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ARTICLE *in* ESTUARINE COASTAL AND SHELF SCIENCE · NOVEMBER 2010

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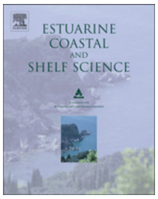

Fish community structure on littoral rocky shores in the Eastern Aegean Sea: Effects of exposure and substratum

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ARTICLE INFO

Article history:
Received 1 December 2009
Accepted 6 August 2010
Available online 13 August 2010

Keywords:
fish assemblages
underwater visual census
Eastern Aegean Sea
exposure
substratum heterogeneity
boulder complexity

ABSTRACT

Littoral rocky shores are important habitats for many coastal fish species providing food, shelter and nursery grounds. Nearshore fish community structure results have been mainly derived from macro-scale habitat characteristics including depth and wave exposure but the influence of, and interaction with, micro-scale habitat substratum features is not well known. This study investigated the structure and functioning of the ichthyofauna composition on rocky substrata around the island of Arki in the Eastern Aegean Sea. Quantitative surveys of fish assemblage composition were carried out by Underwater Visual Census (UVC) at 14 sites assigned to three levels of exposure. The physical substratum of every transect area was described by 14 microhabitat characteristics. Multidimensional scaling (MDS) showed that exposure to wave activity was a significant factor in structuring fish assemblages differing in feeding guilds, species richness and diversity. Substratum heterogeneity, depth, boulder complexity and verticality were the main substratum descriptors that were related with wave exposure and hence were the determining factors defining fish community structure, as revealed by Canonical Correspondence Analysis (CCA). The similarity of percentages (SIMPER) determined the species that typified the different exposure groups. This study has shown that rocky littoral shores are of high ecological importance and their conservation is of great significance to maintain coastal fish diversity.

1. Introduction

Marine shallow nearshore zones (including coastal lagoons, mangroves, estuaries, seagrass beds, coral reefs and rocky shores) possess high productivity, strong seasonality and high physical disturbance (Planes et al., 2000). Such zones are an important habitat for fish worldwide, providing food and shelter from predators (Hindell et al., 2000; Hyndes et al., 2003; Ornellas and Coutinho, 1998) and a nursery ground for numerous species (Cocheret de la Morinière et al., 2002; García-Rubies and Macpherson, 1995; Lloret et al., 2002; Nagelkerken et al., 2000). Spatial and temporal variation in fish community structure is driven by biotic factors (settlement, predation, competition, spawning, etc.) and environmental factors (light and nutrient availability, depth, temperature, algal cover, habitat complexity, etc.). Both sets of factors play a major role in controlling nearshore fish community structure and can be described as the habitat structure, defined by Thrush et al. (2001) as a term encompassing the variety, abundance and spatial arrangement of a variety of physical and biological processes. Increasing disturbance in the coastal zone, as a result of anthropogenic pressures such as urban developments, tourism and the use of destructive illegal fisheries, strongly modifies the habitat structure of littoral ecosystems and as such impacts ecosystem functioning altering fish communities (Fishelson et al., 2002; Guidetti and Boero, 2004; Guidetti et al., 2002; Hughes et al., 2003; Kucuksezgin et al., 2006; Letourneur et al., 2001; Pinnegar and Polunin, 2004).

The fish abundance in the coastal zone of the Mediterranean Sea is highest in highly productive seagrass beds (*Posidonia oceanica*, *Cymodocea nodosa*, *Zostera noltii*) and in shallow rocky habitats. Seagrass beds have been studied in depth, with respect to their role as a spawning ground, a nursery area for juvenile fish and a suitable area for settlement. Fish abundance has been shown to be related to the depth and structural features of the seagrass beds (Guidetti, 2000; Guidetti and Bussotti, 2000; Vega Fernández et al., 2005) and to the diversity of microhabitats in *P. oceanica* beds (Bell and Westoby, 1986). Rocky shores are substrata for macroalgae and sessile invertebrates which, along with topographic features of these sites, result in high habitat complexity (Guidetti and Boero,

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doi:10.1016/j.ecss.2010.08.007

2004). Rocky habitats therefore act as feeding and nursery areas supplying food and refuge to many adult and juvenile fish (Guidetti, 2000). Algal rocky shores are therefore of special ecological importance and their conservation is of great significance in maintaining coastal fish diversity.

The responses of fish assemblages to habitat features of rocky shores have been extensively studied, largely focusing on macro-scale habitat characteristics, i.e. depth, wave exposure and bottom slope topography (Colloca et al., 2003; Gust et al., 2001; Kallianiotis et al., 2000; Kallianiotis et al., 2004; Valesini et al., 2004). This approach is most suitable in highly heterogeneous habitats subject to strong environmental gradients. The relative importance of these processes in structuring ecological communities is still largely unknown. Difficulties in separating the effect of habitat characteristics from other environmental influences, in addition to large geographical variation, create problems when describing the response of fish assemblages to habitat features (McCoy and Bell, 1991). However, on a smaller spatial scale, the influence of micro-habitat features of substratum better describes species abundance and distribution patterns, providing an explanation for the variation in fish community structure within the habitats over a larger scale. Such work has focused on tropical coral reef fish (Aburto-Oropeza and Balart, 2001; Bozec et al., 2005; Chabanet et al., 1997; Friedlander and Parrish, 1998; Garpe and Öhman, 2003), small crypto benthic fish (Costello, 1992; La Mesa et al., 2004; Macpherson, 1994; Wilkins and Myers, 1992), juvenile fish (García-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995), but to a lesser extent for entire fish communities in temperate rocky shores (Harmelin, 1987; Ruitton et al., 2000). However, it has been suggested that increased habitat complexity by large artificial reef units improved the diversity and abundance of fish assemblages (Charbonnel et al., 2002; Diamant et al., 1986; Moreno, 2002; Sánchez-Jerez et al., 2002). Exposure to wave activity has been studied as a macro-habitat characteristic that has a strong influence on the distribution of fish species (La Mesa et al., 2004) but the correlation with microhabitat features of substratum has not been made clear. In this study we attempt to define the importance of the degree of exposure on the physical substratum and the related biodiversity of fish assemblages over algal rocky shores.

The importance of nearshore zones to ichthyofaunal biodiversity has been studied by classical community descriptors, e.g. species richness, abundance and biodiversity indices. However, functional categorisation of marine species can be a useful approach for comparing communities over large spatial scales and for linking the effects of ecological functioning to changes in community structure (Cartes et al., 2002; Franco et al., 2006; Micheli and Halpern, 2005). A variety of functional guilds have been used, mostly based on the biological characteristics of species, i.e. spatial and temporal use of an area, type of food and nature of reproduction (Elliott and Dewailly, 1995). In the present study both the classical community descriptors and the functional guild approach were combined, this combination being of proven value in studies by Bond et al. (1999) and Nagelkerken and van der Velde (2004).

