



Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province

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ABSTRACT: Using a towed camera system, a total of 422 individuals belonging to 62 taxa (including 33 identified species) were counted in the Santa Maria di Leuca (SML) coral province (Mediterranean Sea). Our findings update the knowledge of the biodiversity of this area and of the depth records of several species. The presence of coral mounds mostly in the north-eastern sector of the SML coral province seems to influence the large scale distribution of the deep-sea benthopelagic fauna, playing the role of attraction-refuge with respect to the barren muddy bottoms where fishing occurs in northern areas. Multiple Correspondence Analysis identified 3 main taxa groups: (1) rather strictly linked to the bottom, resting or moving on the seabed, often sheltering and feeding; (2) mostly swimming in the water column and mostly observed on rugged bottoms; and (3) actively swimming or hovering near the seabed. The behavioural patterns largely related to activity and position of the fauna seem to determine their small-scale distribution. The effects of different benthic macrohabitats appear to be less important and the depth within the bathymetric range examined even less so. The behavioural patterns reflect aspects of the species life strategies, revealing common features in phylogenetically and ecologically distant species. The teleost *Helicolenus dactylopterus* exhibited a clear behavioural pattern of resting on the seabed in different macrohabitats. The golden shrimp *Plesionika martia* and the fish *Pagellus bogaraveo* seem to be associated with the presence of corals.

KEY WORDS: Behaviour · Cold-water corals · Mediterranean Sea · Species distribution · Species diversity · Species–environment relationships

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INTRODUCTION

Several studies of Atlantic cold-water ecosystems support the hypothesis that the distribution of cold-water corals worldwide is directly related to topographic highs where enhanced currents prevent burial by deposition of fine sediment and provide transport of fresh and labile food particles to the coral

polyps (Freiwald et al. 1999, 2002, 2004, Reed et al. 2006, Thiem et al. 2006, Kiriakoulakis et al. 2007, Roberts et al. 2009).

The distribution of the Santa Maria di Leuca (SML) cold-water coral community in the Mediterranean (Fig. 1) also seems to be strictly related to the local topography and hydrodynamic regime (Savini & Corselli 2010, Vertino et al. 2010) and, as confirmed

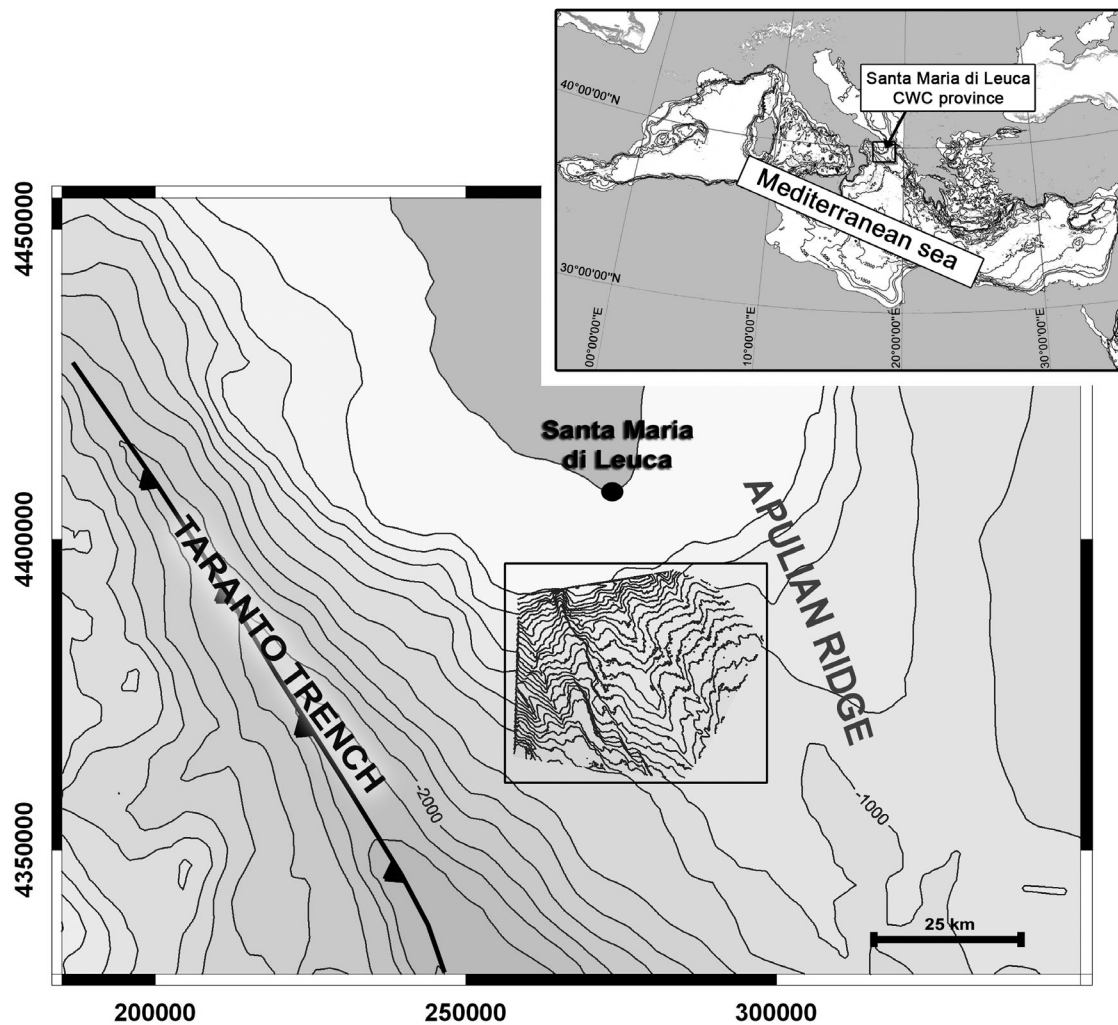


Fig. 1. Study area: Santa Maria di Leuca cold-water coral (CWC) province within the Mediterranean Sea and bathymetric framework within the southern Apulia margin. Universal Transverse Mercator (UTM) projection, zone 32 North with WGS84 datum

by Etiope et al. (2010), cannot be attributed to seeping fluids. Most probably, the main deep current flowing from the Adriatic Sea into the northern Ionian in a northeast to southwest direction (Budillon et al. 2010) provides a continuous and regular supply of nutrients and particulate organic matter to the SML corals. The corals preferentially settle on the top and north eastern upper flanks of the SML topographic heights. The hydrodynamic influence on coral distribution is particularly evident in some zones of the SML coral province where fan-shaped scleractinian colonies, as well as sponges, locally show a NNW to SSE orientation, perpendicular to the main current direction (Vertino et al. 2010). High densities of particulate matter and zooplankton organisms in the water column have been commonly observed in SML

remotely operated vehicle (ROV) videos (Carlier et al. 2009, Mastrototaro et al. 2010). In the long run, such a nutrient-rich current could cause accumulation of a large amount of particulate organic matter along the north eastern flanks of the coral mounds, as observed for sediment deposition due to the action of bottom currents (Malinverno et al. 2010, Savini & Corselli 2010). Since food-rich sediment would be likely to support a richer detrital food web, in turn it would favour a greater abundance of benthic and benthopelagic fauna belonging to different trophic levels (Carlier et al. 2009, Mastrototaro et al. 2010). To date, 222 taxa (202 at species level) have been reported from the SML coral province, with 135 of the species being new for the area (Mastrototaro et al. 2010).

