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# The effectiveness of fish feeding behaviour in mirroring trawling-induced patterns

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The ability to observe and predict trawling-induced patterns at spatial and temporal scales that are relevant to inform realistic management strategies is a challenge which scientists have consistently faced in recent decades. Here, we use fish feeding behaviour, a biological trait easily impaired by trawling disturbance, to depict alterations in fish condition (*i.e.* individual fitness) and feeding opportunities. The benthivorous fish *Mullus barbatus barbatus* was selected as a model species. The observed trends of responses to trawling in prey species confirmed the effectiveness of a non-trawled zone in sustaining higher levels of diet diversity (*e.g.* quantity and quality of ingested prey) and fish condition values (*e.g.* morphometric and physiological Condition Index). Changes observed in fish prey selection confirmed the role of trawling disturbance in modifying the local soft bottoms community, producing alterations of prey availability that trigger shifts in fish diet. Trawling-induced feeding patterns, mirrored through stomach contents, can positively or negatively affect fish condition, the main driver of population dynamics in maintaining carrying capacity levels. Due to the widespread socio-economic value of the red mullet fishery, and the current exploitation status, evidence gathered by the proposed bottom-up trait based approach might inform future trawling adaptation strategies, and tailor spatial conservation measures supporting an Ecosystem-Based Fisheries Management.

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## 1. Introduction

One of the main challenges of the next generation of fisheries scientists and policy makers is the capacity to depict and predict patterns of trawling disturbances at spatial and temporal scales relevant to building-up realistic management measures and plans (van Denderen et al., 2014; Kaiser et al., 2015; Rijnsdorp et al., 2016; Melnychuk et al., 2017). Trawling is a well-recognised source of physical disturbance that shapes the ecosystem integrity in terms of both benthic and fish communities' structures and its dynamics alteration (*i.e.* biotic component), and through large modifications of habitat structure with significant physical, chemical and trophic changes (*i.e.* abiotic component; Kaiser et al., 2006; Tecchio et al., 2013; Clark et al., 2016; O'Neill and Ivanović, 2016; Collie et al., 2017). To date, the study of trawling-induced changes at the community level have represented the most common way to grasp this disturbance phenomenon (*e.g.* species distribution, communities composition and diversity; Queirós et al., 2006; Hiddink et al., 2011; van Denderen et al., 2013, 2014; Lambert et al., 2014). Therefore, similarly to other sources of physical and biological disturbances (Suding et al., 2008) the effects of trawling originate at species level, from significant modifications of species biological traits (*e.g.* behavioural, physiological and morphological), to biodiversity alteration at various range scales and in a variety of marine habitats

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(Kaiser et al., 2006; Svensson et al., 2010; Hiddink et al., 2017). Specifically, by altering the patterns of food availability, trawling can affect fish feeding behaviour, inducing changes in prey selection preferences and altering the carrying capacity of benthivorous fish (*e.g.* loss of preferred prey for highly selective species and increased availability of generic prey for more resilient generalist species; Kaiser and Ramsay, 1997; Frid and Hall, 1999; Garrison and Link, 2000; Rijnsdorp and Vingerhoed, 2001; Pinnegar et al., 2003; Hinz et al., 2005; 2009; de Juan et al., 2007; Fanelli et al., 2009; Hiddink et al., 2007, 2011; Shephard et al., 2010; van Denderen et al., 2013; Johnson et al., 2015). The use of predatory fish diets, through stomach contents analysis, has been described as a useful, indirect and cost-effective method for sampling the benthic community and for exploring trophic aspects of complex systems at broad spatial and temporal scales (Link, 2004; Baker et al., 2014). Empirical and modelling studies, mainly performed on flatfishes along the Northern European shelves, have shown the relationship between trawling impact and fish body condition, underlining potential consequences for population dynamic (Link et al., 2002; Choi et al., 2004; Hinz et al., 2005; Shephard et al., 2010; Hiddink et al., 2011; Johnson et al., 2015). Interestingly, the study of "prey-to-consumer biomass ratio" based on both prey availability and intra- and inter-specific competitor abundance, has allowed to disentangle the direct effects of trawling on benthic prey availability and the effect of competition over food sources caused by concomitant changes in fish population (Hiddink et al., 2016). Despite this, only very few studies have focused on trawling-induced patterns generation and on the effects on fish feeding behaviour in the Mediterranean Sea (mostly dealing with demersal fish species, de Juan et al., 2007; Fanelli et al., 2009, 2010; 2011; Sinopoli et al., 2012; or using stable isotopes Badalamenti et al., 2002, 2008; Romano et al., 2016). This is surprising considering the very sensitive nature of this basin, characterised by low production levels coupled with intense and highly aggregated trawling effort (Mangano et al., 2014) that historically provides seafood to many coastal countries, highly exploited and crowded of human activities (Penas and Lado, 2016; Mangano and Sarà, 2017).

Feeding behaviour is a sensitive trait-based metric (*sensu* Moretti et al., 2017) that may allow to *(i)* elucidate subtle community-level changes associated with shifts in ecological processes otherwise difficult to visualise (Mouillot et al., 2013; Coleman et al., 2015), and *(ii)* observe theoretical emergent ecological patterns as the Intermediate Disturbance Hypothesis (IDH theory *sensu* Connell, 1978) on a large scale (Svensson et al., 2009). This theory represents a pillar of the ecology in examining patterns of diversity and species coexistence under physical disturbance (Connell, 1978). Representing one of the most mentioned theories in ecology (Fox, 2013), featured in numerous ecology textbooks and a common topic for reviews (Mackey and Currie, 2001; Svensson et al., 2009), the IDH has triggered passionate debate among scientists (Fox, 2013). Diversity trends consistent with the IDH predictions have been observed mainly in manipulative studies in both terrestrial and marine ecosystems (Svensson et al., 2007 and references therein). Consequently, practical applications of the IDH theory still remain necessary both to stimulate advances in quantifying and predicting the effects of disturbance on biodiversity patterns and to address conservation efforts and management of ecological resources (Mouillot et al., 2013; van Denderen et al., 2014).