In the eastern part of the Aegean Sea there are few studies carried out on shallow coastal fish assemblages, whereas more research has been conducted in the North Aegean Sea (Kallianiotis et al., 2004; Labropoulou and Papaconstantinou, 2004), and a concentration of fisheries research has been conducted in the South Aegean Sea (Kallianiotis et al., 2000; Tserpes et al., 1999; Tsimenides et al., 1991). The objective of the present study was therefore to understand the structure and functioning of the ichthyofaunal composition on rocky substratum around the island of Arki in the Eastern Aegean Sea. The first aim was to explore variation in fish assemblages (numerical abundance, species richness and diversity) that respond to varying levels of exposure. The second aim was to characterise fish species and biological traits that could be assigned to habitats of different exposure and to assess the relative importance of these different habitats for fish belonging to different trophic levels. The third and final aim was to find descriptors related to the substratum structure, that explain the biological variability among fish communities between sites of different exposure to wave activity.

2. Materials and methods

2.1. Study area and field methods

The study was conducted in the littoral zone around the island of Arki, in the Eastern Aegean Sea (37°23′N, 26°44′E; Fig. 1a). Arki is a small island (approx. 7000 m^2 and highest elevation 111 m). There is no direct nutrient input as Arki lacks any rivers and has no industry or intensive agriculture. As the island is sparsely populated, anthropogenic impacts are limited to disturbance by small-scale fisheries, as well as seasonal tourism and boat impact. Nearshore currents are controlled by the predominant NW wind, and tidal range is negligible. Coastal habitats range from sheltered seagrass beds (*Posidonia oceanica*) to exposed rocky substrata. This study concentrated on shallow waters (3–6 m) as they generally have high levels of primary productivity and correspondingly high secondary productivity maintaining the richest ichthyofauna (García-Rubies and Zabala, 1990).

Fourteen sites around Arki were surveyed (Fig. 1b), differing in physical structure, but not having predictable zonation patterns as described in other geographical regions (Garpe and Öhman, 2003). Therefore only three levels of exposure from wave activity were investigated, with exposure defined by two factors; firstly, the degree of exposure to a direct and north-westerly fetch and secondly, the location in a bay or along the open coast. Among the 14 sites, 5 were identified as sheltered (A: protected from NW fetch and located in a bay), 5 were classified as moderately exposed (B: occasionally exposed to NW fetch but located in a minor bay or protected by surrounding islands) and 4 sites were identified as exposed (C: often exposed to NW fetch and not protected by the bay).

Quantitative surveys of fish assemblage composition and habitat characteristics were carried out in July and August 2005. Sea surface temperature (SST) ranged between 20.8 °C and 26.6 °C. Water turbidity was low, with horizontal Secchi disk readings ranging from 10 to 30 m. Fish surveys employed the non-destructive Underwater Visual Census (UVC) technique, based on the standardised procedures of Harmelin-Vivien et al. (1985). The UVC technique was selected among the available visual methods as this method is non-destructive, inexpensive and it gives rapid results. It can be used on heterogeneous rocky substrata, surveys can be repeated and results can be compared with other studies. However, differences in accuracy occur between observers and fish may be attracted or scared off by the observers (Nagelkerken et al., 2000). To reduce bias, surveys were carried out in this research by one experienced researcher. A 50 m transect was laid out parallel with the substratum slope at 3–6 m depth. After waiting 15 min to minimize disturbance, the observer identified the species and their abundance was recorded on a pre-prepared PVC slate. Species were counted 2.5 m either side of the measuring tape, at a speed of approximately 2.5 m min^{-1} taking 20 min to survey the entire transect area (250 m^2). A series of 5 duck dives covering 10 m^2 was carried out at equal distances along each transect to identify benthic and cryptic species. Surveys were carried out between 09:00 and 17:00 to exclude diurnal patterns on fish behaviour (Gray et al., 1998). This time window also excluded periods of poor visibility caused by low sun angle. Within each sampling site, 6 transects were surveyed continuously along the coast but separated by a minimum of 5 m. Transects were performed in July 2005 and

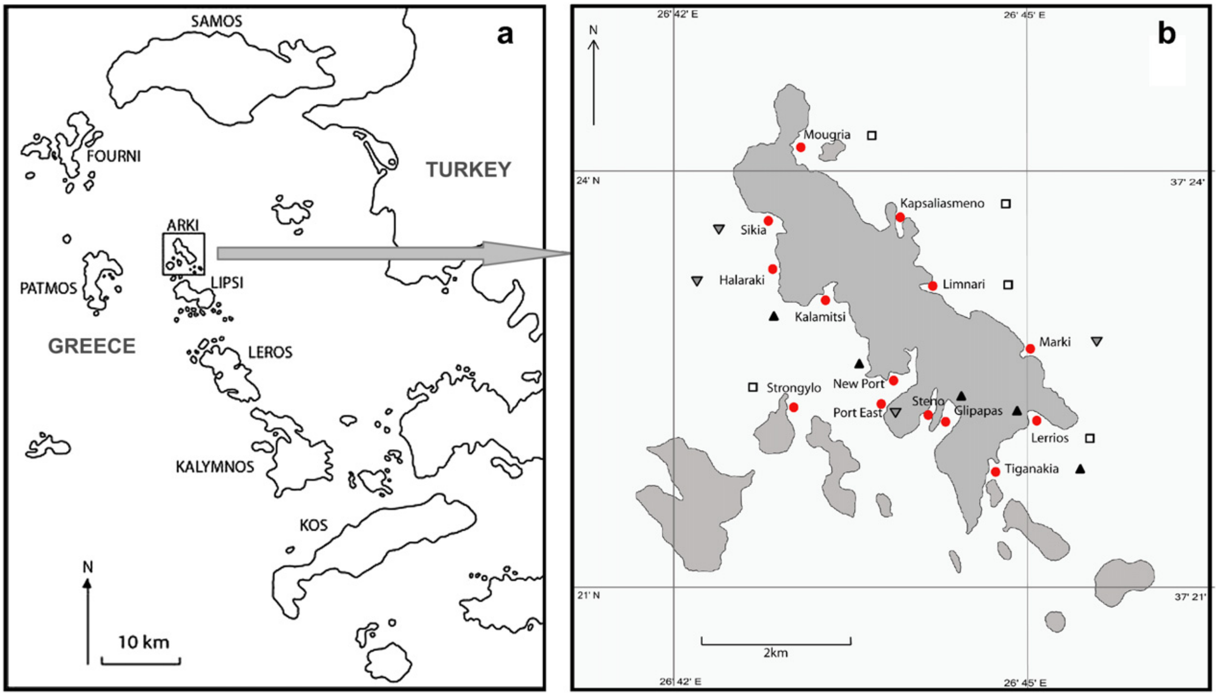

Fig. 1. (a) Geographical location of the study area. (b) Sampling locations in Arki, Greece: sites were either sheltered (Glipapas, Kalamitsi, New Port, Steno, Tiganakia ▲), moderately exposed (Kapsaliasmeno, Lerrios, Limnari, Mougria, Strongylo □) or exposed (Halaraki, Marki, Port East, Sikia ▽) to wave activity.

repeated the following month. After completing the fish survey of each transect, 14 microhabitat descriptors that described the physical habitat/substratum were assigned to each transect area. The relative percentage cover of rock, sand and seagrass was visually estimated and used to calculate the substratum heterogeneity, based on the Shannon Wiener index ($H' \log e$). The deepest and shallowest point at each transect was measured and the verticality was determined as a function of the difference between these depths. The mean depth of each transect was calculated from an average of 6 depth readings along each transect. The percentage of boulders grouped into 5 size classes ($<$10 cm, 10–50 cm, 50 cm–1 m, 1–2 m and $>$2 m) was estimated and used to calculate the boulder complexity based on the Shannon Wiener index ($H' \log e$).