Distribution and abundance of the benthopelagic megafauna (cephalopods, decapod crustaceans and fishes) in the SML coral province have been investigated by fishing with bottom longline and trawl inside and outside the coral area (D'Onghia et al. 2010). The aim of that study was to evaluate the effects of the presence of corals and the virtual absence of fishing inside the coral area, and the absence of corals and the presence of fishing outside. However, the use of fishing gear does not allow the precise definition of the distribution of the species but confound the species and habitat associations over the distance covered by the gear (Ross & Quattrini 2007). Video inspections can provide information on the habitat selection of the species, their position in the water column and their behaviour (e.g. Costello et al. 2005 and references therein). Towed underwater cameras, submersibles and ROVs have been used in the Atlantic to collect information about the association between cold-water corals and fishes (e.g. Mortensen et al. 1995, Freiwald et al. 2002, Fosså et al. 2002, Krieger & Wing 2002, Costello et al. 2005, Ross & Quattrini 2007, 2009, Le Guilloux et al. 2009); however, this type of information is still scarce for the Mediterranean Sea (Tunesi et al. 2001).

In this work, the videos recorded during the APLABES programme (Corcelli 2010) were used: (1) to identify the benthopelagic fauna distributed in the SML cold-water coral province; (2) to investigate their small-scale distribution and relationship with local factors such as depth and substrate; and (3) to examine the behaviour of the individuals by species or taxa. Due to the explorative objective of the APLABES video survey and the difficulties involved in this type of study (e.g. time required to explore unknown deep-sea bottoms with variable and rugged topography using towed cameras, variable sea-weather conditions and strong currents on the bottom), the main results are qualitative.

MATERIALS AND METHODS

Video observations were carried out using the gas scientific package (GAS-SCIPACK) module connected to the mobile docker for underwater science (MODUS) vehicle (hereafter MGS), deployed by the RV 'Universitatis' during May 2005 (Etiope et al. 2010) in 10 geographic sites (Fig. 2). Two of these sites (MS04-Atlantis Mound and MS06-Yellow Chain) have been accurately mapped and described

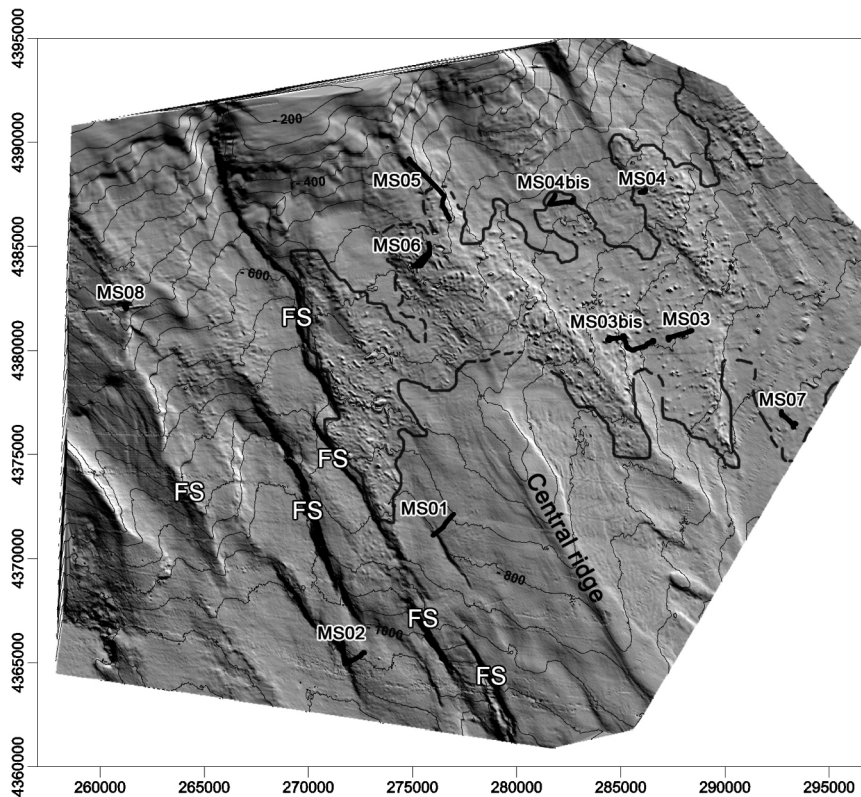


Fig. 2. Three-dimensional view (by multibeam swath sonar) of the study area investigated during the APLABES project. The main seafloor morphologies (FS = Fault Scarpsments; Central Ridge) and locations of video surveys performed by MODUS/GAS-SCIPACK are indicated (MS01 to MS08). Universal Transverse Mercator (UTM) projection, zone 32 North with WGS84 datum

by Vertino et al. (2010). In each of them, a total of 7 main benthic macrohabitats were identified: (1) CF: coral framework; (2) LCF: loose coral framework; (3) CF/H: coral framework and hardground; (4) CR: coral rubble; (5) BR: buried rubble; (6) BS: bioturbated fine-grained sediment; and (7) H: hardground crusts and boulders. In this work, each benthic macrohabitat was considered as a substrate typology or as a small-scale habitat.

Mean, minimum and maximum depths as well as the geographic coordinates of each geographic site are reported in Table 1.

The videos examined herein were recorded by 3 video cameras (Deep Sea Power & Light MULTI-SEACAM 2050 and DL 1040), mounted on one side ('lateral camera') and in front ('front camera') of the MODUS vehicle and at the base ('bottom camera') of the GAS-SCIPACK module. The first 2 cameras were inclined at about 45° with respect to the horizontal plane whereas the latter one was oriented vertically. The system was not equipped with a proper underwater positioning system, therefore its survey track was extrapolated from the offset position of its cable at sea in relation to the vessel DGPS antenna. Since the system did not have a continuous size calibration tool, a 10 cm long 'yellow tube' was attached by a 2 m long rope to the MGS frame. This helped in evaluating the size of the recorded fauna. Video recordings were made during daylight hours.

From a total of 44 h of video recorded, 32 h 45 min in which the MGS was surveying the bottom at close distance were used for data analysis, recording the time spent over each benthic macrohabitat (*sensu* Vertino et al. 2010) at each geographic site (7 benthic macrohabitats × 10 geographic sites). Only non-schooling mobile cephalopods, decapod crustaceans and fishes belonging to benthopelagic megafauna (animals ex-

ceeding 2 cm in length according to Freiwald et al. 2004) were considered in the present study. Video was frequently viewed from all 3 available cameras in order to track each individual or taxon identified, preventing duplicate counting in subsequent frames.

The abundance of video-recorded cephalopods, crustaceans and fishes was standardized for effort, dividing counts by the hours surveyed. Thus, the number of individuals per hour ($N\ h^{-1}$) was computed for all benthic macrohabitats (7) and geographic sites (10) (Table 2). Spatial interpolation of $N\ h^{-1}$ values was carried out by means of ordinary kriging (Webster & Oliver 2001) using ARCVIEW 3.2. In order to evaluate whether the standardized abundance of the fauna ($N\ h^{-1}$) across geographic sites differed significantly from that expected if it was equally distributed across all geographic sites, the goodness of fit test was employed. This statistical test allows the comparison of an observed with a theoretical distribution (Möller 1979).

The taxa identified in the video records were listed with respect to depth, benthic macrohabitat (i.e. substrate typology), position and activity. In particular, the depth was classified into Upper Slope (380 to 800 m) or Middle Slope (801 to 1170 m) (D'Onghia et al. 2004). Following Costello et al. (2005) and Lorange & Trenkel (2006), position with respect to the bottom and activity of the individual organisms were classified in terms of Fauna Position and Fauna Activity, respectively. In particular, Fauna Position was recorded in 3 categories: (1) water column (1 to 2 m above the bottom); (2) near the seabed (within 0.5 to 1 m); and (3) on the seabed. Fauna Activity was recorded in 7 categories: (1) actively swimming; (2) quietly swimming; (3) hovering; (4) moving on the seabed; (5) resting on the seabed; (6) sheltering; and (7) feeding.