Here, we mirrored the trophic adaptation resulting from trawling disturbance looking at the taxonomic composition of benthic invertebrates (ingested prey) and at the fish morphological and physiological condition, along a Mediterranean actively exploited fishing ground. Through stomach contents analysis, we aimed to disentangle dietary preference and diversity, mirroring the magnitude of trawling disturbance in reducing or promoting feeding opportunities along a gradient of intensity. With our trait-based tailored assessment, we expected to enhance the actual understanding of the secondary effect working principles of trawling disturbance (Thrush and Dayton, 2002; Hiddink et al., 2011; Cook and Bundy, 2012; Johnson et al., 2015). Furthermore, the use of a species' biological trait scaled-up into community features may allow the use of species-specific responses in informing an adaptive trawling management plan and in tailoring future conservation measures and strategies. The benthivorous fish *Mullus barbatus barbatus* (Linnaeus, 1758) was selected as a model species as: *(i)* it is widely distributed across the Mediterranean shelves, representing one of the most valuable commercial species, and historically is the most exploited in sustaining fishery-dependent communities (FAO, 2014; Vasilakopoulos et al., 2014); *(ii)* is routinely collected as a target species in the framework of national and international long-term experimental trawl surveys (*e.g.* MEDITS, GFCM); and *(iii)* is potentially subject to a northward shift of expansion range due to climate change (*e.g. Mullus surmuletus;* Sumaila et al., 2011). Our study takes advantage of the presence of a long-term existing Fishery Exclusion Zone (FEZ) and a highly resolute evaluation of trawling intensity through Vessel Monitoring System (VMS); two powerful tools to accurately detect and check for the effects of trawling disturbance. Fish feeding and conditional responses have been tested for differences in fish gender to avoid any confounding effects in our analysis.

## 2. Materials and methods

The study was carried out along the continental shelf off the Northern Sicilian coast (Southern Tyrrhenian Sea, Central Mediterranean; Fig. 1), a commercially important fishing ground encompassing three main gulfs: the Gulf of Termini Imerese, the Gulf of Sant'Agata and the Gulf of Patti (Mangano et al., 2013). The latter gulf, a Fishery Exclusion Zone closed to commercial trawling since 1990, was selected as a reference area that experiences no trawling activity until a certain extension (Fig. 1). The seabed under investigation was characterised by a narrow continental shelf dominated by soft sediments, with a predominant percentage of mud (>80% to see Mangano et al., 2014) mixed with sand and silt (both fractions are similar, accounting for 10% each; Fanelli et al., 2009, 2011; Mangano et al., 2014; Romano et al., 2016). Both infaunal and epifaunal benthic communities from this seabed are shaped by a chronic and highly aggregated trawling disturbance (Mangano et al., 2014, 2015). To avoid any influence of natural variability due to habitat heterogeneity, red mullet were *a priori* sampled across a depth range of 50–100 m continental upper shelf, where this species represented a main component of the associated demersal fish assemblage (Busalacchi et al., 2010). Previous analyses of the trawling intensity along the study area highlighted non-random behaviour of the trawling fleet, characterised by a high degree of patchiness, with medium-large trawling fleets mainly operating over the continental shelf and upper slope (Mangano et al., 2014, 2015). Here we estimated the trawling intensity and spatial distribution through satellite data Vessel Monitoring System (VMS) recorded during the year 2012 for Italian bottom otter trawlers (Bottom Otter Trawls - OTB $\geq$ 12 m). Trawling intensity was calculated by following the point summation technique (*sensu* Lee et al., 2010; see Mangano et al., 2014, 2015 for more details on the applied procedure) and the swept area was estimated on a grid cell size of 1 km $\times$ 1 km. Trawling intensity was expressed as the number of times an area of seabed was swept per year for each cell, and was subsequently grouped into four categories: FEZ (Fishery Exclusion Zone, no trawling), Low (low trawling intensity 0.001–3 swept area per year), Intermediate (medium trawling intensity 3.001–6.5 swept area per year) and High (high trawling intensity

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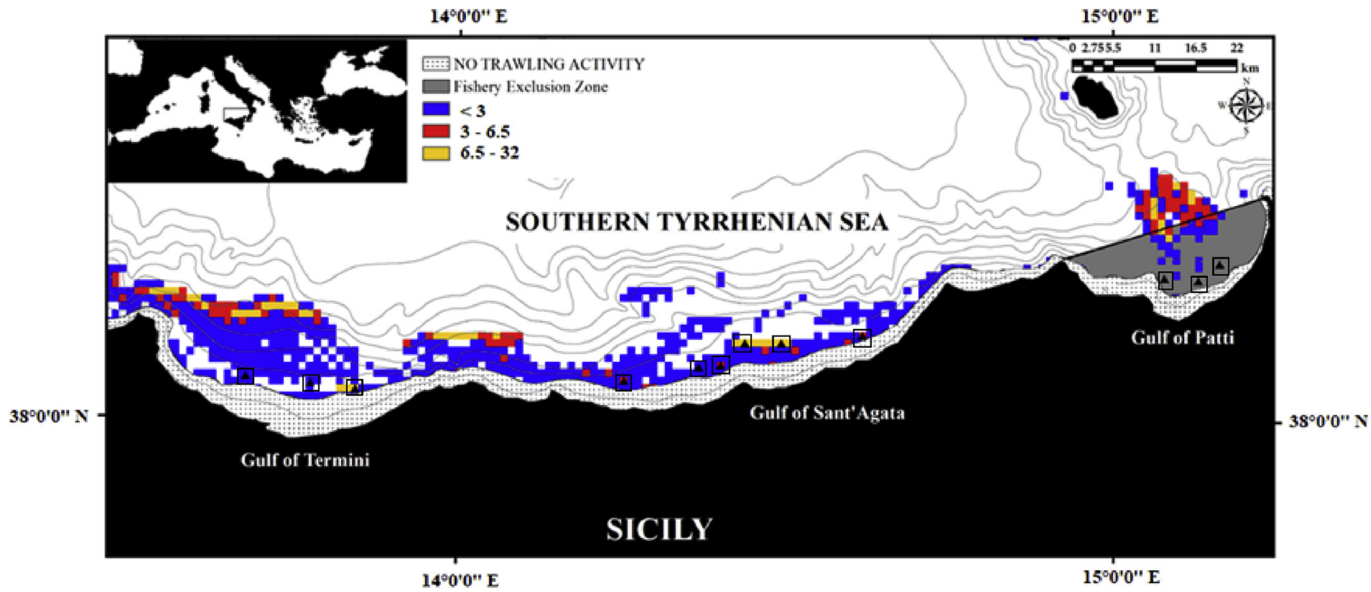


**Fig. 1.** Sampling sites (framed black triangles on a 1 $km^2$ cell size sampling area) and the distribution of trawling intensity along the study area (VMS data analysis for Italian OTB ≤ 12 m operating during 2012; trawling intensity expressed as swept area per year, total extension of mapped trawling activity 2067 $km^2$, maximum depth 800 m; modified as from Mangano et al., 2015). The black line in front of the Gulf of Patti represents the seaward limit of the Fishery Exclusion Zone; sampling sites are represented by black triangles.