2.2. Statistical analysis

Fish assemblages were compared between sites with different level of exposure using classical community descriptors; species richness, abundance and diversity. Species richness was expressed as the number of species (S) found over all transects; abundance was the average number of individuals over all transects (N), diversity was calculated for each transect using Hill's N1 index as a univariate measure of the species diversity (Hill, 1973). This index, which is the exponential of the Shannon Wiener function (exp H'), has been applied in many studies on fish assemblages (Blanchard, 2001; Greenstreet and Hall, 1996). All species analyses were performed excluding the ubiquitous family Atherinidae, due to the large variation in abundance because of an inexact estimation that confounded the normality of species data. Fish species were divided into feeding guilds and habitat area. Six feeding guilds were identified based on published material (Franco et al., 2006) and Fishbase (Froese and Pauly, 2000): herbivorous (HE), herbivorous–invertivorous (HI), invertivorous (IN), carnivorous (CA), planktivorous (PL) and omnivorous feeders (OM). Habitat associated fish species were categorised into pelagic (PE), demersal (DE), benthopelagic (BP) and reef associated (RA). Community descriptors and associations with feeding guilds and habitats were compared between exposure categories using a one-way ANOVA after $\log(x+1)$ transformations to meet the assumptions of normal distribution (Kolmogorov–Smirnov test) and homogeneity of variances (Levene's test criteria) (Sokal and Rohlf, 1995). Tukey's a posteriori test was used to determine where the differences resided. Statistical analyses were carried out using Minitab Version 14 software.

Community composition was analysed by comparing species abundance per transect in each site using the nonmetric multidimensional scaling (MDS) ordination technique of PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 statistical package (Clarke, 1993). From the original samples by species matrix, rarer species ($<$3% of occurrence) were eliminated (Table 1) to produce the final reduced matrix (84×50). The mean abundance of each species was square root transformed to down weigh large numbers and the Bray–Curtis similarity coefficient was calculated to generate a similarity matrix. Multivariate dispersion (MVDISP) was used to compare the degree to which the points for the samples from the three different levels of exposure were dispersed (Somerfield and Clarke, 1997). Averages of fish species per transect per month were used to assess any spatial or temporal trend in fish assemblage composition using a two-way crossed analysis of similarities (ANOSIM) (Clarke, 1993). Where significant differences were found, particular emphasis was placed on the R-statistic values to ascertain the extent of fish composition differences. R-statistic values close to unity indicate high difference in composition of samples, whereas those close to zero indicate a low level of difference. Similarity Percentages (SIMPER) (Clarke and Warwick, 1994) were employed to determine which species contributed the most to any similarities within exposure groups.

Associations between species abundances (square root transformed) and microhabitat descriptors (standardised) were examined with the canonical correspondence analysis (CCA) using CANOCO version 4.0 (ter Braak and Smilauer, 2002). CCA is a weighted

Table 1
Mean abundances (250 m^{-2}) ± standard deviations of all species recorded during the study with visual census averaged over different levels of exposure. Rare species, $<3\%$ of occurrence, were indicated with an asterisk (*). Fish species were assigned to habitat type (HAB): pelagic (PE), demersal (DE), benthopelagic (BP), reef associated (RA) and to feeding guild (FG): herbivorous (HE), herbivorous-invertivorous (HI), invertivorous (IN), carnivorous (CA), planktivorous (PL) and omnivorous (OM).