Table 1. Mean, minimum and maximum depth and geographic coordinates (start and end) of the non-linear transects carried out by means of the MGS system (GAS-SCIPACK module connected to the MODUS vehicle), in the Santa Maria di Leuca (SML) coral province, during the APLABES project

Geographic site	Depth (m)			Start		End	
	Mean	Min	Max	Latitude	Longitude	Latitude	Longitude
MS01	759	729	819	39°27.296'N	18°25.298'E	39°27.643'N	18°23.789'E
MS02	1143	1102	1179	39°24.461'N	18°21.484'E	39°24.767'N	18°20.856'E
MS03	790	775	810	39°33.106'N	18°32.138'E	39°32.914'N	18°31.501'E
MS03bis	771	717	804	39°32.827'N	18°30.994'E	39°32.858'N	18°29.510'E
MS04	648	631	663	39°36.761'N	18°30.571'E	39°36.696'N	18°30.378'E
MS04bis	629	613	634	39°36.463'N	18°28.150'E	39°36.513'N	18°27.511'E
MS05	453	386	498	39°35.858'N	18°24.027'E	39°37.347'N	18°22.636'E
MS06	519	495	556	39°35.207'N	18°23.350'E	39°35.015'N	18°23.379'E
MS07	906	895	919	39°30.748'N	18°35.736'E	39°30.807'N	18°35.671'E
MS08	542	539	547	39°33.269'N	18°13.279'E	39°33.316'N	18°13.292'E

Table 2. Time of video recording (T, h) and number of individuals (N) identified in each geographic site and benthic macrohabitat in the Santa Maria di Leuca (SML) coral province during the APLABES project. Benthic macrohabitat: CF: coral framework; LCF: loose coral framework; CF/H: coral framework and hardground; CR: coral rubble; BR: buried rubble; BS: bioturbated fine-grained sediment; H: hardground crusts and boulders. – : macrohabitat not observed

Geographic site		Benthic macrohabitat							Total
		CF	LCF	CF/H	CR	BR	BS	H	
MS01	T	–	0.204	0.002	0.051	0.845	10.472	0.049	11.623
	N	–	0	0	0	1	32	1	34
MS02	T	–	–	–	–	1.779	1.721	0.085	3.586
	N	–	–	–	–	4	6	1	11
MS03	T	0.251	0.612	0.211	0.510	0.147	1.934	0.125	3.790
	N	2	5	4	2	1	12	4	30
MS03 bis	T	0.010	0.109	0.006	0.155	0.053	3.578	0.043	3.954
	N	0	3	0	1	1	175	3	183
MS04	T	0.085	0.311	0.015	0.047	0.055	0.417	0.139	1.070
	N	2	36	0	0	0	28	1	67
MS04 bis	T	–	0.030	–	0.018	0.059	0.883	0.005	0.995
	N	–	1	–	0	0	10	0	11
MS05	T	–	–	–	–	0.002	2.250	–	2.252
	N	–	–	–	–	0	36	–	36
MS06	T	0.131	0.661	0.260	0.131	0.594	1.854	0.203	3.833
	N	0	5	3	1	7	10	0	26
MS07	T	–	–	–	–	0.308	0.242	–	0.550
	N	–	–	–	–	14	4	–	18
MS08	T	–	0.118	0.011	0.133	0.150	0.635	0.053	1.100
	N	–	0	0	0	3	3	0	6
Total	T	0.477	2.046	0.505	1.044	3.991	23.986	0.702	32.752
	N	4	50	7	4	31	316	10	422

Multiple correspondence analysis (MCA) was applied to describe the relationship between individual/taxon and the variables depth, fauna position, fauna activity and benthic macrohabitat in a low-dimensional space and simultaneously to depict the relationships among the categories for each variable. A joint plot of category points, which is a single plot of the centroid coordinates of each selected variable, was drawn to visualize relationships between the different categories of variables. Percentage variances and discrimination measures associated with each variable were computed according to Meulman & Heiser (2009) using SPSS (SPSS 2009). The goodness of fit test (Möller 1979) was employed for each group resulting from MCA in order to evaluate whether the standardized abundance of the taxa ($N\ h^{-1}$) across benthic macrohabitats, position and activity categories differed significantly from that expected if they were equally distributed across all benthic macrohabitats, position and activity categories. Finally, this statistical test was also applied to the standardized abundance ($N\ h^{-1}$) of the single species that were observed several times during the survey with the aim of verifying their relationships with respect to benthic macrohabitat, position and activity.

RESULTS

A total of 422 individuals were counted in the video records: 36 cephalopods, 201 decapod crustaceans and 185 fish. The spatial interpolation of the standardized $N\ h^{-1}$ of individuals over the study area is shown in Fig. 3, in which the highest densities appear in the north eastern sector of the SML coral province, mostly around the MS04 and MS03bis geographic sites. In this respect, the standardized abundance of the fauna ($N\ h^{-1}$) across geographic sites differed significantly from that expected if it was equally distributed across all geographic sites ($\chi^2 = 198.80$; $df = 9$; $p < 0.01$).

The distribution of the individuals or taxa in the different depths and benthic macrohabitats, and their position and activity are presented in Table 3.

A total of 132 individuals were identified to the species level, belonging to 33 species, and 290 were assigned to 29 higher taxa; 38% of the species identified are of commercial interest. The cephalopods *Ancistroteuthis lichtensteini*, *Brachioeteuthis riisei*, *Chiroteuthis veranyi* and *Onychoteuthis banksi*, the crustacean *Solenocera membranacea* and the fishes *Aulopus filamentosus*, *Nettastoma melanurum* and *Sudis hyalina* represent new records for the SML

