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Trawling disturbance effects on the trophic ecology of two co-generic Astropectinid species

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Abstract

Physical disturbance by trawling can have both negative and positive effects on populations of scavenging benthic organisms. In the present study the impact of fishing activity on feeding behaviour of the two Astropectinids, *Astropecten bispinosus* and *A. irregularis*, was assessed based on stomach contents analysis. The study was carried out along trawled seabed highlighting the positive response of the two facultative scavengers to carrion generated by trawl disturbance. Furthermore, there was greater food specialization in areas that were more heavily exploited by trawling. This specialisation could be linked to the availability of certain prey that results from the passage of fishing gears across the seabed. Interestingly, differences between the two species analysed have been highlighted in term of population dynamic, feeding rate, diet composition and diet diversity, testifying their capacity to coexist in the same fishing grounds.

Keywords: Scavengers, Stomach contents analysis, Energy subsidy, Vessel Monitoring System data, Ecosystem approach, Southern Tyrrhenian Sea.

Introduction

The spatial distribution of fishing activity can strongly influence benthic community structure in many continental shelf marine ecosystems (Collie *et al*., 2000; Kaiser *et al*., 2006; Lambert *et al*., 2014). Communities that are subjected to trawling activity become dominated by resilient fauna that are adapted to frequent trawling disturbance regimes, and tend to be characterised by opportunistic feeding organisms that have low vulnerability (Ramsay *et al*., 1998; Bergman & Santbrink, 2000; Demestre *et al*., 2000; Groenewold & Fonds, 2000; Kaiser *et al*., 2000; de Juan *et al*., 2007, 2011; Tyler-Walters *et al*., 2009). Previous studies have reported temporal aggregations of starfish in areas subjected to chronic trawling activity along the continental shelf of the Southern Tyrrhenian Sea (Mangano *et al*., 2013a, b). This aggregative response may be stimulated through the presence of additional carrion or other feeding opportunities or through the removal of competing species. Prompted by these observations, the present study examined the diet composition of two paxillosid astropectinids: *Astropecten bispinosus* (Otto, 1823) and *A. irregularis* (Pennant, 1977) (Fig. 1). These species belong to one of the most trophically specialized asteroid genera and are known to be both predatory and scavenging in behaviour throughout the world (Koehler, 1921; Tortonese, 1965; Sierra *et al*., 1978; Ramsay *et al*., 1997; Wells & Lalli, 2003; Southward & Campbell, 2006). Both starfish species usually dwell on sandy-muddy seabed habitats in the Mediterranean Sea where they feed primarily on infauna organisms buried in the sediment, particularly molluscs and crustaceans (Massé, 1963; Edwards, 1969; Christensen, 1970; Schwartz & Porter, 1977; Sloan, 1980). As for all the paxillosid starfish, these two Astropectinids have an intra-oral feeding mechanism, such that prey are ingested intact and remain in the stomach for a considerable period of time (Christensen, 1970; Beddingfield & McClintock, 1993). Therefore the stomach contents analysis of these invertebrates can provide reliable information on the diet of these starfish in a natural environment. Although the trophic biology of asteroids is an extensively studied topic, the majority of studies have focused on the feeding biology and strategy, and are primarily laboratory observations or direct observations restricted to shallow waters (for a comprehensive review see Jangoux, 1982 and references therein).

The present study was performed in a commercial fishing ground characterised by highly aggregated fishing intensity ascertained from an *a posteriori* evaluation of Vessel Monitoring System (VMS) data analysis. As prey availability can vary with depth and season (Christensen,

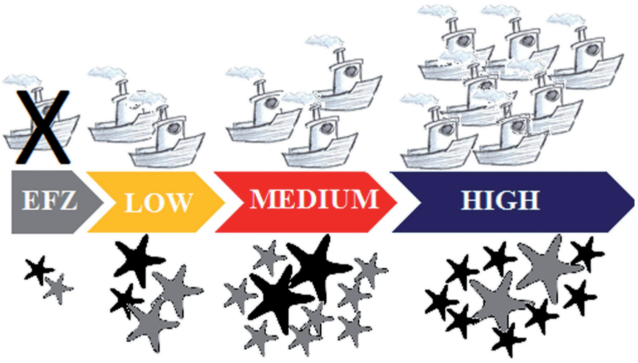

Fig. 1: Conceptual model. Astropectinids aggregation along the detected gradient of fishing intensity. *A. bispinosus* (grey starfish) assemblages are most abundant at medium fishing intensity, specimens with highest dimension populated the most heavily trawled areas and *vice versa* for *A. irregularis* (dark starfish). Fishing intensity categories: EFZ (grey) = no fishing intensity, LOW (yellow) < 3, MEDIUM (red) = 3 – 6.5, HIGH (blue) = 6.5 – 32 swept area/year.

1970; Brun, 1972; Massé, 1975; Morin *et al*., 1985; Freeman *et al*., 2001), hence in the present study the analysed samples were selected within the same bathymetric range during springtime. To investigate and compare the effects of commercial trawling along the different regimes of exploitation, samples were selected from a dataset of two years of otter trawl experimental surveys. The sampled area also encompassed an undisturbed portion of the continental shelf inside the Gulf of Patti which is a Fishery Exclusion Zone where trawling activity has been banned for 25 years. The presence of this closed area provided a robust control area for comparative purposes (Collie *et al*., 1997; Ball *et al*., 2000; Mangano *et al*., 2013b).

To date, several studies on the diet of fish that prey on benthic organisms have been used to infer changes in prey availability and feeding strategies that may arise as a result of fishing activities (Frid & Hall, 1999; Hinz *et al*., 2005; Shephard *et al*., 2010; Hiddink *et al*., 2011; van Denderen *et al*., 2013; Muntadas *et al*., 2014). Here, we tested the hypothesis that bottom trawling affects the diet of benthivorous organisms by altering food availability and generating a positive response of facultative scavengers to carrion. Benthic scavengers feeding on the benthic community that results from the effects of trawling might represent cost-effective samplers, hence diet studies may provide insights into the trophic consequences of such community changes for other components of the ecosystem (Link, 2004; Dell *et al*., 2013; Johnson *et al*., 2015).