Family	Species	Species abbreviation	Highly sheltered	Moderately exposed	Highly exposed	HAB	FG
Apogonidae	*Apogon imberbis*	apim	7.38 ± 7.65	4.05 ± 3.16	7.75 ± 7.06	RA	CA
Atherinidae			411.83 ± 320.39	472.67 ± 365.44	292.08 ± 151.53	PE	
Belonidae	*Belone belone*	bebe	0.02 ± 0.09	0.02 ± 0.09	0.02 ± 0.10	PE	CA
Blenniidae	*Lipophrys trigloides**				0.02 ± 0.10	DE	HI
	Parablennius gattorugine	paga	0.08 ± 0.19	0.08 ± 0.23	0.06 ± 0.17	DE	IN
	Parablennius rouxi	paro	0.63 ± 1.17	0.45 ± 1.18	0.02 ± 0.10	DE	HI
	Parablennius sanguinolentus	pasa	0.08 ± 0.23			DE	HE
	*Parablennius tentacularis**		0.02 ± 0.09			DE	IN
	*Parablennius zvonimiri**				0.02 ± 0.10	DE	HE
Bothidae	*Bothus podas*	bopo	0.10 ± 0.31	0.02 ± 0.09		DE	CA
Carangidae	*Pseudocaranx dentex*	psde	0.10 ± 0.55	0.08 ± 0.23	0.08 ± 0.24	RA	PL
	Trachinotus ovatus	trov	0.05 ± 0.15	0.02 ± 0.09		PE	CA
Gobiidae	*Gobius auratus**		0.02 ± 0.09			DE	HI
	Gobius bucchichi	gobu	1.52 ± 0.99	1.10 ± 1.04	0.90 ± 0.82	DE	HI
	Gobius cobitis	goco	0.12 ± 0.28	0.08 ± 0.23	0.04 ± 0.14	DE	HI
	*Gobius fallax**		0.03 ± 0.13			DE	IN
	Gobius geniporus	goge	2.37 ± 1.80	1.67 ± 1.36	0.73 ± 0.91	DE	IN
	Gobius paganellus	gopa	0.07 ± 0.17	0.02 ± 0.09	0.02 ± 0.10	DE	IN
	Gobius vittatus	govi	1.28 ± 1.70	0.93 ± 1.06	0.19 ± 0.48	DE	HI
Holocentridae	*Sargocentron rubrum*	sarg	0.15 ± 0.33		0.02 ± 0.10	RA	CA
Labridae	*Coris julis*	coju	20.35 ± 7.29	32.87 ± 13.42	29.75 ± 8.53	RA	IN
	Labrus merula	lame	0.07 ± 0.17	0.08 ± 0.23	0.02 ± 0.10	RA	IN
	*Labrus viridis**			0.03 ± 0.18		RA	IN
	Symphodus cinereus	syci	0.52 ± 0.76	0.23 ± 0.41	0.08 ± 0.24	DE	IN
	Symphodus doderleini	sydo	0.88 ± 1.09	0.33 ± 0.51	0.27 ± 0.39	DE	IN
	Symphodus mediterraneus	syme	1.68 ± 1.23	3.28 ± 2.25	2.21 ± 1.18	DE	IN
	Symphodus melanocercus	syml	0.05 ± 0.20	0.37 ± 0.92	0.31 ± 0.48	RA	IN
	Symphodus ocellatus	syoc	0.22 ± 0.58	0.07 ± 0.17		RA	IN
	Symphodus roissali	syrs	1.48 ± 2.01	1.38 ± 1.84	1.13 ± 1.14	RA	IN
	Symphodus rostratus	syrr	0.43 ± 0.69	0.92 ± 0.86	0.60 ± 0.61	RA	IN
	Symphodus tinca	syti	6.85 ± 3.11	6.90 ± 2.90	5.25 ± 1.88	RA	IN
	Thalassoma pavo	thpa	22.65 ± 7.40	22.07 ± 7.79	33.40 ± 13.15	RA	IN
Mugilidae		mugi	4.47 ± 6.25	3.67 ± 5.28	4.06 ± 3.83	BP	OM
Mullidae	*Mullus surmuletus*	musu	2.67 ± 1.82	2.60 ± 2.28	1.08 ± 1.05	DE	CA
Muraenidae	*Murena helena*	muhe	0.15 ± 0.33	0.10 ± 0.33	0.17 ± 0.35	RA	CA
Pomacentridae	*Chromis chromis*	chch	17.57 ± 14.41	29.53 ± 16.74	23.56 ± 14.06	RA	PL
Scaridae	*Sparisoma cretense*	spcr	2.78 ± 2.84	2.38 ± 2.70	4.02 ± 2.61	RA	HI
Sciaenidae	*Sciaena umbra**			0.05 ± 0.27		DE	CA
Scorpaenidae	*Scorpaena maderensis*	scma	0.35 ± 0.54	0.85 ± 1.00	0.71 ± 0.72	DE	CA
	Scorpaena notata	scno	0.02 ± 0.09	0.10 ± 0.24	0.10 ± 0.25	DE	CA
	Scorpaena porcus	scpo	0.12 ± 0.25	0.28 ± 0.39	0.48 ± 0.68	DE	CA
	Scorpaena scrofa	scsc	0.08 ± 0.23	0.15 ± 0.33	0.08 ± 0.24	DE	CA
Serranidae	*Epinephelus costae*	epco	0.02 ± 0.09	0.03 ± 0.13		DE	CA
	Epinephelus marginatus	epma	0.05 ± 0.20	0.08 ± 0.23	0.10 ± 0.25	RA	CA
	Serranus cabrilla	seca	5.67 ± 2.26	5.13 ± 2.41	3.63 ± 1.85	DE	CA
	Serranus scriba	sesc	1.48 ± 1.05	2.75 ± 2.12	3.10 ± 1.55	DE	CA
Siganidae	*Siganus luridis*	silu	0.70 ± 2.00	0.88 ± 1.18	4.27 ± 5.44	RA	HE
Sparidae	*Boops boops*	bobo	1.92 ± 4.57	0.38 ± 1.83	0.85 ± 3.09	DE	OM
	*Dentex dentex**		0.02 ± 0.09	0.02 ± 0.09		BP	CA
	Diplodus annularis	dian	6.37 ± 3.32	4.25 ± 3.83	3.94 ± 2.15	BP	IN
	Diplodus puntazzo	dipu	0.37 ± 0.60	0.25 ± 0.64	0.92 ± 1.10	BP	HI
	Diplodus sargus	disa	4.60 ± 2.79	3.62 ± 2.42	3.54 ± 1.71	DE	IN
	Diplodus vulgaris	divu	3.15 ± 2.50	4.27 ± 2.57	3.10 ± 2.15	BP	IN
	Oblada melanura	obme	4.32 ± 3.65	8.05 ± 5.62	7.67 ± 6.58	BP	OM
	*Pagrus pagrus**			0.02 ± 0.09		BP	CA
	Sarpa salpa	sasa	4.82 ± 3.02	12.58 ± 14.41	12.17 ± 10.83	BP	HI
	Sparus aurata	spau	0.02 ± 0.09		0.04 ± 0.14	DE	HI
Sphyraenidae	*Sphyraena* sp.*			0.02 ± 0.09		PE	CA
Tripterygiidae	*Tripterygion delaisi*	trde	1.38 ± 1.22	1.10 ± 0.96	0.73 ± 0.88	DE	IN
	Tripterygion melanurus	trme	0.88 ± 1.17	2.10 ± 2.48	1.67 ± 1.71	DE	IN
	Tripterygion tripteronotus	trtr	0.27 ± 0.52	0.2 ± 0.34	0.08 ± 0.24	DE	IN
Total species richness			55	53	48		
Total average abundance (without Atherinidae)			133.41 (96.38)	162.42 (111.34)	162.98 (101.64)		

averaging method that directly relates community data to environmental variables by constraining species ordination to a pattern that correlates maximally with environmental variables. Rarer species ($<3\%$ of occurrence) were eliminated in CCA. Inter-set correlations between environmental microhabitat variables and CCA axes were used to assess each variable's contribution. Monte Carlo permutation test (999 permutations) and the forward selection option served us to evaluate the significance of each environmental variable in the faunal assemblage. To avoid colinearity between microhabitat descriptors, the original dataset ($n = 14$) was reduced to 10 microhabitat

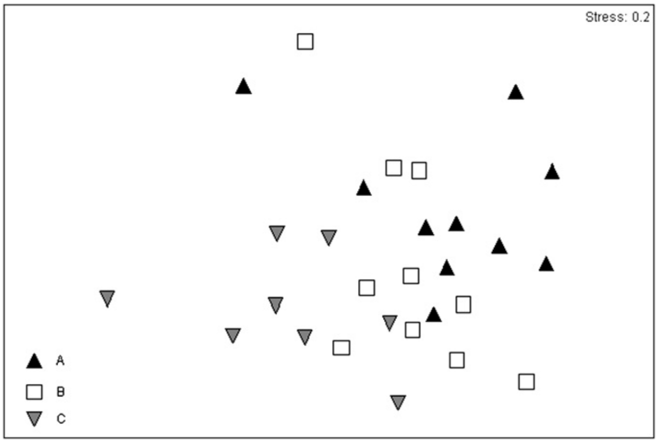

Fig. 2. Nonmetric multidimensional scaling (MDS) ordinations of the average fish abundance data per month recorded at 14 sampling sites around Arki representing three exposure levels (A: sheltered ▲, B: moderately exposed □, C: exposed ▽), stress = 0.20.

descriptors; percentage of 1–2 m boulders and >2 m boulders were pooled due to their highly significant correlation ($r > 0.7$), whereas percentage of <10 cm boulders (negative correlation with percentage >1 m boulders) and percentage rocky and sandy substratum (both negative correlation with substratum heterogeneity) were eliminated from the analysis.