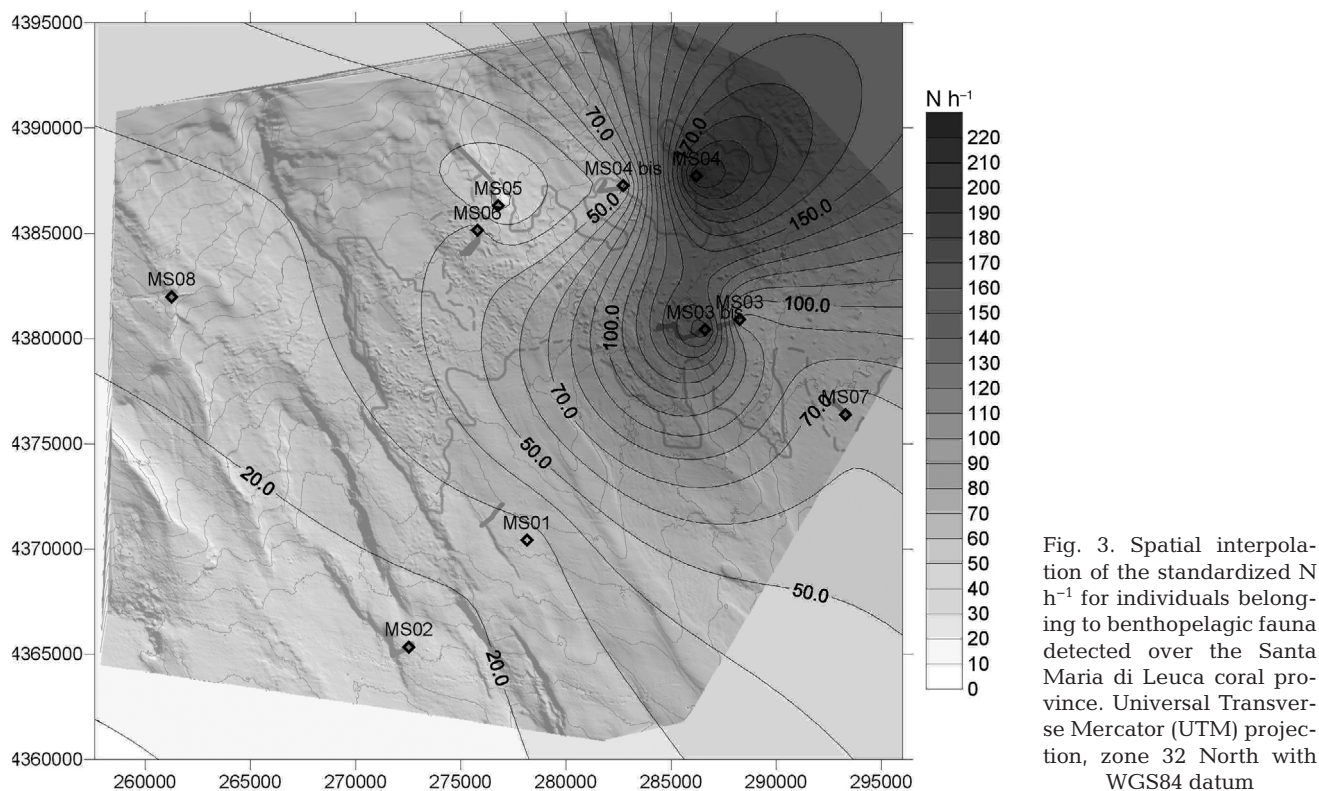


Fig. 3. Spatial interpolation of the standardized $N\ h^{-1}$ for individuals belonging to benthopelagic fauna detected over the Santa Maria di Leuca coral province. Universal Transverse Mercator (UTM) projection, zone 32 North with WGS84 datum

coral area. The present findings of *B. riisei*, *C. veranyi*, *Loligo forbesii* and *Pteroctopus tetracirrhus* represent the deepest records in the Ionian Sea.

The results of the MCA, which was carried out considering all 422 individuals recorded, are presented in Fig. 4. The first 2 dimensions of the MCA represent 52% and 44%, respectively, of the total variance, i.e. more than 95% of the variance in the first factorial plane (Table 4). The role played by the different variables within each dimension is indicated by the discrimination measures reported in Table 5. The activity and position variables showed the greatest discrimination measures for the first dimension of the MCA, indicating a high degree of discrimination between the categories of these variables along this dimension. The habitat and activity variables exhibited the greatest discrimination measures for the second dimension of the MCA. On average the smallest discrimination measure was shown for depth (Table 5).

The MCA defined 3 main species or taxa groups. Group 1 included the species more strictly linked to the bottom, resting or moving on the seabed, often sheltering and feeding (Fig. 4a). These species were represented by the crustaceans *Nephrops norvegicus*, *Bathynectes maravigna* and *Aristeus antennatus*, the fishes *Chlorophthalmus agassizi*, *Helicolenus*

dactylopterus, *Lepidopus caudatus*, *Chimaera monstrosa*, *Galeus melastomus*, *Aulopus filamentosus*, *Caelorinchus caelorhincus*, *Nezumia sclerorhynchus*, *Merluccius merluccius* and, to a lesser extent, *Phycis blennoides*, *Mora moro* and the *Aristeidae* family, which were placed rather centrally in the factorial plane because they were observed in different positions and carrying out different activities (Fig. 4b, Table 3). The only individual of the species *Pteroctopus tetracirrhus*, not shown in Fig. 4b, was observed resting on the seabed (Table 3). Most individuals in this group were observed in the sediment-dominated benthic macrohabitat. However, the goodness of fit test did not show significant differences among the standardized abundances of the species or taxa of this group across all benthic macrohabitats, while significantly greater abundances of the species or taxa were detected on the seabed ($\chi^2 = 38.52$; $df = 2$; $p < 0.01$) and resting on the seabed ($\chi^2 = 68.43$; $df = 6$; $p < 0.01$). Among the most frequently observed species, the records of *Aristeus antennatus* did not show significant differences between the categories of macrohabitats, fauna position or fauna activity. *H. dactylopterus* was mainly recorded on the seabed with a resting behaviour. The statistical test provided significant results for both position

Table 3. Taxa identified during the video analysis in the Santa Maria di Leuca (SML) coral province with indication of depth range, number of individuals (N), benthic macrohabitat, fauna position and fauna activity categories. Benthic macrohabitat: CF: coral framework; LCF: loose coral framework; CF/H: coral framework and hardground; CR: coral rubble; BR: buried rubble; BS: bioturbated fine-grained sediment; H: hardground crusts and boulders. Fauna position: WC: water column; NS: near seabed; OS: on seabed. Fauna activity: AS: actively swimming; QS: quietly swimming; H: hovering; MS: moving on the seabed; RS: resting on the seabed; S: sheltering; F: feeding. ^aSpecies of commercial interest in the Mediterranean Sea

Taxa	Depth range (m)	N	Benthic macrohabitat								Fauna position			Fauna activity					
			CF	LCF	CF/H	CR	BR	BS	H	WC	NS	OS	AS	QS	H	MS	RS	S	F
<i>Ancistroteuthis lichtensteini</i>	774–1102	3						3		2	1			3					
<i>Brachioteuthis riisei</i>	629–1102	4						4		2	2			4					
<i>Chiroteuthis veranyi</i>	772	1						1			1			1					
<i>Loligo forbesi</i> ^a	906	1					1			1				1					
<i>Onychoteuthis banksi</i>	765–796	7			1			6		5	2		1	6					
<i>Pteroctopus tetracirrhus</i>	773	1			1							1					1		
<i>Todarodes sagittatus</i> ^a	713–771	3						2	1	2	1			3					
Ommastrephidae	1109	1					1			1				1					
Onychoteuthidae	740–1102	5					1	4				5		5					
Teuthida	420–796	9	1	1	1			6		1	8		1	5	1				2
Cephalopoda	648	1	1								1			1					
<i>Aristeus antennatus</i> ^a	718–786	17			1			16		5	2	10		7		4	6		
<i>Bathynectes maravigna</i>	496	1						1				1					1		
<i>Nephrops norvegicus</i> ^a	489	1						1				1				1			
<i>Plesionika martia</i> ^a	631–663	13	1	11					1	3	10			13					
<i>Solenocera membranacea</i>	715–774	4				1		3		4				4					
Aristeidae	648–790	14			3			11		2	5	7	1	5		3	5		
Pandalidae	490–781	15	1	1			1	12		14	1		1	9			5		
Solenoceridae	631–663	7			7							7		7					
Dendrobranchiata	648–798	40						40		10	16	14	5	16		2	10	7	
Pleocyemata	509–906	37			11	1		23	1	27	8	2	6	20		1	10		
Decapoda	490–1098	52					11	38	3	20	24	8	28	14		2	1	7	
<i>Chimaera monstrosa</i>	537	1						1				1					1		
<i>Etmopterus spinax</i>	542–1152	6					1	5			6			2	4				
<i>Galeus melastomus</i> ^a	480–787	4						4			3	1		3			1		
Chondrichthyes	613	1						1			1				1				
<i>Arctozenus risso</i>	780	1						1		1				1					
<i>Aulopus filamentosus</i>	444–477	3						3				3					3		
<i>Benthocometes robustus</i>	747	1						1			1			1					
<i>Caelorinchus caelorhincus</i>	774	1						1				1			1				
<i>Chlorophthalmus agassizi</i> ^a	381–403	2						2				2					2		
<i>Conger conger</i> ^a	749–798	3					1	2			3			2	1				
<i>Epigonus</i> sp.	739	1						1			1				1				
<i>Helicolenus dactylopterus</i> ^a	408–774	11			3		1	6			1	10		1			8	2	
<i>Hymenocephalus italicus</i>	760	1						1			1				1				
<i>Lepidion lepidion</i>	1123	1					1				1				1				
<i>Lepidopus caudatus</i> ^a	772–786	5						5				5							5
<i>Merluccius merluccius</i> ^a	500–738	2						2			1	1		1			1		
<i>Mora moro</i>	477–1123	9						8	1		7	2		3	3		2	1	
<i>Nettastoma melanurum</i>	497–760	4						4		1	2	1		2	1			1	
<i>Nezumia sclerorhynchus</i>	521–763	3			1			2			2	1			1		1	1	
<i>Notacanthus bonaparte</i>	648	1			1						1							1	
<i>Pagellus bogaraveo</i> ^a	457–906	12			2	2		3			12		2	4	5			1	
<i>Phycis blennoides</i> ^a	396–496	3						3			2	1		1	1		1		
<i>Sudis hyalina</i>	774	1						1		1				1					
Apogonidae	793	1							1		1			1					
Gadidae	520	1					1				1				1				
Macrouridae	380–781	3					1	1	1	1	2			1	2				
Myctophidae	648–786	3						3		1	2		1	2					
Ophidiidae	629–781	1						1		1				1					
Paralepididae	648–790	15			3	1	1		10	8	7		4	9	1				1
Scorpaenidae	420–482	3						3				3					3		
Sparidae	535	1					1				1			1					
Stomiidae	780	1							1		1			1					

