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Comparing sessile benthos on shallow artificial versus natural hard substrates in the Eastern Mediterranean Sea

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Abstract

Artificial structures cover a considerable part of the Mediterranean coasts. In the Aegean Sea, most studies related to artificial structures have focused in vagile fauna on harbours and marinas but little attention has been given to the sessile biota on coastal defense structures. The aim of this work was to describe for the first time the shallow subtidal sessile benthos on coastal defense structures in Crete (Eastern Mediterranean Sea) in order to identify potential differences in comparison to natural rocky substrates, adopting both a taxonomic and functional (i.e. macroalgal structural complexity) approach. Three shallow (1-3 m) localities were studied in the north coast and three in the south coast of the island (six localities in total). At each locality, two types of hard substrate were selected: an artificial coastal defense structure (rip-rap) and the nearest natural rocky substrates. The percent cover of sessile taxa was calculated using random points counts over photoquadrats (20 x 20 cm). The structure of the assemblage differed between artificial and natural habitats. Values of Shannon-Wiener's diversity index and number of taxa were higher in natural substrates. In addition, cover of arborescent macroalgae was lower on artificial substrates. In conclusion, rip-raps do not function as surrogates of natural hard substrates in the study area since their shallow subtidal assemblages differ in terms of community structure, diversity and functionality. The deficient performance of such artificial structures could be attributed to the combined effects of abiotic factors and biotic processes, including substrate nature and roughness as well as differential grazing pressure.

Keywords: Assemblage structure; defense structures; rip-rap; rocky reefs; surrogates; macroalgae; structural complexity.

Introduction

Shoreline urbanization combined with the increase of tourist, recreational and commercial activities, result in the introduction and proliferation of artificial structures in marine coastal habitats worldwide (Bulleri & Chapman, 2010; Dafforn *et al.*, 2015; Firth *et al.*, 2016a). These structures are mostly linked to coastal defense purposes against sea-level rise, but also to commercial infrastructures, protection against coastal erosion and wave action, extraction of oil (e.g. offshore platforms), energy generation (e.g. wind farms) and aquaculture (Bacchiocchi & Airoidi, 2003; Dafforn *et al.*, 2015; Firth *et al.*, 2016a and references therein). Recently, some eco-engineering interventions have been carried out with the purpose of increasing or maintaining biodiversity inhabiting such structures (see review by Strain *et al.*, 2018). Nevertheless, strict or well-defined ecological criteria and man-

agement practices are lacking during the design stage or after installation of these infrastructures (Moschella *et al.*, 2005; Firth *et al.*, 2014, Dafforn *et al.*, 2015). Their impacts have been largely documented, generally concluding that artificial structures do not function *per se* as surrogates of natural habitats (e.g. Bulleri & Chapman, 2010; Perkins *et al.*, 2015) due to different habitat complexity (e.g. Perkol-Finkel & Benayahu, 2004; Lam *et al.*, 2009; Loke *et al.*, 2015; Mercader *et al.*, 2017), nature of building materials (e.g. Coombes *et al.*, 2015; Sempere-Valverde *et al.*, 2018), surface inclination and orientation (e.g. Moreira *et al.*, 2006; Chapman & Underwood, 2011) and even differential grazing pressure between artificial and natural habitats (Ferrario *et al.*, 2016). Consequently, the importance of ecological characterization of these structures and the incorporation of ecological criteria in their design should not be neglected (Mosquella *et al.*, 2005; Perkins *et al.*, 2015).

The European coasts have been highly modified by the introduction of artificial structures (Airoldi & Beck, 2007). In the Mediterranean Sea, the ecological study of artificial structures as “hot spots” of biological invasions has been particularly prolific, focusing mainly in marinas (e.g. Ros *et al.*, 2014; Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018) or artificial reefs (Fabi *et al.*, 2011; López *et al.*, 2016). However, only few studies have compared communities of natural hard habitats with coastal defense structures (e.g. Gacia *et al.*, 2007; García-Gómez *et al.*, 2015; Ido & Shimrit, 2015). In the Aegean Sea, most studies related to artificial structures have focused in vagile fauna associated with harbours and marinas (Karalis *et al.*, 2003; Chintiroglou *et al.*, 2004; Corsini-Foka *et al.*, 2015; Ulman *et al.*, 2017; Chatzinikolaou *et al.*, 2018; Zenetos *et al.*, 2018), aquaculture facilities (Fernández-González & Sánchez-Jerez, 2017) and artificial reefs (Sinis *et al.*, 2000; Lök *et al.*, 2008; Klaoudatos *et al.*, 2012). Regarding sessile fauna, a recent study in Saronikos Gulf found higher abundances of the cryptogenic coral *Oculina patagonica* over anthropogenic structures compared with natural habitats (Salomidi *et al.*, 2013).

The northern coast of Crete (Eastern Mediterranean Sea, Greece) is greatly affected by urbanization because the largest cities and main tourist infrastructures (e.g. harbours) of the island are located there (e.g. Chatzinikolaou & Arvanitidis, 2016). This has resulted in an increase of maritime traffic and the establishment of various types of coastal defense structures. In spite of this, there is a lack of studies on the impact of these structures on the benthic biota. The aim of this work was to study and compare for the first time the subtidal sessile benthos on coastal defense structures with that of nearby natural rocky substrates around Crete. Our main hypothesis is that the assemblage structure and function (in terms of macroalgal structural complexity) will differ significantly between artificial and natural substrates.