Materials and Methods

Study area and sampling design

Starfish were collected from fishing grounds along the continental shelf off the Northern Sicilian coast from Capo Milazzo (Messina) to Capo Gallo (Palermo), in the Southern Tyrrhenian Sea (Fig. 2). Starfish were sampled from inside the Fishery Exclusion Zone of the Gulf of Patti (Messina) (Regional Law N. 25/90). The study area extended across a total of 708 km^2 on the continental shelf within the 80 to 180 m depth contour. Sediment composition is homogeneous across this area of the seabed, such that the percentage of mud contents is predominant > 80%. Sand and silt fractions are similar to each other at concentration of 10% (Mangano *et al*., 2014). Individuals of the two starfish species were sorted from the catch of otter trawl samples collected as part of experimental surveys (Italian National Research Council, BIOTRI research projects). Starfish were selected at random to ensure that the full size range of animals were represented in the analyses. The otter trawl hauls were carried out from dawn to dusk and had an average duration of approximately an half an hour; the vessel speed was maintained at 2.5 – 3.0 knots. The horizontal and vertical opening of the net was measured by the SCANMAR acoustic system. Thus the swept area was ascertained from the distance towed (measured from GPS) and the mouth aperture of the net. An experimental otter trawl net, with double warps and 20mm stretched mesh size in the cod-end was deployed on board of the Italian Research Vessel (RV) G. Dallaporta. A gear with the same features of an OTMS (Otter Trawl Maireta System gear) was designed *ad hoc* having the main characteristics of the conventional commercial gears commonly used in the Mediterranean basin. The net was designed to catch the violet shrimp *Aristeus antennatus* which is the main target species for the local fleet. Previous studies have demonstrated that this net is an effective sampler of deep-sea megafauna (Sardà *et al*., 1998).

The analysis of population structure and stomach contents of the two starfish species were carried out from a total of twelve hauls selected from the total survey, in order to achieve the minimum statistical number of specimens necessary to obtain a reliable analysis (Underwood, 1997). For each sampling site we calculated fishing intensity values *a posteriori* from the analysis of VMS data.

Estimation of fishing intensity

The estimation of trawling intensities and the spatial distribution of fishing activity was derived using Vessel Monitoring System (VMS) data recorded during the year 2012 for bottom otter trawlers (OTB) operating in the territorial waters of the Southern Tyrrhenian Sea. VMS position, time, speed and anonymous vessel identification data included Italian vessels ≥ 12 m operating on the study area (Council Regulation N. 1224/2009). During the first phase of processing, the data were screened to remove inaccuracies and duplicate records and records close to port (Lee *et al*., 2010). The calculation of fishing intensity was restricted to speeds > 2 and ≤ 4 knots (Piet *et al.*, 2007; Lambert *et al.*, 2012). All analyses were conducted using the VMStools package in R (Hintzen *et al.*, 2012). Fishing intensity was calculated for each year by estimating the area swept by point summation of VMS data on a grid cell size of 1 km × 1 km (Lambert *et al.*, 2011). The point summation technique consists of summing the area swept attributed to each VMS point in a defined cell. VMS position records were projected into the Universal Transverse Mercator (UTM) geographic coordinates system. The sum of the area trawled in each 1 km^2 cell was represented with ArcGIS 9.3, giving the actual fishing frequency per annum (Fig. 2). A more detailed description of considered parameters is given in Mangano *et al.* (2014).

Sampling processing

In each of the twelve selected hauls the number of *Astropecten bispinosus* and *A. irregularis* was recorded and the average abundance was determined and standardised to numbers per km^2. Starfish were preserved in 70% ethanol for subsequent analysis. In the laboratory, a total of 655 *A. bispinosus* and 544 *A. irregularis* were individually measured. The size, in term of radius length between the mouth and the tip of the longest arm of each starfish, was measured to the nearest 0.1 mm using vernier callipers. Each starfish was individually weighed twice, before and after dissection, to the nearest 0.001 g. The measure of weight before the dissection gave us information about the biomass of individuals, whereas the difference of weight recorded before and after dissection was considered as a measure of the weight of the stomach contents. Stomach contents were preserved in 70% ethanol for later analysis.

A sub-sample of extracted stomachs, belonging to 30 individuals of the two species for each haul, was analysed in terms of species composition and quantity. A total of 360 stomach contents for each species were analysed. The percentage of total empty stomachs in each haul was recorded as an indicator of feeding intensity. Food items for each stomach were sorted and identified to the lowest taxonomic level possible; unidentifiable contents were excluded. The identified prey were counted and their relative percentage of occurrence in terms of percentage of numeric abundance, N%, was evaluated for diet composition analysis (%N, abundance of prey per total abundance of recorded prey at each fishing intensity category). We also expressed the species composition in terms of the total number of individuals, the total number of species and species diversity for the stomach contents. These parameters were analysed in relation to fishing intensity at each of the sampling sites.