Table 3 (continued)

Taxa	Depth range (m)	N	Benthic macrohabitat							Fauna position			Fauna activity						
			CF	LCF	CF/H	CR	BR	BS	H	WC	NS	OS	AS	QS	H	MS	RS	S	F
Triglidae	479	1						1				1						1	
Scorpaenoidei	623	1						1			1				1				
Anguilliformes	648–789	3		1				2		2	1		1	2					
Aulopiformes	753–798	2						2		2			1	1					
Gadiformes	523–1170	8		1			2	5				6	2	1	1	3		1	2
Ophidiiformes	790–800	2		1				1		1	1		1	1					
Perciformes	471–779	6					1	5		1	5		3	3					
Osteichthyes	386–800	56		2		1	2	51		10	30	16	12	15	14		14	1	

($\chi^2 = 16.54$; $df = 2$; $p < 0.01$) and activity ($\chi^2 = 32.91$; $df = 6$; $p < 0.01$) of this fish. No significant differences were detected in the distribution of this fish among the different benthic macrohabitats. All 5 *L. caudatus* individuals, which measured approximately <30 cm, were observed feeding in the sediment.

Group 2 mostly consisted of the species quietly swimming in the water column (Fig. 4a), such as the teleost fishes *Sudis hyalina* and *Arctozenus risso*, the squids *Ancistroteuthis lichtensteini*, *Brachioteuthis riisei*, *Chiroteuthis veranyi*, *Onychoteuthis banksi* and *Todarodes sagittatus*, and crustaceans showing a more pelagic habit, such as the shrimps *Plesionika martia* and *Solenocera membranacea*. Several families were included in this group even though the individuals were observed in different positions and activities (Fig. 4b, Table 3). Species or taxa of this group were mainly observed in CF, LCF and H benthic habitats (2nd dimension of the MCA in Fig. 4a). In this respect, the standardized abundance of the species or taxa across all benthic habitats differed significantly from that expected if they had been equally distributed across all benthic habitats ($\chi^2 = 18.91$; $df = 6$; $p < 0.01$). The goodness of fit test also showed significant differences in the abundance of the species or taxa between the categories of fauna position ($\chi^2 = 36.51$; $df = 2$; $p < 0.01$) and fauna activity ($\chi^2 = 273.54$; $df = 6$; $p < 0.01$). The most frequently observed species, *Plesionika martia*, clearly distinguishable due to its long rostrum, was significantly mostly observed in habitats with corals (LCF) ($\chi^2 = 18.89$; $df = 6$; $p < 0.01$), near the seabed ($\chi^2 = 12.15$; $df = 2$; $p < 0.01$) and quietly swimming ($\chi^2 = 78.01$; $df = 6$; $p < 0.01$).

Group 3 was made up of species actively swimming and hovering near the seabed (Fig. 4a). This group was represented by the squid *Loligo forbesii* and the fishes *Lepidion lepidion*, *Etmopterus spinax*, *Pagellus bogaraveo*, *Hymenocephalus italicus*, *Conger conger* and *Nettastoma melanurum*. The families

Gadidae, Macrouridae, Ommastrephidae and Onychoteuthidae were also included in this group (Fig. 4b). This group was associated with the Middle Slope depth category most probably in relation to the deepest species (*Lepidion lepidion*) and families (Ommastrephidae and Onychoteuthidae) observed within the depth range examined (Table 3). The goodness of fit test showed significant differences in the abundance of the species or taxa of this group among the categories of fauna position ($\chi^2 = 41.44$; $df = 2$; $p < 0.01$) and fauna activity ($\chi^2 = 38.34$; $df = 6$; $p < 0.01$). Most individuals were observed in BR macrohabitat (2nd dimension of the MCA in Fig. 4a). However, the standardized abundance of the species/taxa of this group did not differ significantly among the benthic macrohabitats. The velvet belly shark *E. spinax* and the teleost *P. bogaraveo* were exclusively observed near the seabed. The goodness of fit test applied to *P. bogaraveo* showed significant results due to greater standardized abundance in habitats with corals ($\chi^2 = 14.57$; $df = 6$; $p < 0.05$), for near seabed position ($\chi^2 = 24.11$; $df = 2$; $p < 0.01$) and hovering activity ($\chi^2 = 14.83$; $df = 6$; $p < 0.05$).

DISCUSSION

Fauna distribution

Despite the explorative objective and the difficulties involved in this type of survey, the results of this study reveal a heterogeneous distribution of the megafauna in the SML coral province. The highest abundance of individuals observed in the north-eastern sector (Fig. 3) seems to be directly linked to the typical hummocky seafloor features (much less extended in the south-western sector), characterized by widespread mound-like reliefs, generally topped with live or dead cold-water corals (Savini & Corselli 2010). The current-induced mechanism which seems