6.501–32 swept area per year) (Fig. 1). The categories were classified employing the Jenks Natural Breaks classification method (Jenks, 1967) based on an optimal break classification algorithm creating ideal numbers of classes by minimizing the variance within the class and maximizing the variances among classes (Slocum, 1999). The number of Jenks' classes was determined by computing the Goodness of Absolute Deviation Fit (GADF). GADFs were then plotted on a graph and the number of classes was selected considering the point at which the curve begins to flatten out. This categorical approach was preferred due to the aggregate fleet behaviour, in order to maximize the chance of detecting the effect of trawling (Mangano et al., 2015).

### 2.1. Data collection

Twelve sampling sites were selected along the detected gradient of trawling intensity, as well as three sampling sites per each of the four categories of trawling activity, and an experimental otter trawl was performed at each sampling site (on a sampling box of 1 $km^2$ cell size; Fig. 1). The demersal fish community was sampled in June 2012 using an experimental otter trawl. Each haul had a duration of 60 min (OTMS gear, Otter Trawl Maireta System; Sardà et al., 1998; Mangano et al., 2015). At each sampling site, a subsample of red mullet specimens ($N_{sampling\ site} = 30$) of a fixed total length (TL) of 110–115 mm was sorted from the total catch and selected for stomach contents analysis ($N_{tot} = 360$, of which 90 per trawling intensity category) to avoid any size and/or ontogenetic effects. Each red mullet was measured and weighed on board, sexual maturity was recorded and stomachs were extracted, formalin-fixed (8% buffered), labelled and stored until dissection in the laboratory. The stomachs were dissected and the content was weighed after blotting (to the nearest 0.001 g wet mass). Food items were sorted under stereomicroscope, counted and identified to the lowest taxonomical level depending on the degree of digestion. To provide an estimate of infaunal prey abundance in the environment the benthic infaunal community was sampled at each sampling site by taking two 0.25 $m^2$ Van Veen grabs; samples were sorted on a 0.5 mm sieve and fixed in 70% alcohol until the laboratory identification to the lowest taxonomic resolution possible.

### 2.2. Data analysis: fish condition indices and dietary descriptors

Two condition indices were used to quantify the effect of trawling intensity on fish growth in each category: the morphometric Fulton's Index and the physiological Digestive-Somatic Index (Lloret et al., 2013). We combined the information coming from the two indices to, respectively, observe the change in individual weigh-length of fish, and to investigate changes in the digestive tract as a response of changes in the consumption of particular prey types highlighting the consequent plasticity in the digestive tract.

The Fulton's (K) condition factor (Ricker, 1975), the first morphometric condition factor used in fisheries science, was expressed as:

$$K = 100(W/L3)$$

where W was the total weight and L is the total length of the single specimens; the constant = 3, assumes an isometric growth in fish (*i.e.* *b*-value of the weight–length relationship must be close to 3 as in the case of *Mullus barbatus barbatus* where $b = 3.36$; *sensu* Lloret et al., 2002). Moreover, by comparing specimens with similar length structures (fixed class size, TL 110–115 mm), we avoided any confounding effect of length and/or allometry on the computation of this index. The index uses 1 as a benchmark for the condition: fish above or below 1 are considered in relatively better or worse condition than a standard fish, depending on their distance from the benchmark.

The Digestive-Somatic Index (DSI) expresses the size of the gut relative to the mass of the body of the animal, as a condition indicator:

$$DSI = (DW/W) \times 100$$

where DW is the weight of the digestive tract (stomach plus intestine) and W is the weight of the whole individual (eviscerated weight). This index has been computed in several demersal fish in the Mediterranean including red mullet (Lloret et al., 2002).

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Five dietary descriptors were used to quantify differences in feeding strategy responses over the trawling intensity categories, respectively: the Chesson's Index of prey selectivity, the Hyslop's Index of stomach fullness and the three indices of diversity based on prey, species richness (d), Shannon-Wiener Diversity Index (H′) and Simpson Dominance (D) hereafter referred and used as proxies of diet composition and diversity (*sensu* de Juan et al., 2007; Mangano et al., 2015).

We computed the Chesson's Index (standardised forage ratio, $\alpha_a$) to check for differences in prey preferences, as appropriate for situations when prey is removed without replacement (Chesson, 1978, 1983). Chesson's Index shows preferred prey types by comparing the availability of a prey item in the environment with the presence of the prey in the stomach contents. The stomach contents of all 90 specimens within a trawling intensity category were combined, and only the common prey species (prey occurring more than 10 times in the diet across all the sampling sites, respectively 12, 4, 7 and 3 prey at FEZ, Low, Intermediate and High accounting for 24, 19, 18 and 30% of the diet in each category) were included in the index calculation (*sensu* Johnson et al., 2015). The index, expressed as standardised forage ratio is:

$$\alpha_a = 1/m$$

where $m$ is the total number of different prey species in the stomachs of the fish ($m$ = 49, 21, 38, 10 at FEZ, Low, Intermediate and High). The standardised forage ratio $\alpha_a$ ranges between 0 (complete avoidance) and 1 (exclusive preference), thus values above $\alpha_a$ indicates a positive selection, and values below indicates avoidance (value equal to $\alpha_a$ indicates a random-feeding, *i.e.* particular prey are consumed in proportion to abundance in the environment, Pinnegar et al., 2003).

The Hyslop's Index (Hyslop, 1980) of stomach fullness expressed as:

$$W_{\text{stomach content}}/TW$$

the ratio of food ingested weight ($W_{\text{stomach content}}$) to fish body weight (TW) (Baker et al., 2014).

The prey abundance in the stomach and in the environment were also tested for differences along the gradient of trawling intensity.

### 2.3. Data analysis: effects of trawling on fish condition and feeding behaviour

The effect of trawling intensity on the diet of fish was analysed by multivariate techniques using PRIMER statistical package (v.6) with PERMANOVA extension (Anderson et al., 2008). Data of prey whose percentage abundance was less than 5% of the total dataset were removed from the analyses, as they were not consistently collected through the stomach contents. The obtained dataset was square-root transformed prior to analysis, in order to reduce the influence of dominant species and to increase the importance of less common species. A similarity matrix was computed using the Bray-Curtis similarity index on the relative abundance of prey in the stomachs from every sample at each site. An Analysis of Similarity (ANOSIM) test was used to find detailed differences in prey species composition among trawling intensities. The obtained dataset was analysed with a SIMPER routine, to determine the contribution of each prey item to the dissimilarities between trawling intensity categories.