Data analysis

All the statistical analyses were performed separately for each of the two sampled starfish species. Average abundance, individual biomass, stomach weight and percentage of occurrence of empty stomachs were statistically tested with univariate analysis using a one-way analysis of variance (ANOVA) test after checking that the data conformed to the necessary assumptions regarding homogeneity of variance and normality. Prior to performing the tests for significance, the twelve sample sites were grouped into four fishing intensity categories (three for each). Fishing intensity was expressed as the number of times an area of seabed was swept/year for each 1 km^2 cell and was grouped into four categories:

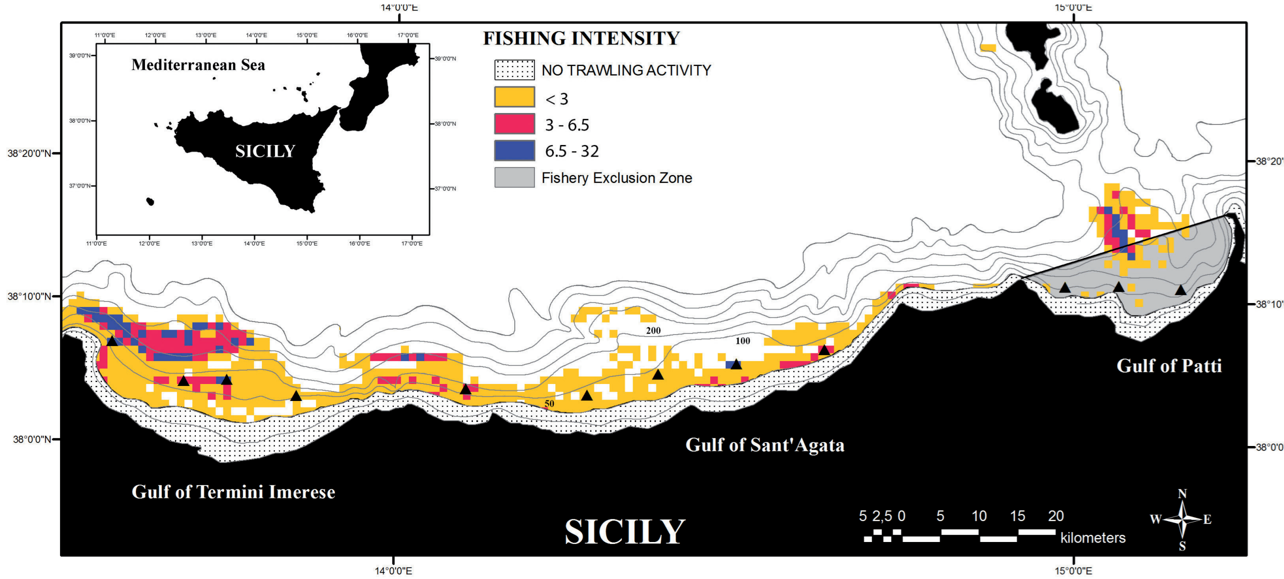

Fig. 2: Location of the study area and spatial distribution of sample sites (black triangles) within the investigated fishing grounds. Fishing intensity categories: EFZ (grey) = no fishing intensity, LOW (yellow) < 3, MEDIUM (red) = 3 – 6.5, HIGH (blue) = 6.5 – 32 swept area/year. Notes: the stippled band represents the depth range closed to otter trawl fishing activity at national level; the black line in front of the Gulf of Patti delineates the seaward limit of the extension of the Fishery Exclusion Zone.

zero (no fishing), low < 3 times swept area/year, medium from 3 to 6.5 times swept area/year, high from 6.5 to 32 times swept area/year.

The size distribution of starfish (based on radial arm length) in relation to fishing intensity was undertaken using the non-parametric Kolmogorov-Smirnov Test at $p < 0.05$. The two-sample Kolmogorov-Smirnov test uses the maximal distance between cumulative frequency distributions of two samples to test significant similarity.

Differences between the diet composition of each species of starfish at each category of fishing intensity were assessed using multivariate techniques using the PRIMER (v.6) software package. A similarity matrix was computed using the Bray-Curtis similarity index computed from the abundance data after four-root transformed to down weight the influence of extremely abundant species. Differences in stomach contents species composition were related to fishing intensity categories and tested for significant differences using an Analysis of Similarity (ANOSIM) test. A categorical approach was adopted to improve the statistical power to detect the effect of fishing. A Similarity Percentage (SIMPER) routine was run to determine the species that contributed mostly to the similarity dissimilarity for those stomachs that experienced the same (categorical) fishing intensity. An ANOVA test was performed to test differences on diet composition, testing the percentage of numeric abundance of prey ingested along fishing intensity gradient. Similarly categorical approach and ANOVA test were used to ascertain diet diversity testing for the three indices: number of species collected inside the stomach (S), number of preys (N) and Shannon's index diversity (H'). Prior to perform the ANOVA test the statistical assumptions required by the test were tested using Anderson-Darling and Levene's tests, respectively for normality and homogeneity of error variance, the indices were $\log_{10}(x + 1)$ transformed when necessary. The non-parametric Kruskal-Wallis test was performed on untransformed data to determine significant differences between fishing intensity categories when the normality assumptions were not achieved. The Tukey's *post hoc* multiple comparison test was undertaken to detect significant pairwise differences among the analysed factor when a significant interaction term was obtained ($p < 0.05$).

Results

VMS data

The fishing intensity distribution across the study area showed that fishing behaviour was highly aggregated presumably in relation to the distribution of the target species, the historical patterns of performance and the regulatory restrictions (Fig. 2). The heavy fishing pressure aggregation is mainly located in proximity to the portion of the slope in front of the Gulf of Termini Imerese (Palermo) and outside the Gulf of Patti (Messina). Other areas had a steady lower level of exploitation (e.g. the Gulf of Sant'Agata, Messina).

Astropecten bispinosus

The average abundance, individual biomass and stomach weight differed significantly with fishing in-

Table 1. Results of the one-way ANOVA on the three population descriptors: average abundance, individual biomass and individual stomach weight with fishing intensity set as a factor. Post-hoc multi-comparison Tukey's test results are presented, asterisks indicate p values: * p < 0.05, ** p < 0.01, *** p < 0.001. Log indicate that data were Log 10(x+1) transformed. Non-parametric Kruskall-Wallis test on the three diet diversity descriptors: number of ingested prey (N), Shannon's diversity index (H') and number of species ingested.