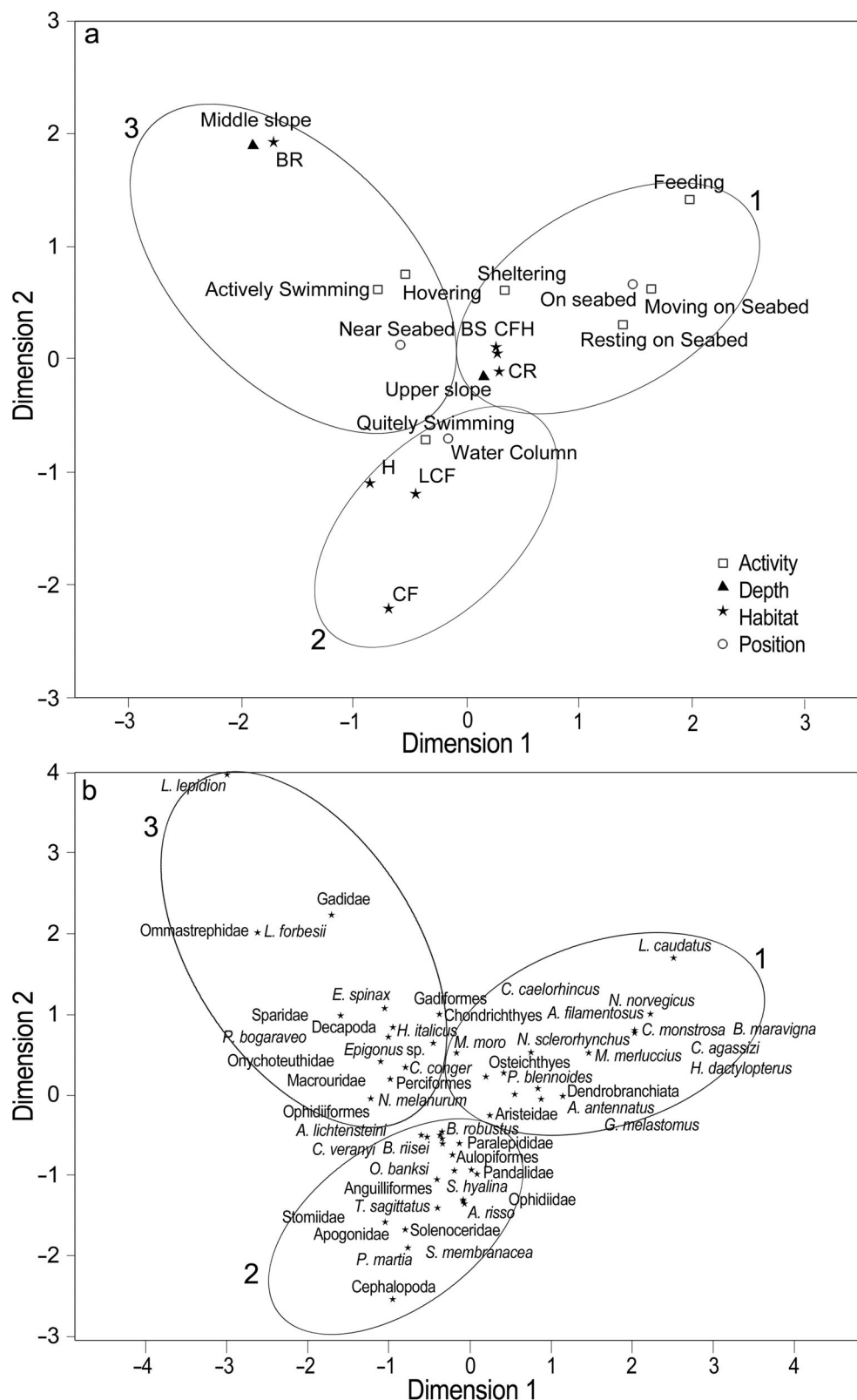


Fig. 4. Category plots obtained by multiple correspondence analysis (MCA). (a) Joint plot of category points of activity, position, benthic habitat and depth of all taxa recorded in the Santa Maria di Leuca (SML) coral province. Benthic macrohabitat: CF: coral framework; LCF: loose coral framework; CF/H: coral framework and hardground; CR: coral rubble; BR: buried rubble; BS: bioturbated fine-grained sediment; H: hardground crusts and boulders. (b) Category plot of species or taxa identified

Table 4. Eigenvalues, inertia and percent variance of the first 2 dimensions of the multiple correspondence analysis (MCA) carried out on the fauna recorded in the Santa Maria di Leuca (SML) coral province

	Variance accounted for		
	Eigenvalue	Inertia	% of variance
1	2.580	0.516	51.605
2	2.179	0.436	43.572
Total	4.759	0.952	

Table 5. Discrimination measures associated with each variable for the first 2 dimensions of the multiple correspondence analysis (MCA) carried out on the fauna recorded in the Santa Maria di Leuca (SML) coral province

	Dimension		Mean
	1	2	
Habitat	0.317	0.518	0.418
Position	0.654	0.261	0.458
Activity	0.677	0.439	0.558
Depth	0.283	0.283	0.283
Species	0.648	0.677	0.663
Active total	2.580	2.179	2.379
% of variance	51.605	43.572	47.588

to favour the settlement of frame-building corals and associated benthic organisms on the north-eastern flank of a single SML coral mound might be invoked, on a larger scale, to explain the highest abundance of frame-building corals on the upcurrent side of the central ridge (Fig. 2) (Vertino et al. 2010). The greater presence of corals and sponges in the eastern part of the SML area might enhance a refuge for small planktonic and benthic invertebrates, which in turn may be preyed upon by the mobile fauna observed in this study. Although not quantified, the high concentration of small invertebrates observed in the north-east side of SML, which is characterized by coral mounds with a high heterogeneity of substrates, most probably represents the attracting factor for the benthopelagic fauna.

The functional effect that structurally complex habitats can have on mobile megafauna is well known (e.g. Auster et al. 2005, Tissot et al. 2006, Caddy 2007) and cold-water corals provide the major contribution to deep-sea habitat complexity and heterogeneity. However, a clear direct link between fish and corals has still not been proved. Although deep-sea coral reefs seem to be important for some fish species (Mortensen et al. 1995, Husebø et al. 2002, Costello et al. 2005) and strong specificity to deep-sea habitats has been observed for some others

(Tissot et al. 2006, Ross & Quattrini 2007), it is not yet known whether corals themselves or only their structural complexity is the attracting factor. Auster et al. (2005) suggested that deep coral reefs play the same role as other reef structures. Stone (2006) reported that some associations that appear 'active' may occur simply because certain species and emergent epifauna prefer the same substrate type. In our opinion, the whole SML coral province, including different benthic macrohabitats (i.e. substrates), plays the role of attraction-refuge with respect to the barren muddy bottoms around it where fishing occurs (D'Onghia et al. 2010). Hard substrates interspersed with coral mounds and muddy bottoms are less accessible to fishing activities and thereby can provide a natural refuge for mobile fauna, as observed in submarine canyons (Yoklavich et al. 2000). In fact, the benthopelagic fauna distributed in the SML coral province is not taxonomically different from the overall regional fauna (Matarrese et al. 1996, D'Onghia et al. 1998, 2003, Capezzuto et al. 2010). D'Onghia et al. (2010) detected greater abundances and sizes in the coral area (the area in Fig. 2), where fishing occurs in some peripheral zones, than outside where fishing is fully developed on muddy bottoms. Refuge effects were detected in the former area and fishing effects in the latter.

Despite the heterogeneous distribution on a regional scale, the MCA results show little effect of benthic macrohabitat typology (i.e. substrate) on the distribution of the examined megafauna. This could be due to the fact that the fauna investigated is rather mobile and moves within mesohabitats (large-scale habitats) where benthic macrohabitats (small-scale habitats) gradually evolve into each other. Thus, the present results do not demonstrate a specific tie of mobile fauna as a whole to corals. They seem to indicate that the benthopelagic fauna is widespread over different benthic macrohabitats (small-scale habitats) and mostly on the north-east side of the SML coral province due to greater food availability.