3. Results

3.1. Fish assemblages and effect of exposure

A total of 21 families and 61 species of fish were recorded for rocky substrata at the 14 survey sites (Table 1). Species richness was underestimated, as individuals belonging to Atherinidae and Mugilidae were not identified to species level due to the difficulty of specific determination by direct visual observation. A total of 44 species (72%) were common between sites of different exposure level. Families most represented at species level were Labridae (12 species), Sparidae (10), Gobiidae (6) and Blenniidae (6). Gregarious species such as *Thalassoma pavo*, *Coris julis* and *Chromis chromis* collectively dominated the fish assemblage, representing 50% of total fish abundance for all transects. The number of species observed per census ranged from 35 in a sheltered site (Tiganakia) to 16 in a moderately exposed site (Kapsaliasmeno). Independent of sampling site and exposure level, 13 fish species accounted for >90% of the frequency of occurrence in the total 84 transects. These species belonged to 6 families; Atherinidae, Apogonidae, Labridae, Pomacentridae, Serranidae and Sparidae. Cryptic and benthic species of the families of Gobiidae, Trypterigiidae and Blenniidae accounted for 96%, 95% and 39% of the frequency of occurrence respectively.

Two-way crossed ANOSIM did not detect differences in fish composition between July and August ($R = 0.092$, $p = 0.883$). However, fish assemblage composition differed significantly between sites with different exposure ($R = 0.283$, $p < 0.001$). The ANOSIM pairwise test indicate that the greatest differences in ichthyofaunal composition occurred between the highly exposed sites and the highly sheltered sites ($R = 0.465$, $p < 0.001$) and the moderately exposed sites ($R = 0.206$, $p = 0.003$) respectively, while the least difference was detected between the latter two categories ($R = 0.195$, $p = 0.020$). MDS ordination plots derived from the average fish abundance data per month per site (Fig. 2) confirmed that fish communities in sheltered and exposed sites formed two discrete groups. Fish communities in moderately exposed sites were less distinct in composition possessing characteristics from both exposed and sheltered sites. This pattern is reflected in a higher dispersion value for moderately exposed sites (1.031) compared to sheltered sites (0.986) and exposed sites (0.974).

Analysis of Variance (ANOVA) revealed that mean species richness did not differ significantly between sites with different exposure levels, whereas the mean abundance was significantly lower in sheltered sites compared to both moderately exposed and exposed sites. The species diversity, or Hill's coefficient, was, in contrast, significantly higher in sheltered sites compared to both moderately exposed and exposed sites. Moderately exposed and exposed sites did not differ significantly in mean abundance or species diversity (Table 2).

3.2. Fish traits and species separated by exposure

Within feeding guilds (Fig. 3a), the most abundant group was the invertebrate feeders (23 species), followed by plankton feeders (2), carnivorous feeders (19), herbivorous-invertebrate feeders (10), and omnivorous fish (3). Herbivores (3) accounted for less than 3% of the total number of individuals observed. There was no significant difference in total abundances of herbivorous–invertivorous, invertivorous and carnivorous feeders between exposure levels.

Table 2
Results of analysis of variance (ANOVA) performed on community descriptors, feeding guild and habitat of the fish from 6 transects in 14 sites representing different exposure levels (A–B–C), with their average value ± standard deviation. Values are expressed after log ($x + 1$) transformation. Levels of significance; ns, not significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

		Highly sheltered (A)	Moderately exposed (B)	Highly exposed (C)	df	*F* Ratio	*p* Values Tukey post-hoc
Community descriptors							
Species richness	S	1.41 ± 0.05	1.39 ± 0.08	1.39 ± 0.06	2	0.15^{ns}	
Abundance (without atherinidae)	N	2.12 ± 0.08	2.19 ± 0.13	2.20 ± 0.08	2	8.77^{***}	$0.0023^{B>A}$, $0.0012^{C>A}$
Hill's coefficient	N1	1.14 ± 0.07	1.06 ± 0.09	1.05 ± 0.07	2	8.71^{***}	$0.0026^{A>B}$, $0.0011^{A>C}$
Feeding guild							
Herbivorous	HE	0.31 ± 0.60	0.49 ± 0.53	1.20 ± 1.08	2	10.30^{***}	$0.0001^{C>A}$, $0.0022^{C>B}$
Herbivorous–Invertivorous feeders	HI	2.45 ± 0.42	2.64 ± 0.82	2.78 ± 0.75	2	1.63^{ns}	
Carnivorous feeders	CA	2.89 ± 0.36	2.78 ± 0.39	2.80 ± 0.63	2	0.47^{ns}	
Invertivorous feeders	IN	4.31 ± 0.17	4.42 ± 0.31	4.46 ± 0.19	2	3.15^{ns}	
Omnivorous feeders	OM	2.25 ± 0.68	2.35 ± 0.74	2.75 ± 0.59	2	3.85^{*}	$0.0253^{C>A}$
Planktivorous feeders	PL	2.63 ± 0.85	3.24 ± 0.71	3.01 ± 0.75	2	4.58^{*}	$0.0099^{B>A}$
Habitat area							
Benthopelagic	BP	3.15 ± 0.32	3.36 ± 0.63	3.47 ± 0.51	2	3.02^{ns}	
Demersal	DE	3.37 ± 0.25	3.28 ± 0.42	3.08 ± 0.36	2	4.33^{*}	$0.0129^{A>C}$
Pelagic	PE	0.05 ± 0.14	0.04 ± 0.14	0.03 ± 0.11	2	0.19^{ns}	
Reef associated	RA	4.37 ± 0.25	4.58 ± 0.35	4.71 ± 0.28	2	8.50^{***}	$0.0004^{C>A}$, $0.0274^{B>A}$

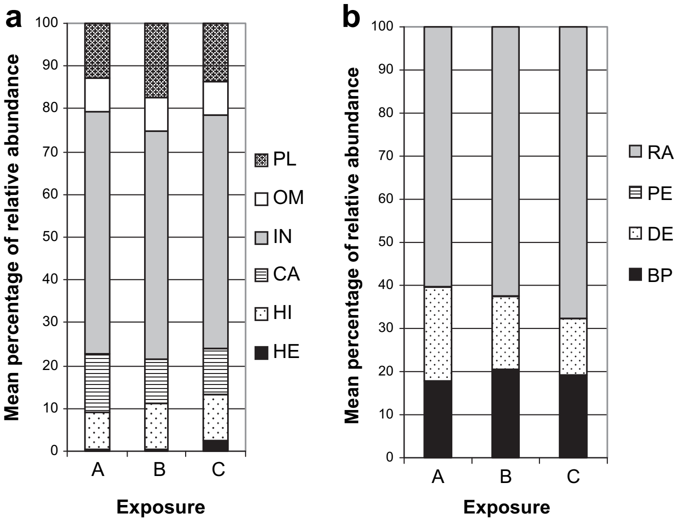

Fig. 3. Mean percentage of relative abundance of fish associated with different (a) feeding guild (HE, herbivorous; HI, herbivorous-invertivorous; CA, carnivorous; IN, invertivorous; OM, omnivorous; PL, planktivorous) and (b) habitat (BP, benthopelagic; DE, demersal; PE, pelagic; RA, reef associated) averaged over all transects belonging to the same exposure level.