Astropecten bispinosus				
	d.f.	F	p	Tukey's test
Abundance Log	3	9.66	p = 0.016	MEDIUM > EFZ, LOW, HIGH *
Biomass Log	3	13.34	p < 0.001	LOW, HIGH > EFZ ***; LOW > MEDIUM **; HIGH > MEDIUM ***
Stomach weight Log	3	13.71	p < 0.001	EFZ > MEDIUM *; LOW > MEDIUM ***; LOW > HIGH *; HIGH > MEDIUM **
	d.f.	H	p	
N. of ingested prey N	3	19.02	p < 0.001	-
Shannon's diversity H'	3	17.14	p < 0.001	-
N. of ingested species S	3	1.57	p = 0.673	-
Astropecten irregularis				
	d.f.	F	p	Tukey's test
Abundance Log	3	9.02	p = 0.024	HIGH > MEDIUM, LOW, EFZ *
Biomass Log	3	66.48	p < 0.001	LOW, MEDIUM, HIGH > EFZ***; MEDIUM > LOW, HIGH***
Stomach weight Log	3	23.74	p < 0.001	MEDIUM > EFZ, LOW, HIGH***
	d.f.	H	p	
N. of ingested prey N	3	41.65	p < 0.001	-
Shannon's diversity H'	3	50.09	p < 0.001	-
N. of ingested species S	3	25.46	p < 0.001	-

tensity (Table 1, Fig. 3). *A. bispinosus* occurred at the highest abundance at the medium level of fishing intensity with an average of 4062 Ind/km^2 whereas the lowest value (837 Ind/km^2) was recorded inside the unfished area in the Fishery Exclusion Zone in the Gulf of Patti. Mean individual biomass reached the highest values at low and high fishing intensity areas. The mean individual stomach weight was lowest at medium fishing intensity compared with all the other categories, moreover low fishing intensity areas had significantly higher values than the high fishing intensity areas. The smallest starfish were collected at medium fishing intensity sites, whereas the dimension of starfish in all the other categories was similar (Table 2). The distribution frequencies of radius length at each category of fishing intensity was significantly different between, zero and low, zero and medium, low and medium and medium and high fishing intensity (Table 3, Fig. 4). The percentage of empty stomachs was consistent along the gradient of fishing intensity (ANOVA Test, $F_{1,4} = 0.72$, $p = 0.49$).

The Analysis of Similarity (ANOSIM) test suggested the presence of significant differences between diets re-

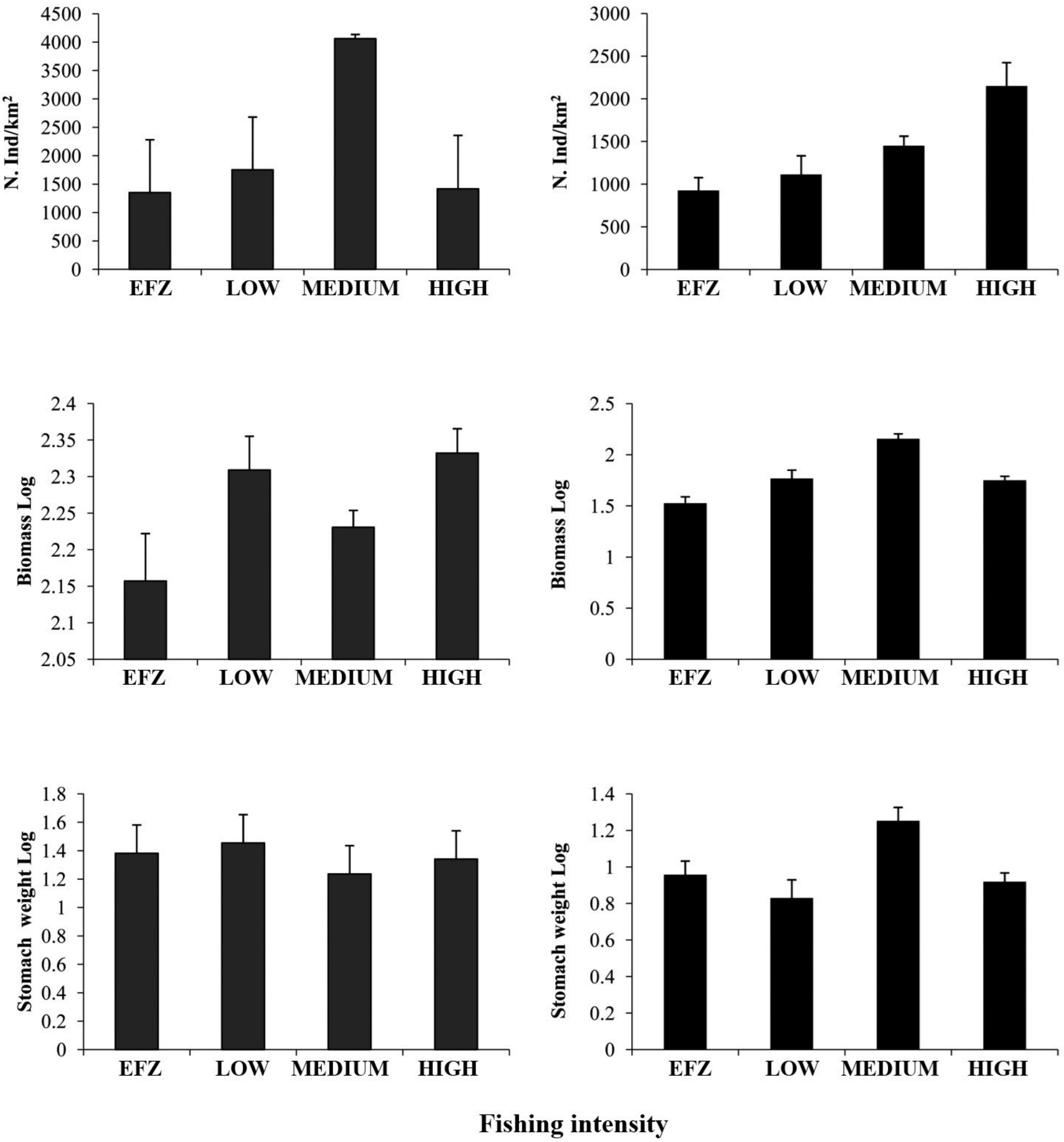

Fig. 3: Trends of the three population descriptors (mean±C.I.): average abundance, individual biomass and individual stomach weight along the investigated fishing intensity gradient. Grey histograms represent values for *Astropecten bispinosus*; black histograms represent values for *A. irregularis*. Log indicate that data were Log 10(x+1) transformed.