Fauna composition and behaviour

Although the MGS system is very large and cumbersome, the towed cameras used in this study gave the opportunity to record several species not previously found in the SML coral province using more traditional sampling methods. The cephalopods *Ancistroteuthis lichtensteini*, *Brachioteuthis riisei*, *Chiroteuthis veranyi*, *Onychoteuthis banksi*, the shrimp *Solenocera membranacea*, and the fishes *Aulopus fil-*

amentosus, *Nettastoma melanurum* and *Sudis hyalina* represent new records for the SML coral area. The findings of *B. riisei*, *C. veranyi*, *Loligo forbesii* and *Pteroctopus tetracirrhus* are also depth records for the Ionian Sea. In this respect, it is well known that cephalopods are also considered 'non-conventional' resources in relation to the difficulty of catching them with conventional fishing gear (Boyle 1990). Thus, the use of towed cameras has updated the knowledge of the biodiversity of the SML coral area, adding 8 species to the 222 taxa reported by Mastrototaro et al. (2010). Furthermore, this study provides new insights into the Mediterranean deep-sea fauna, previously almost exclusively known from sampling with fishing gear. Although species behaviour refers to daylight hours, it is in agreement with their lifestyle and feeding strategies (Table 6).

The MCA results show some behavioural patterns mostly related to activity and position, while effects of benthic macrohabitat typology were only detected in the second species or taxa group and only in some species. Most individuals were observed on the upper slope, most probably due to the greater number of video records examined in this depth range. Activity and position patterns were generally confirmed by the goodness of fit test by group and single species. These patterns seem to reflect the life strategies of the different species, revealing common features in phylogenetically and ecologically distant species, as observed by Lorange & Trenkel (2006) for Atlantic ones. However, due to the phylogenetic and ecological distances between the different species or taxa recorded, each group cannot be considered as an exclusive homogeneous ecological unit.

In the first group, the most sedentary species, strictly linked to the bottom and probably almost undetectable to predators due their orange-red (e.g. *Bathynectes maravigna*, *Helicolenus dactylopterus*), greyish (e.g. *Chlorophthalmus agassizi*) and dark (e.g. *Nezumia sclerorhynchus*) colour or their burrowing activity (*Nephrops norvegicus*), were associated with more active predator fishes, such as *Merluccius merluccius* and *Lepidopus caudatus*, and the shrimp *Aristeus antennatus*, known as a species capable of remarkable horizontal and vertical displacement (Relini et al. 2000). With regard to *L. caudatus*, the video records provided a new contribution to the understanding of the behaviour of juveniles, which seem to feed mostly in the sediment, while adults have a more pelagic feeding behaviour (Macpherson 1979, Demestre et al. 1993). This could explain the fact that large individuals are selectively caught by longline in the study area, while small

ones are mostly fished during trawling (D'Onghia et al. 2000, 2010). In addition, Uiblein et al. (1996) reported a bigger-shallower trend for this fish. The individuals observed between 772 and 786 m in depth in this study were all small in size and were observed feeding in the sediment.

Even *Aristeus antennatus* was grouped with other species linked more to the bottom. It did not show any particular position or behavioural pattern. This could be due to the fact that this shrimp has a highly diverse diet based on a wide variety of small benthic-suprabenthic organisms and pelagic macrofauna and micronekton (Cartes et al. 2008). In this respect, day-time migrations in the water column have been detected for this shrimp, with a more pelagic behaviour at night (e.g. Cartes et al. 1993, Matarrese et al. 1995).

The teleost *Helicolenus dactylopterus* exhibited a clear behavioural pattern of resting on the seabed in different macrohabitats of the SML coral province. Indeed, this fish uses a wide range of habitat and is tightly associated with the bottom (Bourcier & Zibrowius 1973, Tunesi & Diviacco 1997, Uiblein et al. 2003, Reed et al. 2006). It is also frequently observed in coral habitats and available photos show solitary individuals resting on the substrate near corals (Costello et al. 2005, Foubert et al. 2005, Reed et al. 2006, Ross & Quattrini 2007, Le Guilloux et al. 2009, D'Onghia et al. 2010, Vertino et al. 2010). *H. dactylopterus* seems to be a typical sit-and-wait ambush predator feeding mainly on benthic crustaceans and fishes as well as on plankton organisms (Mianzan et al. 1996, Nouar & Maurin 2000, Uiblein et al. 2003, Consoli et al. 2010). Since it can also be a potential prey of larger deep-sea predators, the observed behaviour can be considered as a trade-off between feeding strategy and predator avoidance (Table 6).

The shark *Galeus melastomus* and the teleost *Mora moro* were also included in the first group. The former has a diet based on epibenthic (mostly *Calocaris macandreae*) and benthopelagic species (euphasids, ommastrephidae, *Pasiphaea multidentata*, mesopelagic fishes) (Carrassón et al. 1992), the latter is an active predator of suprabenthic and epibenthic fauna. In particular, the food items found in the stomachs were mostly represented by decapods (*Aristeus antennatus* and *Munida* sp.), cephalopods (*Bathypolypus sponsalis*) and fishes, all from the benthic fauna (Carrassón et al. 1997). In the Bay of Biscay, *G. melastomus* was observed displaying a high rate of forward locomotion close to the bottom, while *M. moro* frequently showed station-holding behaviour (Uiblein et al. 2003).

Table 6. Relationship among observed behaviour (position and activity), benthic macrohabitat, lifestyle and feeding habit in benthopelagic species observed in the SML coral province. See Table 3 legend for abbreviations

Species	Observed behaviour	Benthic macro-habitat	Lifestyle	Main food
<i>Aristeus antennatus</i>	WC, NS, OS – QS, MS, RS	BS, LCF	Benthopelagic species (23; 26), with diel and seasonal migrations (6; 17)	Small benthic-suprabenthic organisms, pelagic macro fauna and micronekton (5)
<i>Plesionika martia</i>	WC, NS – QS	LCF, CF, H	Benthopelagic, diel and seasonal migrations (7; 16)	Active predator of macroplankton, mainly benthopelagic crustaceans. Small fishes, polychaetes and sergestidae represent secondary prey (3)
<i>Solenocera membranacea</i>	WC – QS	BS, CR	Benthic with burying habit (10; 13). Swimming ability (24)	Large polychaetes (10; 13) and benthic organisms (4)
<i>Etmopterus spinax</i>	NS – QS, H	BS, BR	Benthopelagic, diel and seasonal migrations	Active predator of benthic and free swimming organisms, mostly cephalopods (2; 30)
<i>Galeus melastomus</i>	NS, OS – QS, RS	BS	Benthopelagic, diel and seasonal migrations	Epibenthic (<i>Calocaris macandreae</i>) and benthopelagic species (euphausiidae, ommastrephidae, <i>Pasiphaea multidentata</i> , mesopelagic fishes) (2)
<i>Aulopus filamentosus</i>	OS – RS	BS	Benthopelagic	Feeds mainly on cephalopods, finfish and benthic crustaceans (9)
<i>Conger conger</i>	NS – QS, H	BS, BR	Benthopelagic, roaming on the bottom	Scavenger; feeds mainly on fishes (28)
<i>Helicolenus dactylopterus</i>	NS, OS – QS, RS, S	BS, LCF, CR, BR	Benthic, sitting and resting behaviour (29), ontogenetic migrations (12)	Benthic crustaceans, fishes and planktonic organisms (8; 15; 21; 27; 29)
<i>Lepidopus caudatus</i>	OS – F	BS	Benthopelagic, pelagic, vertical swimming	Pelagic feeding in adults (11; 14; 22) and zoobenthic feeding in juveniles (14)
<i>Mora moro</i>	NS, OS – QS, H, RS, S	BS, H	Benthic, hovering, station holder (29)	Suprabenthic and epibenthic fauna (<i>Aristeus antennatus</i> , <i>Munida</i> sp., <i>Bathypolypus sponsalis</i> , benthic fishes (1)
<i>Nettastoma melanurum</i>	WC, NS, OS – QS, H, S	BS	Benthopelagic	Predator hunting macrofauna. It feeds mainly on crustaceans and finfish (25)
<i>Nezumia sclerorhynchus</i>	NS, OS – H, RS, F	BS, LCF	Benthopelagic (14; 18), searching in the sediment	Generalist feeder: epibenthic and infaunal invertebrates (14; 18)
<i>Pagellus bogaraveo</i>	NS – AS, QS, H, S	BS, BR, LCF, CF/H	Benthopelagic, hovering	Benthic prey near the bottom and pelagic species in the water column (19; 27)
<i>Phycis blennoides</i>	NS, OS – QS, H	BS	Benthic, hovering, station holder (29)	Epibenthic species, decapods, mysids and teleosts (20)