To investigate the variation of condition indices (Fulton's K and DSI) within the factors sex and trawling intensity, a 2-way ANOVA was performed considering these two categorical predictors after checking that the data conformed to the necessary assumptions regarding homogeneity of variance and normality. A 2-way mixed ANOVA was performed to detect changes in the dietary descriptors (Chesson's and Hyslops's indices, and the diet diversity indices S, H′ and D) among the trawling intensity categories with a trawling disturbance as a fixed factor (as expressed by trawling intensity, 4 levels) and a nested random factor with two levels (Haul, site factor). Differences among categories were tested using the SNK, Student–Newman–Keuls test (significant interaction term were considered at $p < 0.05$ *, $p < 0.001$ **; $p < 0.0001$ ***). The same 2-way ANOVA approach was applied to test differences within trawling intensity on mean prey abundance both inside the stomachs and in the environment, and on each single most abundant species. The non-parametric Kruskal-Wallis test was performed when ANOVA assumptions were not satisfied by data after transformation.

## 3. Results

The red mullet specimens sampled along the detected categories of trawling disturbance displayed different values of morphological condition on Fulton's Index (K, $F_{1,3} = 8.54$, $p < 0.0001$; SNK pairwise test are reported in Fig. 2a) showing the lowest values of fish weight-at-length in highly trawled areas. Looking at the effects of trawling on the physiological condition, the DSI showed a typical IDH hump-shaped trend (DSI, $F_{1,3} = 28.34$, $p < 0.0001$; SNK pairwise test are reported in Fig. 2b). Specimens at the non-trawled FEZ gulf showed highest DSI values that decrease at lowest trawling intensity, which then increase at intermediate disturbance and reach the lowest value at the highest level of disturbance (Fig. 2b). No significant correlation between both Fulton's and DSI indices with sex of *M. barbatus barbatus* were detected ($F_{1,3} = 2.18$, $p = 0.142$). Looking at the dietary descriptor of prey preference, according to the Chesson's Index ($\alpha_a$), the red mullet showed to feed actively (exclusive feeding) on the highest number of prey at FEZ, mostly polychaetes (Fig. 3, thresholds of standardised forage ratio are reported for each trawling intensity category, together with the main abundance of preferred prey found on the total sampled stomach per category). At Low and High disturbance red mullets prefer a fewer number of different items, respectively Ampharetidae and Capitellidae *vs* Tellinidae and Sternaspidae. The three preferred prey at Intermediate disturbance were Tellinidae, Foraminifera and fragment of Amphipoda (Fig. 3). The index of stomach fullness showed the same hump-shaped trend of the DSI with the highest values at both the FEZ and at the Intermediate level of disturbance (Hyslop's, $F_{1,3} = 5.73$, $p < 0.0001$; SNK post-hoc test are reported in Fig. 4a). The total abundance of infaunal prey in the diet was highest at FEZ and Intermediate trawling disturbance compared to Low and High (prey diet, $F_{1,3} = 9.30$, $p = 0.012$; $N_{\text{tot prey}} = 1366$; SNK pairwise test are reported in Fig. 4b). The total abundance of prey in the environment was highest at FEZ and Low compared to Intermediate and High disturbance (prey environment, $F_{1,3} = 119.08$, $p = 0.013$, $N_{\text{tot prey}} = 3326$; SNK pairwise test are reported in Fig. 4c). Looking at the selected proxies of diet diversity indices, a highly diversified diet was detect at the FEZ, both the species richness Index (d, $F_{1,3} = 35.83$, $p < 0.0001$, Fig. 5a) and the Shannon's-Wiener diversity Index (H′, $F_{1,3} = 27.49$, $p < 0.0001$, Fig. 5b) showed a significant hump-shaped trend along the gradient of trawling disturbance, with significant differences between the FEZ and the areas opened to fisheries (both indices showed the highest values at FEZ; SNK test all significant reported into Fig. 5a and b). The Simpson's Dominance Index showed an opposite trend with the highest value at High levels of trawling intensity (D, $F_{1,3} = 14.78$, $p < 0.0001$; SNK pairwise tests are reported in Fig. 5c).

The abundance of ingested prey along the gradient of trawling intensity was significantly different (ANOSIM test R = 0.431, $p < 0.001$ all pairwise test were significant at $p < 0.001$); a SIMPER

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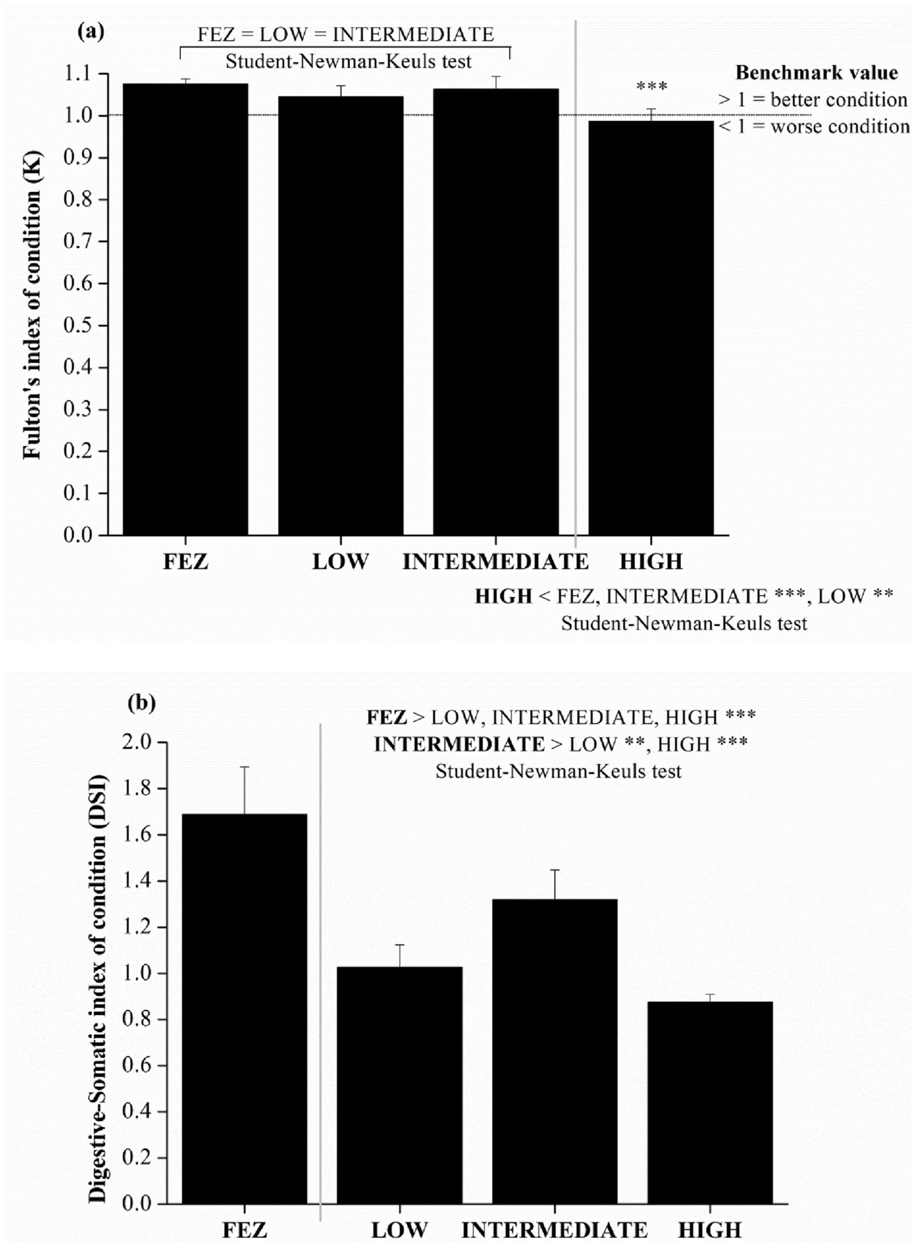