However post-hoc comparisons showed a higher abundance of herbivorous feeders in exposed sites compared to sheltered and moderately exposed sites, as well as a higher abundance of omnivorous feeders in exposed sites compared to sheltered sites and a higher abundance of planktivorous feeders at moderately exposed sites compared to sheltered sites (Table 2).

The most abundant group, defined by habitat (Fig. 3b), were demersal fish (32 species), followed by reef associated fish (17 species). The benthopelagic and pelagic species were only represented by 8 and 4 species, respectively. Consequently, the pelagic and benthopelagic fish abundances did not differ between exposure levels but the abundance of demersal fish was significantly higher in sheltered sites compared to exposed sites, whereas the reef associated fish were significantly more abundant in the moderately exposed and exposed sites compared to the sheltered sites (Table 2).

SIMPER analysis performed on ichthyofaunal data (Table 3) detected a relatively high within-group similarity for the identified fish assemblages in the three exposure groups in which 17 species accounted for >90% of the similarity within groups. Fish assemblages in all exposure levels were mainly typified (when contributing a similarity >5%; column 3 of Table 3) by schooling species; *Thalassoma pavo*, *Coris julis* and *Chromis chromis* occurred consistently and accounted for >8% within each exposure group. *Symphodus tinca* also typified all exposure groups. In contrast, other species typified only 1 exposure group; *Diplodus annularis* and *Apogon imberbis* distinguished the fish fauna in sheltered sites, *Serranus cabrilla* distinguished the fish fauna in both sheltered and moderately exposed sites, *Oblada melanura* was typical for only moderately exposed sites and *Sarpa salpa* typified exposed sites. Ephemeral species which were recorded consistently in a particular exposure group (and thus produced relatively high average similarity to standard deviation ratios), but with a lower frequency of occurrence, did not contribute a high percentage to the within-group similarity for the fish assemblages. However, it should be noted that ephemeral species, with a lower contributing similarity percentage, were considered to be important components characterising fish fauna composition for specific exposure groups. As such, those species are represented in column 4 of Table 3.

3.3. Physical microhabitat and link with exposure and fish assemblages

The CCA ordination pattern relating the sites (samples) to the microhabitat descriptors and exposure groups presented a separation of sites from different exposure groups along the first axis. This confirmed that the environmental variables measured in this study were a valuable set to measure the effect of exposure on microhabitat differences between sampling sites. For this analysis, 50% of the variability between sites was explained by all 10 microhabitat descriptors as represented by the first two axes depicted in Fig 4. Axis 1 generally separated the exposed sites from the sheltered sites, accounting for a variation of 33%, and was positively correlated with substratum heterogeneity (0.85) and percentage 10–50 cm boulders (0.47) and negatively correlated with the average depth (−0.74), the deepest (−0.69) and shallowest (−0.56)

Table 3
SIMPER analysis showing average similarity percentages within exposure groups. The average abundance (root transformed) and percentage contribution of typifying species to within-group similarity for the identified fish assemblages in the three exposure groups are shown, both for species contributing >5% to within-group similarity (column 1) and less abundant but regularly occurring in 1–2 exposure groups (column 2).

Exposure groups	Av. Sim.	>5% Contributing species			Regularly but less abundant species		
		Typifying species	Av. Ab.	Contr. %	Typifying species	Av. Ab.	Contr. %
Highly sheltered	71.41%	*Thalassamo pavo*	22.65	12.19	*Mullus surmuletus*	2.67	3.21
		Coris julis	20.35	11.36	*Gobius geniporus*	2.37	3.19
		Chromis chromis	17.57	8.38	*Gobius buchichi*	1.52	2.38
		Symphodus tinca	6.85	6.25	*Tripterigion delaisi*	1.38	1.94
		Serranus cabrilla	5.67	6.01	*Gobius vittatus*	1.28	1.12
		Diplodus annularis	6.37	5.67			
		Apogon imberbis	7.38	5.24			
Moderateley exposed	70.58%	*Coris julis*	32.87	13.6	*Mullus surmuletus*	2.6	2.89
		Chromis chromis	29.53	11.7	*Gobius geniporus*	1.67	2.11
		Thalassamo pavo	22.07	11.52	*Tripterigion melanurus*	2.1	1.95
		Symphodus tinca	6.9	6.31			
		Oblada melanura	8.05	5.69			
		Serranus cabrilla	5.13	5.26			
Highly exposed	74.01%	*Thalassamo pavo*	33.4	13.37	*Sparisoma cretense*	4.02	4.13
		Coris julis	29.75	13.18	*Siganus luridus*	4.27	1.76
		Chromis chromis	23.56	9.73			
		Sarpa salpa	12.17	5.68			
		Symphodus tinca	5.25	5.37			

point of the transect, the boulder complexity (−0.62) and the percentage of >1 m boulders (−0.55). The second axis was negatively correlated with the percentage large boulders (−0.41) and positively correlated with the verticality (0.40). The variation along the second axis explained a further 17% of the variance between species–environment. This axis divided the moderately exposed sites from both the sheltered and exposed sites. CCA eigenvalues of the first four multivariate axes were 0.036 (CCA1), 0.018 (CCA2), 0.013 (CCA3) and 0.010 (CCA4).

The correlation of the biotic pattern with these substratum variables is illustrated in the patterns of ichthyofaunal composition in relation to the microhabitat descriptors (Fig 5). Species–environment correlation coefficients for the first four axes were 0.78, 0.62, 0.66 and 0.61. Cumulative percentage of variance of species for the first four axes (CCA1–4) was 12.6. The first and second axes modelled 6% and 3% of species data, respectively, and they cumulatively accounted for 50% of variance of species–environment relationship modelled by CCA. The test of significance for the first axis and overall CCA was highly significant ($p = 0.005$; Monte Carlo permutation test).

4. Discussion

This study has shown that exposure to wave activity was a significant factor in structuring fish assemblages on littoral rocky shores on the island of Arki (Eastern Aegean Sea). Less abundant but more diverse fish communities exploited sheltered sites compared to exposed sites. Multivariate analysis showed that assemblages in the three different exposure levels were distinctively different, although the R value was smaller than in other studies (Guidetti et al., 2002; Valesini et al., 2004) reflecting the smaller spatial and temporal scale of this study. Evidence from other studies confirm that exposure and depth are the main macro-scale factors driving community composition (Gaertner et al., 1999; García-Rubies and Zabala, 1990; La Mesa and Vacchi, 1999).