Table 2. Basic statistical analysis measures of radius length.

RADIUS LENGTH *ASTROPECTEN BISPINOSUS*					
Fishing intensity	N	Mean	Median	Q1	Q3
EFZ	54	27.07	27	22.75	30
LOW	102	28.265	27.5	23	32
MEDIUM	329	25.894	25	22	29
HIGH	170	29.141	27	25	33
Radius length ***Astropecten irregularis***					
Fishing intensity	N	Mean	Median	Q1	Q3
EFZ	81	13.647	14	11	16
LOW	89	17.539	18	13	22
MEDIUM	116	24.241	25	19	27
HIGH	258	17.143	15	13	22

Table 3. Comparisons of radius length frequencies at the categories: of fishing intensity two-sample Kolmogorov-Smirnov test results (K-S Test at p < 0.05, significant values in bold).

Kolmogorov-Smirnov Test		
Astropecten bispinosus		
Fishing intensity	K-S test Statistic	K-S Critical value
EFZ - LOW	**0.378**	0.219
EFZ - MEDIUM	**0.738**	0.207
EFZ - HIGH	0.273	0.185
Low - MEDIUM	**0.411**	0.191
Low - HIGH	0.14	0.167
Medium - HIGH	**0.489**	0.152
Astropecten irregularis		
Fishing intensity	K-S test Statistic	K-S Critical value
EFZ - LOW	0.188	0.228
EFZ - MEDIUM	0.157	0.199
EFZ - HIGH	0.161	0.212
LOW - MEDIUM	**0.216**	0.154
LOW - HIGH	0.143	0.17
MEDIUM - HIGH	**0.191**	0.128

lated to fishing intensity categories ($R = 0.247$; $p < 0.001$) (all pairwise comparisons significant, $p < 0.05$). A list of species that contributed most to the similarity in the species composition of the diet at each fishing intensity category is presented in Table 4. The gastropods pyramidellids *Odostomia* sp. and *Eulimella* sp. together with the murchisonellids *Ebala* sp. contributed most to the average similarity of diet irrespective of fishing intensity. The diet was composed mainly of gastropods, whereas the megalopa of Crustacea were found at low intensity fishing sites and in the unexploited areas. The greatest average values of dissimilarity were recorded between the zero and low fishing intensities with the highest (respectively 86.74 and 85.44). The presence of some of the species found in the stomach contents changes significantly along the gradient of fishing intensity. The Gastropod *Cerithium* sp. and the crustaceans, Mysidae and Cumacea, were found most often inside the stomachs contents of starfish collected within the un-trawled Fishery Exclusion Zone. The diet of *Astropecten bispinosus* at low disturbed areas was composed of the highest percentage of the bivalve *Corbula gibba* and the gastropod *Odostomia* sp. The occurrence of otoliths, in particular otoliths of the gobiid *Lesueurigobius friesii* together with the bivalve *Nucula nucleus* have characterised the diet of starfish in medium fishing intensity areas. The gastropods *Eatonina* sp. and *Weinkauffia* sp. were more abundant in the diet of starfish collected from the high intensity fishing area (Table 5). The occurrence of otoliths in the diet coincided at sites with the highest levels of fishing intensity and were absent from stomachs in the un-trawled areas.

Only two of the three investigated indices of diet diversity have been significantly different along the fish-

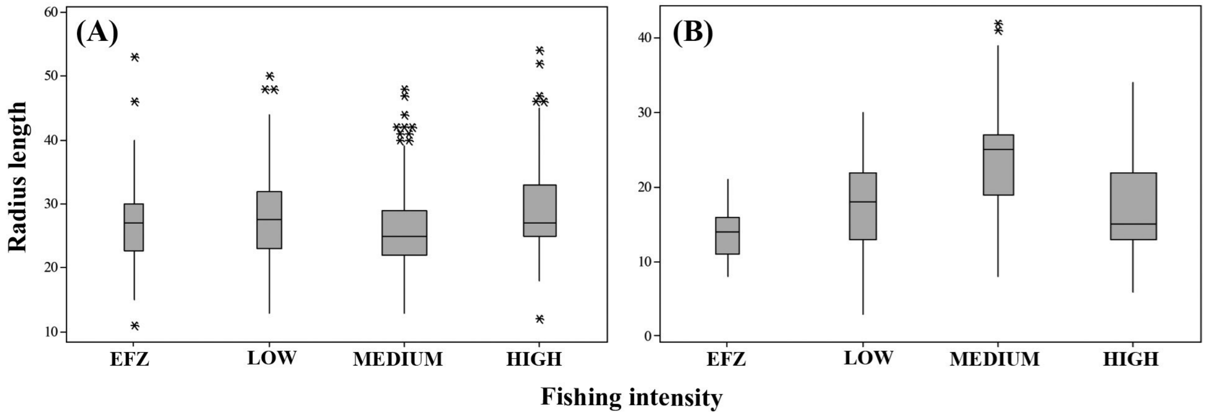

Fig. 4: Frequency distributions, median and the lower and upper quartiles, of Radius length measure, respectively *A. bispinosus* (A) and A. irregularis (B) (the box plot width reflect the number of points in the given group or sample, asterisk represent the outliers).

ing intensity gradient. The number of ingested prey was highest in more exploited areas where in opposition the Shannon's diversity index reached the lowest value (Table 1, Fig. 5).