**Fig. 2.** Trends of the morphometric Fulton's (K) Index (a) and the physiological Digestive-Somatic Index (DSI) Index (b). Fulton's (K) benchmark threshold is reported. Trawling intensity categories: FEZ = Fishery Exclusion Zone, no trawling intensity; LOW = 0.001–3 swept area/year; INTERMEDIATE = 3.001–6.5 swept area/year; HIGH = 6.5–32 swept area/year (the swept area was evaluated on a sampling box of 1 $km^2$ cell size) Student-Newman-Keuls post-hoc test results are reported, asterisks indicate different p-values: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.0001$ [as from Fig. 1 and equally valid at each table and figure through the text].

analysis highlighted those taxa that accounted for the differences between the different trawling intensity categories (Table 1). The highest values of average similarity characterised the FEZ and the Intermediate level of trawling intensity (Table 1). At the FEZ the diet was dominated by gastropod molluscs, amphipods, and foraminifers, whereas decapod crustaceans, polychaetes and bivalve mollusc were dominant at Low trawling intensity. Molluscs gastropods *Retusa* sp. and bivalves Tellinidae dominated the diet at the Intermediate and High trawling intensity; the gastropods *Odostomia* sp. dominated the diet inside the FEZ (Tables 1 and 2). Crustaceans fragments (chelae and carapaces) were found at both FEZ and highly trawled areas. Polychaete Spionidae, Capitellidae, Maldanidae and Sternaspidae were more abundant inside the FEZ; Ampharetidae and Cirratulidae were present inside the stomach of fish at both FEZ and Intermediate disturbance (Tables 1 and 2). Otholits and the gobiid fish, *Lesueurigobius* sp., were most abundant at High trawling intensity (Table 2). Foraminifera showed the highest abundance inside the non-trawled gulf. The crustacean Gammaridae, and Cumacea together with the decapod *Alpheus glaber* were more abundant at FEZ. Phoxocephalidae and Tanaidacea showed not significant differences in abundance between FEZ and Intermediate trawling intensity (Tables 1 and 2).

## 4. Discussion

Our outcomes confirm the power of trawling disturbance in shaping the benthic community and in generating trawling-induced feeding patterns by removing, or adding, preferential

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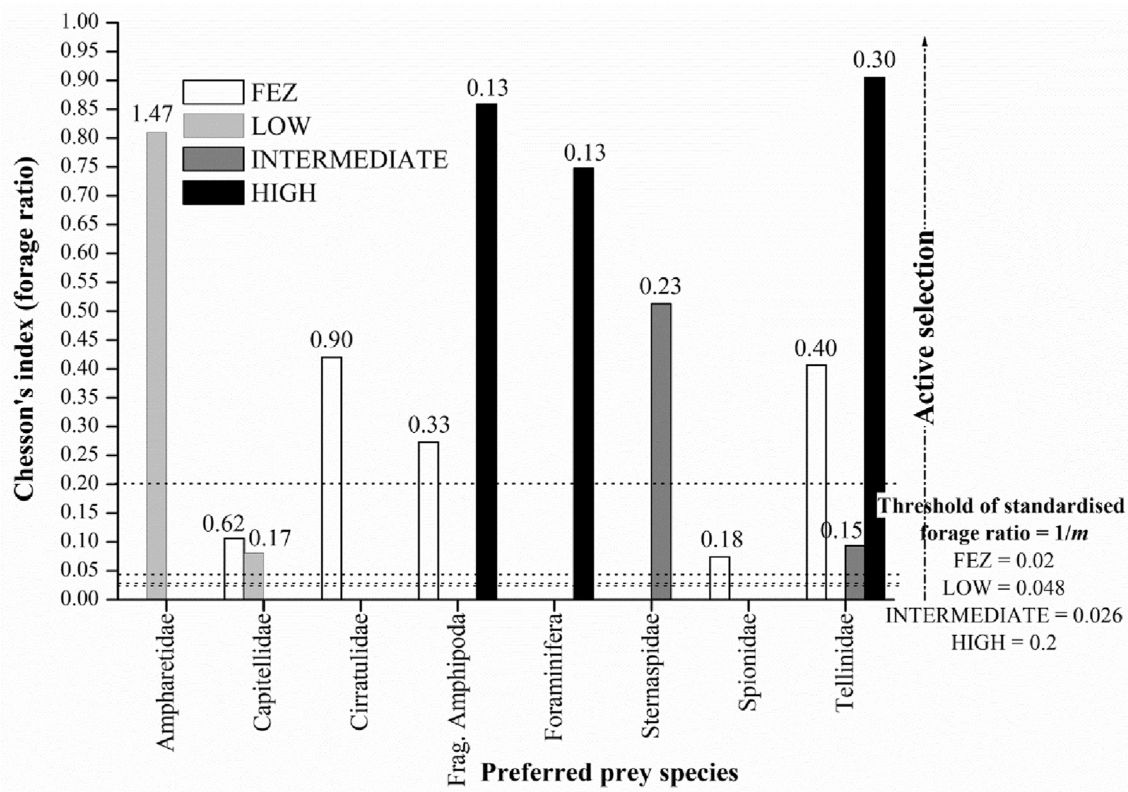


**Fig. 3.** Prey preferences (Chesson's index, $\alpha_a$) for the most common infaunal prey species at each trawling intensity category, the thresholds of standardised forage ratio $\alpha_a$ values at each trawling intensity category are reported (dotted lines). The mean density value for each prey in the environment per trawling intensity category is reported above each bar.

species on the diet of benthivorous fish, with a consequent effect on fish condition and the future of high valued fish stocks (*e.g.* red mullet; Hiddink et al., 2008, 2011, 2017; Johnson et al., 2015). The proposed bottom-up approach provided new insights into the indirect effect induced by trawling disturbance on fish populations mediated through diet, not previously reported in a Mediterranean context at a fishing ground scale. This direct link can trigger several cause-effect relationships along hierarchical levels, from species diversity to ecosystem functioning, with high repercussions on fish stock exploitation and fisheries sustainability (Cardinale et al., 2002; Hinz et al., 2017; Collie et al., 2017; Melnychuk et al., 2017).