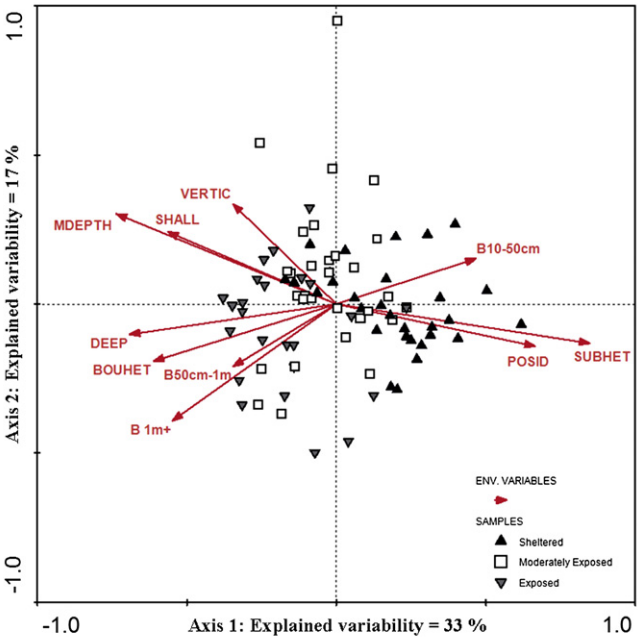

Fig. 4. Ordination diagram of the first two axes from a Canonical Correspondence Analysis (CCA) with 10 microhabitat descriptors and 84 transects (samples) representing three exposure levels.
VERTIC, verticality; SHALL, shallowest point; DEEP, deepest point; MDEPTH, mean depth; BOUHET, boulder heterogeneity; POSID, percentage of seagrass; SUBHET, substrate heterogeneity; B, percentage of boulders of different size classes.

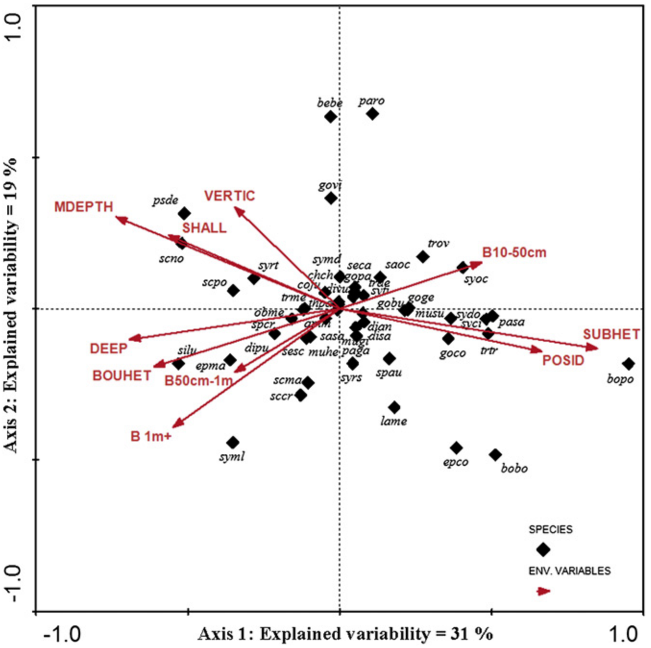

Fig. 5. Ordination diagram of the first two axes from a Canonical Correspondence Analysis (CCA) with 10 microhabitat descriptors and 61 species.
VERTIC, verticality; SHALL, shallowest point; DEEP, deepest point; MDEPTH, mean depth; BOUHET, boulder heterogeneity, POSID, percentage of seagrass; SUBHET, substrate heterogeneity; B, percentage of boulders of different size classes and find species abbreviations in Table 1.

The most important substratum characteristic responsible for these different species assemblages, and high species diversity, in littoral shores with different exposure levels to wave activity was substratum heterogeneity. The availability of a good mixture of sandy patches, *P. oceanica* beds, and rocky walls in sheltered sites was beneficial for a variety of species. These more heterogeneous habitats are known to provide specific substrata for feeding, recruitment and refuge from predators (Aburto-Oropeza and Balart, 2001; Ruitton et al., 2000). In contrast, the exposed sites with predominantly rocky >1 m boulders provide a smaller range of niches resulting in lower species diversity. The mean depth was lower in the sheltered sites explaining the positive effect of shelter on species diversity. The findings of the present study are consistent with previous research where deeper and more homogeneous habitats harbour fewer species, which are highly characteristic of those habitats (Aburto-Oropeza and Balart, 2001). The boulder complexity and boulder size distribution was another important habitat characteristic reflecting influence of exposure on species assemblages. Small boulders are optimal to create small cavities, which are crucial for shelter for small or juvenile fish, as also reported elsewhere (Diamant et al., 1986). Therefore it is likely that the abundance of 10–50 cm boulders gives a good picture of shelter availability in sheltered and moderately exposed sites. Verticality was an important factor distinguishing mainly fish composition in moderately exposed sites. This shows that a high volume of coastal water in some sites was beneficial for certain fish species.

Substratum heterogeneity, water depth, boulder complexity, and verticality were the main contributors to exposure differences, and hence were the determining factors defining fish community structure. However the cumulative percentage of variability in ichthyofaunal composition explained by the first four axes in the CCA was 12.6%; only a small part was directly attributed to measured habitat characteristics. Hence, the role of investigated habitat variables in structuring fish community can be reasonably hypothesized, but other physical, chemical or biological variables not incorporated in the present study could likely account for the unexplained variation. Factors such as structure and coverage of macroalgal communities, which increase habitat complexity and are well supported by rocky reefs in temperate regions, may influence the community structure (Guidetti and Boero, 2004). Macrobenthic and invertebrate communities play an important role in providing food and may also be a determinant of fish structure. Besides the external heterogeneity of a habitat, i.e. that imposed by the variation of environmental factors, variability can emerge as a result of biological processes such as species interactions, dispersal, and colonization (García-Charton and Pérez Ruzafa, 1999). The interactions among these physical, chemical, and biological aspects of any nearshore marine environment will determine the structure of the faunal assemblage.