Astropecten irregularis

Mean abundance, individual biomass and individual stomach weight all varied significantly with fishing intensity. *Astropecten irregularis* was significantly more abundant in areas with the highest values of fishing intensity (Table 1, Fig. 3), with an average of 2150 Ind/km^2. The lowest value (925 Ind/km^2) was recorded inside the undisturbed area, the Fishery Exclusion Zone. The individual biomass was generally highest in proximity to the disturbed area, reaching the highest values at medium fishing intensity category. Similarly the measure of individual stomach weight showed the highest values occurred at medium fishing intensity. The maximum size, radius length measure, was recorded for starfish collected at medium fishing intensity sites, whereas starfish the smallest starfish were founded in the undisturbed area (Table 2, Fig. 4). The comparison of radius length frequencies distribution at each category of fishing intensity revealed significant differences between low and medium and medium and high fishing intensity sites (Table 3). The percentage of empty stomachs was significantly different along the gradient of fishing intensity (ANOVA Test, $F_{1,4}$= 6.21, p = 0.05). Analysis of Similarity (ANOSIM) suggested the presence of significant differences in diet composition that was related to fishing intensity (R = 0.281; p < 0.001) (all pairwise p < 0.05). A list of species that contributed most to the similarity of diet at each category is presented in Table 4. In general along the investigated categories of fishing intensity the gastropods more than the bivalves contributed to the internal similarity. Interestingly fragments of crustaceans were an important contributor to the diet at the medium fishing intensity site. The bivalve *Kelliella miliaris* was

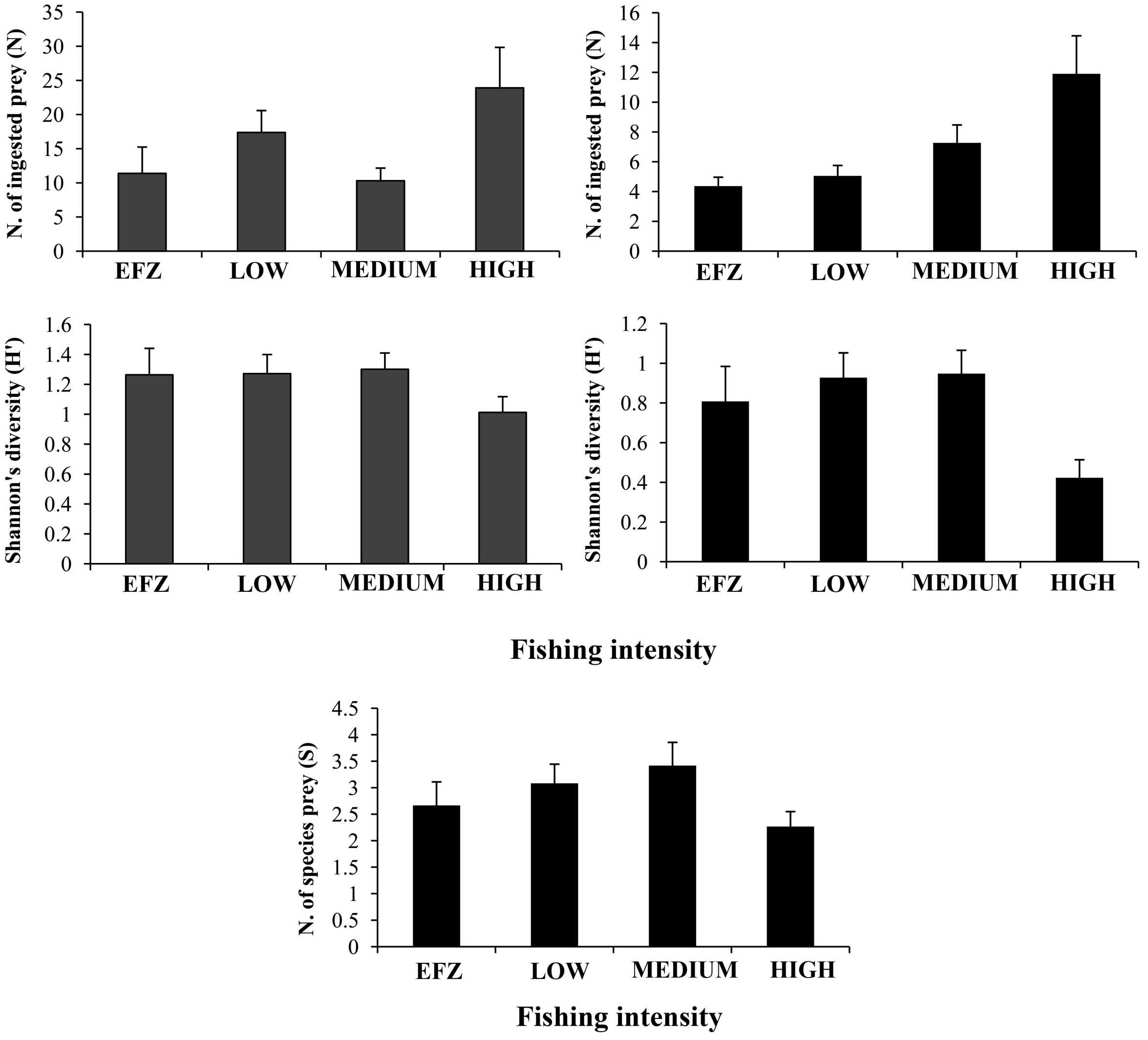

Fig. 5: Trend of the diet diversity descriptors (mean±C.I.): number of prey ingested (N), Shannon's diversity index (H') and number of species ingested (S) along the investigated gradient of fishing intensity. Grey histograms represent values for *Astropecten bispinosus*; black histograms represent values for *A. irregularis*.

Table 4. Output from a SIMPER analysis showing those species that contributed to 90% to the similarity for sites within each of the different fishing intensity categories respectively *A. bispinosus* left and *A. irregularis* right side.