The lowest value of morphometric condition at the highest trawling disturbance confirmed the detrimental effects exerted on fish growth resulting from a reduction of available prey and diversity of species. Moreover, by coupling a physiological index of condition, here we depicted significant difference between the non-trawled area and the intermediately trawled, potentially due to the plasticity in the digestive tract that adapts to the consumption of particular prey types. This change can be the result of a shift in diet from prey of different structure or size. The bivalves belonging to the Tellinidae family, for example, were the most frequently preyed-upon molluscs along the study area, preferred by the red mullet at three of the four levels of disturbance, but representing a primary sources of food in the heavily trawled areas. Overall, as previously observed by various authors discussing other benthivorous fish species diet within the Mediterranean basin (de Juan et al., 2007 *Citharus lingulata*; Fanelli et al., 2009, 2010 *Arnoglossus laterna* and *Pagellus erythrinus*; Sinopoli et al., 2012 *Merlucciu merluccius*), a general increase in the ingestion of small fish (gobiid fish, *Lesueurigobius* sp.) and otoliths was recorded at the fished site. The highest level of condition inside the non-trawled zone indicates, v*iceversa,* the presence of suitable habitat conditions with available food resources sustaining energy reserves. This latter trait is crucial to describe the future population success in term of growth, reproduction and survival (Lambert and Dutil, 2000; Lloret et al., 2013). Inadequate energy reserves under poorer condition levels, (*i.e.* under low and high trawling disturbance) might influence survival chances leading both to an increase of natural mortality and major vulnerability to predation and detrimental environmental change (*e.g.* parasites, increasing temperature and pollution; Wood et al., 2014; Bottari et al., 2016). Our evidence confirmed the FEZ as an effective measure in protecting benthic community's biodiversity that is able to sustain community heterogeneity and host healthier fish (Fanelli et al., 2011; Pipitone et al., 2014; Sciberras et al., 2015). Near-surface dwelling polychaetes belonging to the family Spionidae, which feed on freshly settled organic matter at or near the sediment surface, together with the sub-surface deposit-feeding Capitellidae and Maldanidae polychaetes, which ingest degraded organic matter within the sediment, were more abundant inside the FEZ which also represents a preferential source of food for the red mullet. Gammaridae and Cumacea filter and/or suspension feeders, which showed a higher sensitivity to trawling activities, were mostly found in the FEZ suggesting a well-structured and less disturbed community (Fanelli et al., 2009, 2011). The red mullet showed the ability to maximize the foraging efficiency by selecting available food resources, confirming an opportunistic feeding behaviour as showed by peaks of physiological condition and trophic descriptors at intermediate level of trawling disturbance (Machias and Labropoulou, 2002; Sieli et al., 2011).

Fish condition and trophic descriptor values at Intermediate trawling disturbance could also be interpreted in the light of the

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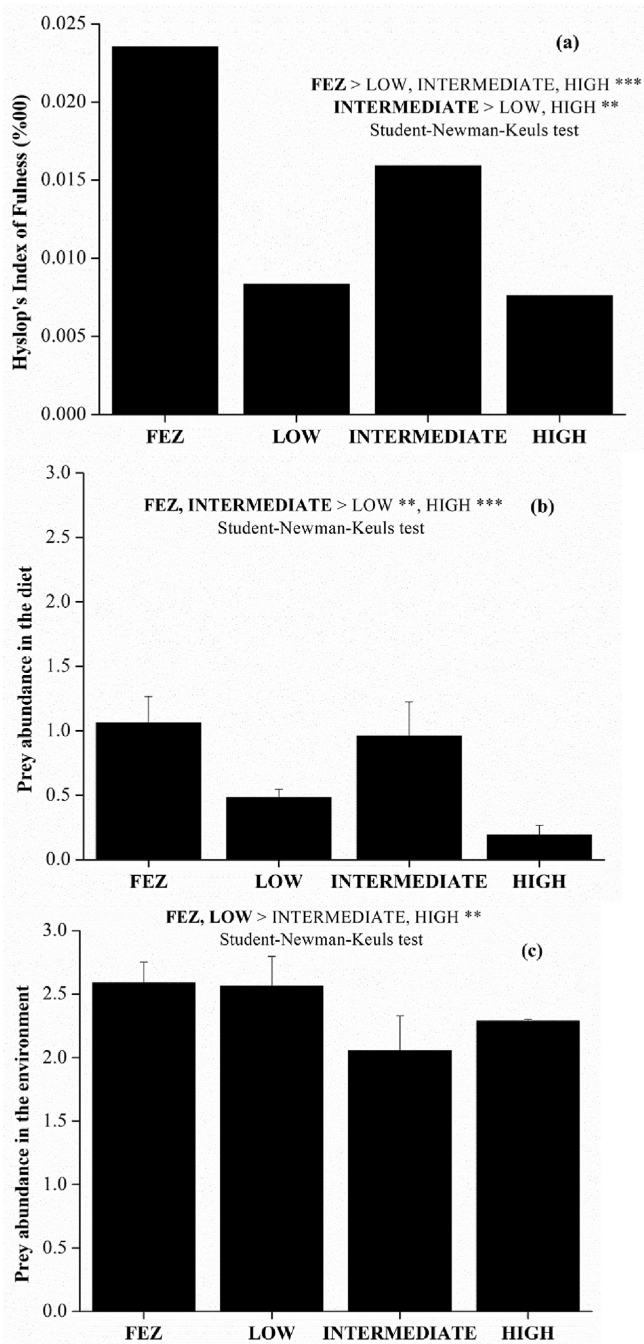


**Fig. 4.** The main feeding descriptors are reported: stomach fullness, Hyslop's Index (a); prey abundance in the stomachs (b); prey abundance in the environment (c). Abundance measurement are based on weights expressed in mg. Mean values were reported ± 95% CI (Confidence Interval), N = 360.