The census data of this study indicate that nearshore ichthyofauna is a relatively homogenous assemblage of fish and a similar species pool, 44 species or 72%, co-occurred between the three exposure levels. Most common families recorded in this study were Labridae and Sparidae (a family of prominent commercial interest in the Mediterranean), as is usually the case on Mediterranean rocky substrata (Harmelin, 1987; Mariani, 2006; Ruitton et al., 2000). *Thalassoma pavo*, *Coris julis* and *Chromis chromis* accounted for a total abundance of 50% in this study and their distribution did not differ between exposure levels, indicating their tolerance to fluctuating environmental conditions on a small spatial scale and responding to variations in quantity of available resources. In contrast, certain species had a restricted distribution, largely confined to a particular exposure level. Species typifying highly sheltered sites in this study have also been confirmed elsewhere to benefit from the high habitat heterogeneity as we found characteristic to sheltered sites. *Diplodus annularis* was found to be most abundant in highly sheltered sites, which had a high percentage of *P. oceanica* meadows in the vicinity. Other studies confirm that this species is seagrass associated (Bell and Harmelin-Vivien, 1982), where it feeds on a variety of invertebrates. *Apogon imberbis* was found to be an abundant typifying species for the sheltered sites in this study and Riggio et al. (2000) confirms that it is a good indicator species of the maturity of reef communities. *Mullus surmuletus* was highly indicative for sheltered sites in this study, consistent with descriptive studies of Vega Fernández et al. (2005), which found that they forage along seagrass boundaries and in sandy corridors. *Gobius bucchichi* and *Gobius geniporus* were regular but less abundant typifying species in highly sheltered areas, additionally, Miller (1986) reported that they inhabit inshore areas on sandy and muddy substrata with seagrass. *Tripterygion delaisi* preferentially inhabits flat habitats, sheltered from the open sea and covered by small boulders, however, this species can also be found on more exposed rock walls (La Mesa et al., 2004). The presence of *Gobius vittatus* in the sheltered sites is interesting, as this species is known to be rare in the Mediterranean Sea (La Mesa and Vacchi, 1999). Moderately exposed sites are characterised by high boulder complexity and this is reflected by the occurrence of the typifying species *Oblada melanura*, *Mullus surmuletus*, *Gobius geniporus* and *Tripterygion melanurus*. La Mesa et al. (2004) confirmed that *Tripterygion melanurus* is associated with a more complex habitat of cobbles and boulders. Exposed sites had another specific subset of typifying species in this study: *Sarpa salpa*, *Sparisoma cretense* and *Siganus luridus*. The fact that those fish are all herbivorous feeders suggests a good algal growth on the large boulders that typify the exposed sites. Studies of Verlaque (1990) provide evidence that *S. salpa* scrapes boulders in sites dominated by encrusting algae, as they found substratum fragments in stomach contents. *S. salpa* is a distinct diurnal feeder and rests at night, mostly in deeper water (Jadot et al., 2006), suggesting it is likely that shelter availability in the exposed sites is of lower concern for this species and its occurrence is attributed to the high availability of encrusting algae. However, other populations persistently occupy the same sites both day and night so the importance of large boulders for shelter cannot be excluded. As a result, more measurements should be taken to provide absolute certainty about the functional role of exposed sites for herbivorous fish species.

A functional approach is highly valuable to understand how ecological functioning varies with macro- and micro-scale habitat variability. As commented before, exposed sites are highly important for reef associated fish, for obtaining shelter, and for herbivorous feeders, for obtaining their food. Highly sheltered sites demonstrated a higher density of demersal fish. Fish inhabiting moderately exposed sites were not habitat specific but more planktivorous fish, e.g. *Chromis chromis* were abundant at these sites. Planktivores are commonly found along reef edges close to deep water (Friedlander and Parrish, 1998) because of a greater volume of water in which they can feed. The findings in this study that verticality is linked with moderately exposed sites where a high abundance of planktivores occur, supports this hypothesis. Furthermore, pelagic, shoaling species were not found to be directly associated with specific habitats. The use of trophic guilds is not widely used for fish (Cartes et al., 2002; Guidetti et al., 2002; Micheli and Halpern, 2005) and could be subject to criticism. It is not surprising that the attribution of a certain feeding groups or guilds differs between studies, as many fish are euryphagous capable of altering their diet depending on size and season (Cartes et al., 2002). For example, *Diplodus annularis* has shown shifts in diet in the absence of *Posidonia oceanica* meadows (Sánchez-Jerez et al., 2002). Nevertheless one must aim towards a better standardisation between studies to offer comparative results.

The Mediterranean Sea has a long history of overexploitation and depletion of species (Planes et al., 2000), but the Lessepsian migration from the Red Sea has greatly enriched the littoral zone of the Eastern Mediterranean (Fishelson et al., 2002). Corsini-Foka and Economidis (2007) listed 41 species of alien ichthyofauna occurring in Hellenic waters. For example, *Siganus luridus* and *Sargocentron rubrum* are Red Sea immigrants that efficiently utilized an "unsaturated niche" (Golani and Ben-Tuvia, 1985). Continued monitoring of these prolific, colonizing species may produce additional insight into the ecological impact on the pre-existing fish fauna. Migrant species, less common in the Western Mediterranean, likely explain the higher overall species richness in this study (61 species of 21 families) than found by other researchers using the visual census technique in other areas of the Mediterranean Sea; 27 species of 12 families (Guidetti et al., 2002), 54 species of 23 families (Diamant et al., 1986; García-Charton and Pérez Ruzafa, 1999); 40 species of 17 families (Charbonnel et al., 2002); 21 species of 9 families (Guidetti, 2000); 46 species of 16 families (Ruitton et al., 2000); whereas numbers are lower in the vicinity of polluted or over fished impacted sites 32 species of 14 families; 19 species of 11 families and 17 species of 6 families (Guidetti et al., 2002). Alternatively, some species such as members of the Scorpaenidae were under recorded compared to some previously mentioned UVC studies. Various hypotheses could explain this. Some features of the investigated area might not reflect their habitat preference. This might be especially true for *Scorpaena maderensis*, which has been recorded between 20 and 40 m depth (La Mesa et al., 2004). Or the UVC sampling method, which has been criticised for underestimating the density of cryptic reef fish (Willis, 2001). This could especially be true when the crypto benthic fish are also nocturnal species, e.g. the scorpion fish *Scorpaena porcus*, as there is no active interference with sampling activities.

Both the spatial and temporal scale of this study was limited. We recommend additional research to compare seasonal effects on ichthyofaunal abundances and composition in this area, since it has affected fish communities in other studies (Maci and Basset, 2009; Maravelias et al., 2007; Stergiou et al., 2006). A strong etesian winds blowing in the entire Aegean Sea during summer has been associated with upwelling resulting in favourable feeding conditions and lesser mortalities of numerous fish species (Stergiou, 1992).

Among all species observed, there were two that are protected in Europe according to the Bern Convention (Convention on the conservation of the European Wildlife and natural habitats) and Barcelona Convention (Convention for the protection of the Marine Environment and the Coastal Region of the Mediterranean); the grouper *Epinephelus marginatus* and the brown meagre *Sciaena umbra*, which are also highly-priced target fisheries species. Higher abundances of commercially important species in shallow coastal zones have been reported by Labropoulou and Papaconstantinou (2004). Our study area is very important for small-scale fisheries in the Greek prefectures (Tzanatos et al., 2005) and we emphasize the need for long term studies to investigate changes in fish community structure resulting from increased (or decreased) fishery pressure and application of different management schemes.

In conclusion this study has shown that rocky littoral shores are of vital importance to the maintenance of fish diversity. Exposure to wave activity was a significant macro-scale habitat factor in structuring fish assemblages. Substratum heterogeneity, depth, boulder complexity and verticality were the main microhabitat descriptors related with exposure and hence were the determining factors defining fish community structure. The inventory in this study can serve as baseline data prior to management strategies, as preparative work is undertaken for the establishment of the *National Nature Reserve of the North Dodecanese Islets*, to ensure sustainable conservation of the environment of the area.

Acknowledgements

Thanks to the directors of Archipelagos, to provide logistics and guidance to undertake this survey. We are grateful to all the marine researchers and especially Catriona Lynch, Maria Segovia, Nick Lewis and Rick Mimpen for their fisheries knowledge, assistance during field work, help with mapping and criticism to improve this manuscript. We gratefully acknowledge the fishermen and locals for sharing their knowledge of the area. The authors wish to thank two anonymous reviewers for their constructive criticisms.

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