Astropecten bispinosus	Av. Density	Con. %	Code	***Astropecten irregularis***	Av. Density	Con. %	Code
EFZ				**EFZ**			
Average similarity: 14.55				Average similarity: 29.16			
Ebala sp.	0,64	25,98	Ga	*Kelliella miliaris*	0.9	81.35	Bi
Asterigerinidae	0,49	18,92	Fr	*Eatonina* sp.	0.31	7.62	Ga
Eulimella sp.	0,42	18,69	Ga	*Alvania testae*	0.21	3.6	Ga
Odostomia sp.	0.23	5.45	Ga				
Cerithium sp.	0.29	5.42	Ga				
Turritella communis	0.17	2.48	Ga				
Diastylidae	0.13	2.58	Cr				
Mysidae	0.17	2.46	Cr				
Retusa sp.	0.2	2.01	Ga				
Weinkauffia sp.	0.17	1.59	Ga				
Miliolidae	0.16	1.74	Fr				
Megalopa of Xanthidae	0.13	1.6	Cr				
Pandora pinna	0.14	1.55	Bi				
Low	Av. Density	Con. %	Code	**Low**	Av. Density	Con. %	Code
Average similarity: 17.97				Average similarity: 13.42			
Eulimella sp.	0.96	49.61	Ga	*Kelliella miliaris*	0.46	41.00	Bi
Diastylidae	0.29	5.87	Cr	*Odostomia* sp.	0.29	17.31	Ga
Asterigerinidae	0.29	5.83	Fr	*Eatonina* sp.	0.32	16.02	Ga
Odostomia unidentata	0.39	5.73	Ga	Diastylidae	0.19	5.01	Fr
Ebala sp.	0.25	4.6	Ga	*Hyala vitrea*	0.16	3.81	Ga
Odostomia silesui	0.27	3.64	Ga	*Eulimella* sp.	0.13	2.56	Ga
Ebala pointeli	0.26	3.29	Ga	Miliolidae	0.12	2.1	Fr
Miliolidae	0.25	3.28	Fr	*Antalis panorma*	0.1	1.64	Sc
Odostomia turrita	0.24	2.65	Ga	*Acanthocardia aculeata*	0.09	1.39	Bi
Caecum clarkii	0.23	1.93	Ga				
Megalopa of Liocarcinidae	0.18	1.87	Cr				
Cerithium sp.	0.16	1.84	Ga				
Medium	Av. Density	Con. %	Code	**Medium**	Av. Density	Con. %	Code
Average similarity: 27.96				Average similarity: 17.18			
Eulimella sp.	1.08	48.01	Ga	*Kelliella miliaris*	0.61	35.71	Bi
Ebala sp.	0.62	18.21	Ga	*Eulimella* sp.	0.51	29.67	Ga
Diastylidae	0.45	11.85	Cr	*Antalis panorma*	0.29	7.94	Sc
Asterigerinidae	0.36	5.17	Fr	Diastylidae	0.21	5.65	Fr
Odostomia sp.	0.23	3.2	Ga	*Ebala* sp.	0.2	4.25	Ga
Turritella communis	0.24	2.76	Ga	*Odostomia* sp.	0.18	3.37	Ga
Eatonina sp.	0.21	1.83	Ga	*Odostomia turrita*	0.17	2.66	Ga
				Crustacean fragments	0.13	2.55	Ga
High	Av. Density	Con. %	Code	**High**	Av. Density	Con. %	Code
Average similarity: 19.75				Average similarity: 51,25			
Ebala pointeli	0.96	32.34	Ga	*Kelliella miliaris*	1.58	96	Bi
Eulimella sp.	0.48	13.82	Ga				
Ebala sp.	0.5	11.75	Ga				
Asterigerinidae	0.45	11.57	Fr				
Odostomia sp.	0.33	7.39	Ga				
Retusa sp.	0.29	4.44	Ga				
Turritella communis	0.24	4.16	Ga				
Bittium submamillatum	0.26	3.72	Ga				
Diastylidae	0.19	1.91	Cr				

Abbreviation codes: Av. Density = average density (N/km^2), Con. % = percentage contribution, Bi = Bivalves, Cr = Crustacean, Fr= Foraminifera, Ga = Gastropods, Sc = Scaphopods.

the species mostly frequently found at each fishing intensity category. Overall the recorded values of average similarity have been low and only a reduced numbers of species accounted for the similarity values. The highest value of similarity was recorded at high category of fishing intensity in which *Kelliella miliaris* contributed to the 96% of similarity. The average dissimilarity was highest when comparing the zero and low fishing intensities with the highest (respectively 83.94 and 81.19). The analysis of stomach contents along the gradient of fishing intensity showed that the two bivalves *Kelliella miliaris* and *Timoclea ovata* were more abundant in the stomachs collected at low fishing intensity disturbance, as well as the three gastropods pyramidellids *Odostomia* sp., *O. nitens* and *O. unidentata*. The gastropod *Turritella communis* was most abundant in the diet of starfish collected at the highest intensity fished area (Table 5).

The three indices of diet diversity all differed significantly along the fishing intensity gradient (Table 1, Fig. 5). The number of species ingested (S) was highest at medium fishing intensity site, whereas the number of prey ingested (N) was highest at high fishing activity where Shannon Wiener diversity was lowest.

Discussion

Although co-occurrence of the different species of the genus Astropecten has been previously documented on shallow sandy ground in the Mediterranean Sea (Massé, 1966; Ribi *et al*., 1977; Sierra *et al*., 1978; Schmid & Schaerer, 1981; Baeta & Ramon, 2013), similar relationship was never tested at the continental shelf depths on muddy ground and, more interestingly niche partitioning phenomena have never been tested along fishing grounds. Bottom-trawl fishing generates a range of different carrion resources that may provide energy subsidies for some species but not others (Ramsay *et al*., 1997, 1998). The partitioning of different resources can allow the co-existence of similar species (Hutchinson, 1959; Menge & Menge 1974; Schoener 1982; Garneau *et al*. 2007), whereas trawling disturbance may disproportionately favour one species over another forcing species to adapt their feeding strategies to avoid competition in a new scenario (Conceptual model, Fig. 1). In relation to trawl intensity the two species showed a highly opportunistic feeding strategy and co-occurred at all sites by showing differences in their diet preferences (Ribi *et al*., 1977) and shifting in size-frequency distributions. Our results support the hypothesis that bottom trawling affects the fitness of benthivorous organisms by altering the food availability and generating a positive response of facultative scavengers to carrion (Demestre *et al.,* 2000; Link, 2004; Dell *et al*., 2013; Johnson *et al*., 2015).