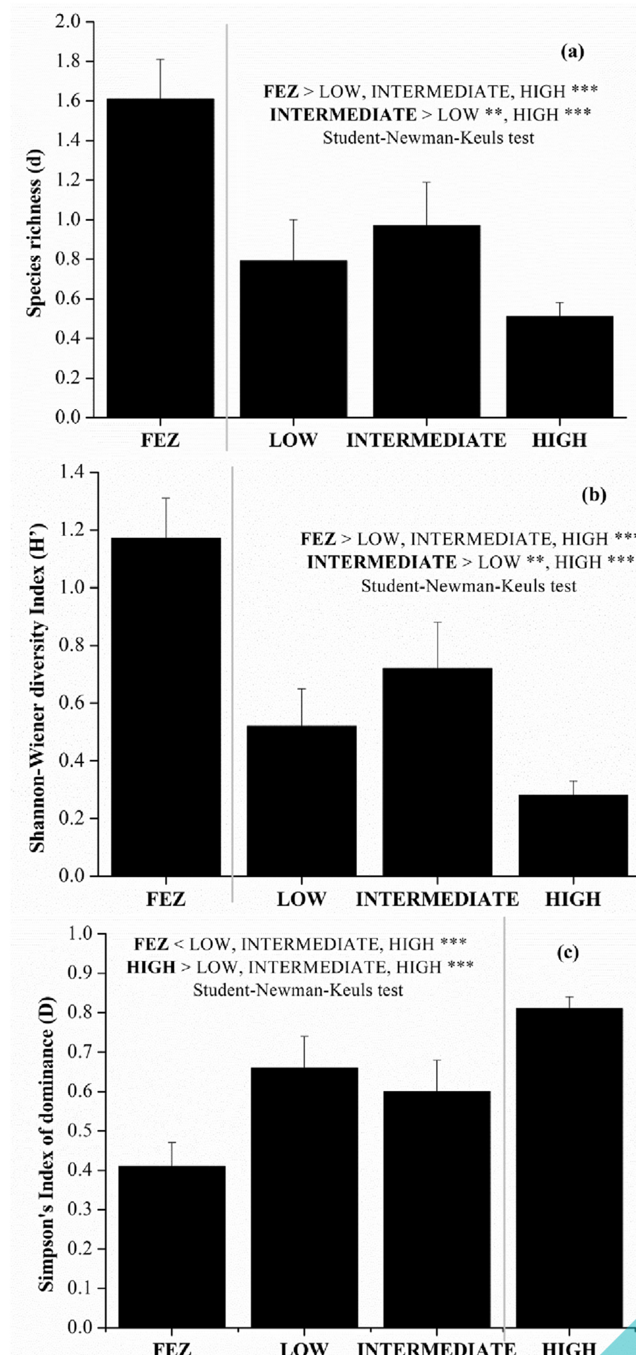


**Fig. 5.** Trends of the three selected diet diversity descriptors analysed along the gradient of trawling intensity: (a) Species richness, (b) Shannon-Wiener's diversity index H′ and (c) Simpson dominance D′. Mean values were reported ± 95% CI (Confidence Interval), N = 360.

IDH theory, in relating disturbance to community structure (*sensu* Connell, 1978) and the related alterations of competitive hierarchy theory (Veale et al., 2000). Although the IDH theory represents a pillar of ecological theory and may be important for the maintenance of biodiversity (Mackey and Currie, 2001; Kimbro and Grosholz, 2006; Svensson et al., 2012) data to support it in marine ecosystems are still limited (van Denderen et al., 2014). Nevertheless, our data showed a well-shaped classic IDH pattern with higher diversity at intermediate disturbance pressure. Thus, at an intermediate disturbance level, trawling could increase the availability of temporary variable extra-food sources which may be represented by the carrion and/or by an increasing recruitment rate, which are well supported by the IDH theory. The increase in diet diversity and richness can originate from the presence of opportunistic species (attracted or generated by the carrion) in comparison to other less or more trawled areas. Fragments of Amphipoda and Decapoda were found in stomachs from High trawling activity potential may result by a highest vulnerability to amphipods to trawling. This can be a good example of carrion source generated by the passage of the net and re-suspended and

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**Table 1**
SIMPER results.

| FEZ | Av. Abundance | Cont. % | LOW | Av. Abundance | Cont. % | INTERMEDIATE | Av. Abundance | Cont. % | HIGH | Av. Abundance | Cont. % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Retusa* sp. | 1.03 | 41.67 | Frag. Crustacea | 0.15 | 37.73 | Tellinidae | 0.59 | 54.68 | Tellinidae | 0.18 | 54.54 |
| Phoxocephalidae | 0.42 | 14.68 | Phoxocephalidae | 0.24 | 33.68 | *Retusa* sp. | 0.45 | 24.6 | Frag. Crustacea | 0.09 | 23.79 |
| Frag. Decapoda | 0.25 | 13.18 | Sternaspidae | 0.12 | 11.48 | Phoxocephalidae | 0.29 | 9.01 | Frag. Amphipoda | 0.08 | 13.67 |
| Foraminifera | 0.33 | 8.35 | Tellinidae | 0.08 | 4.39 | Sternaspidae | 0.09 | 2.01 | Foraminifera | 0.06 | 6.03 |
| Capitellidae | 0.25 | 3.88 | *Processa* sp. | 0.06 | 3.25 | Cirratulidae | 0.18 | 3.28 | Cirratulidae | NF | NF |
| Tellinidae | 0.19 | 3.03 | Cirratulidae | NF | NF | Ampharetidae | 0.21 | 2.44 | Ampharetidae | NF | NF |
| Sternaspidae | 0.16 | 2.78 | Ampharetidae | NF | NF | | | | | | |
| Frag. Amphipoda | 0.07 | 6.88 | | | | | | | | | |
| Cirratulidae | 0.14 | 2.07 | | | | | | | | | |
| Ampharetidae | 0.11 | 1.02 | | | | | | | | | |
| Av. Similarity: 16.41 | | | Av. Similarity: 6.17 | | | Av. Similarity: 12.23 | | | Av. Similarity: 7.88 | | |

Trawling intensity categories: FEZ = Fishery Exclusion Zone, no trawling intensity; LOW = 0.001–3 swept area/year; INTERMEDIATE = 3.001–6.5 swept area/year; HIGH = 6.5–32 swept area/year (swept area was evaluated on a sampling box of 1 $km^2$ cell size). NOTE: NF = Not Found species into the stomachs; Cont. % = Percentage contribution of each species; Av. Abundance = Average Abundance; Av. Similarity = Average Similarity. Cut off for low contributions: 90,00%.