1: Carrassón et al. (1997); 2: Carrassón et al. (1992); 3: Cartes (1993); 4: Cartes (1995); 5: Cartes et al. (2008); 6: Cartes et al. (1993); 7: Company & Sardà (1997); 8: Consoli et al. (2010); 9: Costa (1991); 10: Demestre & Abelló (1993); 11: Demestre et al. (1993); 12: D'Onghia et al. (1996b); 13: Heegaard (1967); 14: Macpherson (1979); 15: Mianzan et al. (1996); 16: Maiorano et al. (2002); 17: Matarrese et al. (1995); 18: Mauchline & Gordon (1984); 19: Morato et al. (2001); 20: Morte et al. (2002); 21: Nouar & Maurin (2000); 22: Palandri & Orsi Relini (1992); 23: Relini et al. (2000); 24: Rufino et al. (2006); 25: Saldanha (1986); 26: Sardà et al. (1997); 27: Stergiou & Karpouzi (2002); 28: Sulak et al. (2007); 29: Uiblein et al. (2003); 30: Wurtz & Vacchi (1978)

Chlorophthalmus agassizi is another fish particularly abundant in the Ionian Sea for which a schooling habit is supposed (D'Onghia et al. 2006). Its presence in this 'benthic' group confirms observations by

Ross & Quattrini (2007) of solitary individuals closely associated with the bottom, revising the opinion on the schooling habit of this fish deduced from trawl surveys. The occurrence of the gadiform fish *Phycis*

blennoides in the first group seems to be due to its feeding on epibenthic species, mostly decapods, mysids and teleosts (Morte et al. 2002). However, *P. blennoides* was observed displaying station-holding behaviour slightly above the bottom in the Bay of Biscay (Uiblein et al. 2003).

A benthopelagic habit was confirmed for the macrourid fishes *Nezumia sclerorhynchus* and *Caelorinchus caelorhincus*, which feed primarily on epibenthic and infaunal invertebrates and appear to be generalist feeders (Macpherson 1979, Mauchline & Gordon 1984). On the contrary, since *Hymenocephalus italicus* shows a more pelagic feeding habit than the other 2 species (Marshall & Merrett 1977, Geistdoerfer 1978, Macpherson 1979), it was included in Group 3 together with other Macrouridae fishes not specifically identified. In the cold-water coral reefs off the south eastern USA, *N. sclerorhynchus* was found to be very abundant in reef, transition reef and off reef habitats, while *C. caelorhincus* was only collected in transition and off reef and *H. italicus* only off reef (Ross & Quattrini 2007, 2009).

Only the second species or taxa group identified in the MCA factorial plane seems to be influenced by the macrohabitat typology. The standardized abundance of species or taxa in this group exhibited a linkage with coral and hardground habitats, showing a pelagic habit. Most probably, these species or taxa need to make reference to 3D structures in their daytime vertical migration. In addition, the corals might be attractive as a habitat and hydrographically mediated small-scale factors could increase the density of zooplankton which may be preyed upon by these pelagic fauna (Husebø et al. 2002). All cephalopod species recorded in this group are known as mesopelagic squids, covering a wide depth range during their daytime vertical migration searching for food (Roper & Young 1975, Guerra 1992). Although they have been previously recorded in the Ionian Sea (Tursi et al. 1994, D'Onghia et al. 1995, 1996a, Maiorano et al. 1999), their detection is rather rare when using bottom trawl nets. Their general behaviour, swimming in the water column, seems to be typical of most Teuthoidea species which are generally attracted by light sources. The shrimp *Plesionika martia*, widely distributed in the Ionian Sea (Maiorano et al. 2002, 2010), was also included in this group of taxa mostly recorded in the water column. *P. martia* exhibited a clear behavioural pattern of quietly swimming near the seabed in habitats characterized by the presence of corals. Its occurrence with species mostly recorded in the water column is a result of the MCA, which is particularly influenced

by activity and position in the first dimension and macrohabitat typology and activity in the second dimension. In fact, all *P. martia* individuals were recorded quietly swimming like almost all the species or taxa in this group, and all *P. martia* individuals were recorded in CF, LCF and H benthic macrohabitats, like many other individuals in this group. The golden shrimp *P. martia* is an active predator of macroplankton, feeding mainly on benthopelagic crustaceans, while small fishes, polychaetes and sergestidae represent secondary prey. Daily and seasonal changes in the diet have also been described for this shrimp (Cartes 1993). *Solenocera membranacea* was always recorded in the water column. Although this shrimp seems to have a high affinity for muddy bottoms where it feeds on large polychaetes at night (Heegaard 1967, Demestre & Abelló 1993) and other benthic organisms (Cartes 1995), a low influence of the substrate and the lack of significant correlations with sediment has recently been reported, probably in relation to its large size and strong swimming ability (Rufino et al. 2006).

The endemic Mediterranean deep-water species *Lepidion lepidion* together with *Pagellus bogaraveo*, *Conger conger* and *Etmopterus spinax* that probably cruise near the seabed actively searching for epibenthic or demersal prey were included in Group 3. Although *P. bogaraveo* was observed in different macrohabitats, its distribution seems to be influenced by the presence of corals. Moreover, this fish showed the typical behaviour of hovering near the seabed. *P. bogaraveo* is mostly caught using longlines in the Ionian Sea and fishermen report that the SML coral area is an attractive fishing ground for this fish (D'Onghia et al. 2010). It also feeds both near the bottom on benthic prey and in the water column on pelagic species (Morato et al. 2001, Stergiou & Karpouzi 2002). Considering observations of exclusive occurrence in coral areas (D'Onghia et al. 2010), *P. bogaraveo* seems to be energetically dependent on the hydrographically mediated food production of the whole SML coral area, even though it is still not known whether its occurrence is directly linked to corals.

The deep-water velvet shark *Etmopterus spinax* is an active predator feeding on a wide range of benthic and free-swimming organisms, mostly represented by cephalopods (Wurtz & Vacchi 1978, Carrassón et al. 1992). The observed behaviour appears to be linked to its active search for food (Mauchline & Gordon 1983).

The recorded mobile fauna distributed over the upper and middle slopes of the SML coral province act as predator, prey or scavenger according to their

life stage and opportunistic encounter in the environment (Table 6). Thus, the observed behaviour can be regarded as a combination of different feeding strategies and a trade-off between foraging and predator avoidance (Lorance & Trenkel 2006). However, since most of the species observed carry out noteworthy daily and seasonal migrations, often varying position, feeding and activity and, consequently, general behaviour throughout their life cycle, different association patterns from those detected in this study cannot be excluded.

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