The presence of individuals of *A. bispinosus* of a larger body size at heavily exploited areas may be explained by the deeper burrowing behaviour of this species (Ribi *et al*., 1977). In addition, *A. bispinosus* appeared to be more robust than *A. irregularis* and appeared to sustain

Table 5. One-way ANOVA test of the responses of preyed species to different levels of fishing intensity. Post-hoc multi-comparison Tukey's test results are given, asterisks indicate p values: * p < 0.05, ** p < 0.01, *** p < 0.001. Log indicate that data were Log 10(x+1) transformed.

Astropecten bispinosus	F	d.f.	p	Tukey's test	Code
Cerithium sp.	7.19	3	< 0.05	EFZ > HIGH*	Ga
Corbula gibba	9.06	3	< 0.05	LOW > EFZ*	Bi
Crustacean fragment Log	10.69	3	< 0.05	MEDIUM > LOW*	Cr
Cumacea Log	17.76	3	< 0.01	EFZ > LOW, HIGH**; EFZ > MEDIUM*	Cr
Eatonina Log	15.5	3	< 0.05	MEDIUM > HIGH*	Ga
Mysidae Log	12.76	3	< 0.05	EFZ > LOW*	Cr
Nucula nucleus	6.9	3	< 0.05	MEDIUM > HIGH*	Bi
Odostomia sp	13.04	3	< 0.05	LOW > EFZ, HIGH*	Ga
Otolith of *Lesueurigobius friesii* Log	31.89	3	< 0.01	MEDIUM > LOW, HIGH***	Fs
Otolith	7.12	3	< 0.05	MEDIUM > LOW, HIGH*	Fs
Weinkauffia sp. Log	14.85	3	< 0.01	HIGH > LOW, MEDIUM*	Ga
Astropecten irregularis	**F**	**d.f.**	**p**	**Tukey's test**	**Code**
Kelliella miliaris	16.26	3	< 0.001	LOW > EFZ, MEDIUM*; LOW > HIGH**	Bi
Odostomia sp.	15.59	3	< 0.05	LOW > EFZ*, LOW > MEDIUM, HIGH*	Ga
Odostomia nitens	13.42	3	< 0.05	LOW > HIGH*	Ga
Odostomia unidentata Log	42.25	3	< 0.01	Low > EFZ, HIGH**; LOW > MEDIUM*	Ga
Timoclea ovata Log	38.14	3	< 0.01	LOW > EFZ, MEDIUM*; LOW > HIGH**	Bi
Turritella communis Log	38.23	3	< 0.001	HIGH > EFZ, LOW, MEDIUM***	Ga

less damage during the sorting phase on deck and the dissection procedure in laboratory (pers. obs.). *A. bispinosus* had a broader diet than *A. irregularis*. There was strong evidence of the utilisation of carrion generated by fishing activity indicated by fragments of large decapod crustaceans together with fishes scales, fish fragments and a considerable number of otoliths of different fish such as *Lesueurigobius friesii* and *L. suerii* (these gobiid's species are typically discarded in the study area; Sartor *et al*., 2003; Sánchez *et al*., 2007; de Juan *et al*., 2013).

The significant increase in the number of the starfish *Astropecten irregularis* with increasing fishing intensity indicates that they may aggregate in response to the carrion generated by trawling disturbance (directly on the seabed or through discarded material) and possibly by the increase in abundance of preferred prey species within the benthic community. Previous studies have demonstrated that the energy subsidy generated by fishing activity attracts starfish in high numbers (Demestre *et al*., 2000). However, within the heavily fished areas, the increase in terms of abundance was not mirrored by an increase in terms of biomass. This observation could be explained by the increased vulnerability of larger starfish beyond a threshold of fishing intensity which increased the vulnerability of large individuals to mortality directly associated with the physical impact of the fishery on the seabed. There is probably a trade-off between fishing mortality and the advantage incurred from fisheries generated carrion in the diet as reflected in the size distribution of starfish at the medium fishing intensity sites. At medium levels of fishing intensity the high values of stomach contents' weight indicate greater feeding opportunities for these starfish. The diversity of diet composition suggest that the quality of food ingested is more diverse than in areas where trawling disturbance does not occur or is low, as testified by a highest Shannon's index diversity and number of species ingested.

In general some common traits were observed between the two astropectinids as the dependence of the growth rate to the amount and the quality of available food (Christensen 1970; Nojima, 1982); the close dependence of the assemblages with food availability (Sloan 1980); the highest occurrence of ingested prey in areas subjected to fishing disturbance.

In this study we have utilised the analysis of diet of two astropectinids scavengers to gain additional insights into changes in a benthic community subjected to fishing activity disturbance. We have argued that the observed evidence of changes in the two populations and in the stomach contents composition match with the effects of trawling disturbance. The existence of such changes would highlight the need to explicitly incorporate considerations on the benthic ecosystem into the management framework of a precautionary approach. At medium to high fishing intensities, there appears to be a strong proliferation of scavengers such as the two species of starfish reported here leading to a significant change in the dominance of benthic community structure. The proliferation of predatory asteroid starfishes could slow the recovery of other components in the benthic ecosystem due to the increase in predation from starfish. The availability of reference areas provides a useful baseline against which a more natural composition of the benthic community can be assessed. Such comparator sites are important when attempting to assess ecosystem indicators such as descriptors of Good Ecological Status (GES).

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