**Table 2**
Ingested prey responses along the gradient of fishing intensity (ANOVA test).

| Prey | df | ANOVA test | p | Taxon | Student-Newman-Keuls post-hoc test |
|---|---|---|---|---|---|
| *Alpheus glaber* | 3 | F = 20.6 | <0.000 | C | FEZ > LOW, HIGH ***, INTERMEDIATE ** |
| Capitellidae | 3 | F = 11.65 | 0.001 | P | FEZ > LOW, HIGH ***, INTERMEDIATE ** |
| Cumacea | 3 | F = 15.26 | 0.002 | C | FEZ > LOW, INTERMEDIATE, HIGH ** |
| Foraminifera | 3 | F = 6.68 | <0.000 | F | FEZ > LOW, HIGH **, INTERMEDIATE *** |
| Gammaridae | 3 | F = 11.58 | 0.009 | C | FEZ > LOW, INTERMEDIATE, HIGH * |
| Maldanidae | 3 | F = 11.58 | 0.009 | P | FEZ > LOW, HIGH *, INTERMEDIATE ** |
| *Odostomia* sp. | 3 | F = 12.46 | 0.006 | M | FEZ > LOW, INTERMEDIATE * |
| Phoxocephalidae | 3 | F = 8.81 | 0.011 | C | FEZ > HIGH * |
| Spionidae | 3 | F = 15.36 | 0.002 | P | FEZ > LOW, HIGH * |
| Tanaidacea | 3 | F = 15.21 | 0.002 | C | FEZ > LOW, HIGH ** |
| *Retusa* sp. | 3 | F = 20.87 | <0.000 | M | FEZ, INTERMEDIATE > LOW, HIGH *** |
| Sternaspidae | 3 | F = 6.98 | 0.032 | P | FEZ, LOW > INTERMEDIATE * |
| Frag. Crustacea | 3 | F = 7.84 | 0.04 | C | LOW > INTERMEDIATE * |
| Frag. Decapoda | 3 | F = 24.82 | <0.000 | C | HIGH > FEZ, LOW, INTERMEDIATE *** |
| Frag. Amphipoda | 3 | F = 10.98 | 0.005 | C | HIGH > FEZ, LOW, INTERMEDIATE * |
| *Lesueurigobius* sp. | 3 | F = 14.48 | 0.005 | Fi | HIGH > FEZ, LOW, INTERMEDIATE * |
| Otholits | 3 | F = 10.33 | 0.003 | Fi | HIGH > FEZ, INTERMEDIATE, LOW * |
| Prey | | Kruskal-Wallis test | p | Taxon | |
| *Acanthocardia aculeata* | 3 | H = 9.08 | 0.028 | M | |
| Ampharetidae | 3 | H = 15.25 | 0.002 | P | |
| Cirratulidae | 3 | H = 11.63 | 0.009 | P | |
| *Crangon crangon* | 3 | H = 9.21 | 0.025 | C | |
| Glyceridae | 3 | H = 8.66 | 0.034 | P | |
| Lysianassidae | 3 | H = 12.15 | 0.007 | C | |
| Megalopa di Paguridae | 3 | H = 8.73 | 0.033 | C | |
| Nereididae | 3 | H = 8.52 | 0.02 | P | |
| Tellinidae | 3 | H = 22.58 | 0.000 | M | |
| *Timoclea* sp. | 3 | H = 9.01 | 0.021 | M | |

Abbreviation codes at the column "Taxon": M = Mollusca; C = Crustacea; P = Polychaeta; F = Foraminifera; Fi = Fish. Asterisks indicate different p-values: *p < 0.05, **p < 0.001, ***p < 0.0001.

release of damaged and doomed species on the seabed (Groenewold and Fonds, 2000; Kaiser and Hiddink, 2007; Mangano et al., 2015). These results represent a significant case study in the marine ecosystem, based over a large spatial scale relevant to trawling disturbance and on infaunal communities inhabiting muddy trawled seabed (Thrush and Dayton, 2002; Mackey and Currie, 2001; Kimbro and Grosholz, 2006; Svensson et al., 2012).

### 4.1. Synthesis and applications

Ecological studies can provide evidence-based information to help in deriving metrics, parameters or indicators to be used in models for the management of fisheries and their ecosystems. In this context, our outcomes can be used to inform proactive management strategies and dynamic monitoring plans of trawling activities, both in an EU context and at a regional level in the Mediterranean Sea. The community alteration generated by trawling disturbance mirrored by the proposed trait-tailored assessment (a bottom-up approach looking at individual level trait response - feeding behaviour - to detect trawling disturbance effects), allowed the observation of: *i)* an effective protection effects at the FEZ on benthic communities and the related beneficial effects on fish growth; *ii)* a detrimental effect of trawling disturbance at the lowest levels of disturbance by producing a loss of prey diversity and generating an emergence of more resilient fauna at the highest one; *iii)* an opposite increase of prey diversity due to chronic trawling practice and the related production of carrion (*i.e.* fragment of damaged species) at Intermediate disturbance.

The observed trawling induced patterns confirmed the value of VMS data analysis as a reliable tool to study and monitor the disturbance intensity distribution and the power of a species traits-based metrics comparable to the traditional metrics of diversity (Badalamenti et al., 2008; Coleman et al., 2015; Hiddink et al., 2011, 2017; Hinz et al., 2009, 2017; Lambert et al., 2014; Mouillot et al.,

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2013; van Denderen et al., 2015).

Following the Ecosystem-Based Fisheries Management principles and in line with the main European policies (*e.g.* Marine Strategy Framework Directive, Common Fishery Policy), here we support the importance of assessing the effectiveness of in-place spatial management measures in maintaining biodiversity hot spots and providing Essential Fish Habitats for numerous commercially exploited fish species by creating feeding grounds/patches able to sustain more healthy fish (Pikitch et al., 2004; Link, 2010; Caddy, 2014; Pipitone et al., 2014). Studies of dietary and fish condition shifts may provide useful insight during the assessment and monitoring steps of fishery management and conservation measures.

In conclusion, although linking individual conditions to biodiversity at community levels can represent a challenge (Stuart-Smith et al., 2013), species functional including life-history traits are useful in that scaling up process, from species to community to design spatial measures. On the other hand, altered patterns of food availability in the habitat, directly affecting the amount of energy reserves (*sensu* Kooijman, 2010) and may drive the energy flux towards somatic and reproduction maintenance as well as growth and reproduction allocation (Sarà et al., 2014). Insufficient food availability constrains the amount of energy available for vital processes, influencing individual performances, and this translates in increasing natural mortality, augmented chances of predation likelihood and a larger vulnerability to environmental stressors (Wood et al., 2014).


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