan, J., Morgan, L.E., Mouillot, D., Palacios-Abrantes, J., Possingham, H.P., Rechberger, K. D., Worm, B., Lubchenco, J., 2021. - Protecting the global ocean for biodiversity, food and climate. Nature 592, 7854.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication, by CE Shannon (And Recent Contributions to the Mathematical Theory of Communication). *W. Weaver*. University of illinois Press.

Shannon, L., Coll, M., Bundy, A., Gascuel, D., Heymans, J.J., Kleisner, K., et al., 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. Mar. Ecol. Prog. Ser. 512, 115–140.

Sinopoli, M., Pipitone, C., Badalamenti, F., D'Anna, G., Fiorentino, F., Gristina, M., et al., 2022. Effects of a trawling ban on the growth of young-of-the-year European hake, Merluccius merluccius in a Mediterranean fishing exclusion zone. Regional Studies in Marine Science 50, 102151.

Sinopoli, Mauro, Fanelli, Emanuela, D'Anna, Giovanni, Badalamenti, Fabio, Pipitone, Carlo, 2012. Assessing the effects of a trawling ban on diet and trophic level of hake, Merluccius merluccius, in the southern Tyrrhenian Sea. Sci. Mar. 76 (4), 677–690.

Stergiou, K.I., 1990. Prediction of the Mullidae fishery in the eastern Mediterranean 24 months in advance. Fish. Res. 9 (1), 67–74.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096.

Sumaila, U.R., Charles, A.T., 2002. Economic models of marine protected areas: an introduction. Nat. Resour. Model. 15 (3), 261–272.

Sweeting, C.J., Badalamenti, F., D'Anna, G., Pipitone, C., Polunin, N.V.C., 2009. Steeper biomass spectra of demersal fish communities after trawler exclusion in Sicily. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 66 (1), 195–202.

Sweeting, C.J., Barry, J., Barnes, C., Polunin, N.V.C., Jennings, S., 2007a. Effects of body size and environment on diet-tissue δ15N fractionation in fishes. J. Exp. Mar. Biol. Ecol. 340, 1–10. https://doi.org/10.1016/j.jembe.2006.07.023.

Sweeting, C.J., Barry, J.T., Polunin, N.V.C., Jennings, S., 2007b. Effects of body size and environment on diet-tissue δ13C fractionation in fishes. J. Exp. Mar. Biol. Ecol. 352, 165–176. https://doi.org/10.1016/j.jembe.2007.07.007.

Vassiliopoulou, V., Papacostantinou, C., 1993. Feeding habits of red mullet (Mullus barbatus) in a gulf in Western Greece. Fishery Research 16, 69–83.

Wirszubski, A., 1953. On the Biology and the Biotope of the red mullet Mullus barbatus L. Sea Fishery Research Station, vol. 7. Bulletin, Haifa, pp. 1–20.