Materials and Methods

Study area

Crete (Greece) is located between the Aegean and Libyan Seas in the Eastern Mediterranean Sea, one of the most oligotrophic marine areas (Boetius *et al.*, 1996) and among the main hotspots for marine bioinvasions worldwide (Rilov & Galil, 2009). Six localities around Crete (Fig. 1) were studied: three in the north (South Aegean Sea) and three in the south (Libyan Sea) coast of the island. Northern localities were Kato Galatas (35.513° N, 23.964° E), Bali (35.413° N, 24.784° E) and Gournes (35.336° N, 25.299° E), while southern localities were Hora Sfakion (31.198° N, 24.136° E), Agia Galini (35.094° N, 24.689° E) and Tsoutsouros (34.150° N, 25.287° E).

At each locality, two types of hard substrates were sampled in the upper subtidal zone (1-3 m deep): (a) artificial boulder-like coastal defense structures (hereafter “rip-raps”) deployed in marinas more than 10 years ago, and (b) nearby natural rock (Habitat type “1170 Reefs”

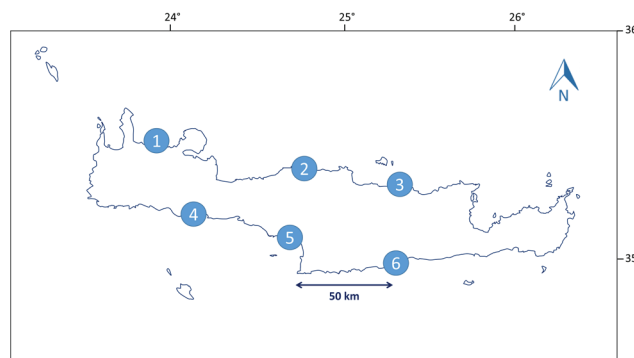


Fig. 1: Sampling localities in Crete Island. 1: Kato Galatas; 2: Bali; 3: Gournes; 4: Hora Sfakion; 5: Agia Galini; 6: Tsoutsouros.

according to the EU Directive 92/43/EEC). Natural substrates within each locality were predominantly adjacent to rip-raps, except for one locality (Gournes) where the only available natural hard substrate was located approximately 1 km away from the rip-raps. The sampled substrates faced North/North-east in the three northern localities and to South in the southern ones.

Sample collection and processing

Sampling took place in July 2017. At each locality, three random sites located tens of meters apart, were selected for each substrate type. Within each site, three quadrats were photographed using an Olympus TG4 camera with a Subacqua Helios 1700 focus light. A total of 108 photoquadrats were collected (3 photoquadrats * 3 sites * 2 substrates * 6 localities). Photoquadrats were randomly taken while snorkeling at a depth of 1-3 m by placing a 20 x 20 cm aluminum square frame (Bianchi *et al.*, 2004). At each site, the first quadrat was placed at the first available subtidal vertical surface orientated seawards. Subsequent quadrats were placed at the first available surface at least 3 m away or further. Cover of sessile species was measured by spawning 100 random points using PhotoQuad software (Trygonis & Sini, 2012). Sessile taxa that were present in the photoquadrats but did not fall below a random point were given an arbitrary value of 0.5% cover (Bacchiocchi & Airoldi, 2003; Marzinelli *et al.*, 2011; Ostalé-Valriberas *et al.*, 2018). Qualitative samples of the main benthic taxa present in the photoquadrats were also collected when needed for accurate taxonomic identification in the laboratory.

Statistical analyses

Taxa cover percentages were calculated for each photoquadrat, and based on these data, values of three diversity indices were further determined: number of taxa (S), Shannon-Wiener’s diversity (H') and Pielou’s evenness (J'). In order to test the null hypothesis of no difference in the aforementioned parameters between substrates and orientations and among localities and sites, multivariate

and univariate statistical analyses were applied.

Four-factor permutational multivariate analysis of variance (PERMANOVA) was used to examine the effect of substrate type, orientation, locality and small-scale heterogeneity (sites within locations) on the structure of the sessile assemblage (based on taxa cover percentages). Thus, four factors were considered: 'Substrate' (Su), a fixed factor with two levels (*Natural, Artificial*); 'Orientation' (Or), a fixed factor with two levels (*North, South*) and crossed with Substrate; 'Locality' (Lo), a random factor nested in Or with three levels for each orientation (North: *Kato Galatas, Bali, Gournes*; South: *Hora Sfakion, Agia Galini, Tsoutsouros*); and 'Site' (St), a random factor nested in Su, Or and Lo, with three levels for each locality (*Site 1, Site 2, Site 3*).

PERMANOVA was run on a triangular similarity matrix derived from Bray-Curtis dissimilarity index of square-root transformed data. In cases of small numbers of unique permutations, P-values were obtained through a Monte Carlo test (Anderson *et al.*, 2008). When significant differences for a given factor or interaction of factors were detected, the sources of variation were identified based on Pair-wise comparisons. Additionally, in order to test the dispersion among samples for the fixed factors Su and Or, a permutational analysis of multivariate dispersions (PERMDISP) was used. No action was taken when there was heterogeneity of variances, since PERMANOVA is largely unaffected by heterogeneity in cases of balanced design (Anderson & Walsh, 2013).

Multivariate non-metric multidimensional scaling (MDS) was also used, along with the Bray-Curtis similarity index to visualize patterns in assemblage structure between substrates, orientations and localities. Kruskal's stress coefficient was used to test whether the ordination was reliable (Kruskal & Wish, 1978). The data (taxa cover percentages) were square-root transformed.

The contribution of each taxon to the Bray-Curtis similarity within each substrate type was determined with the SIMPER (SIMilarity PERcentages) analysis.

A four-factor analysis of variance (ANOVA) following the abovementioned design was used to examine whether the number of taxa, Shannon-Wiener's diversity and Pielou's evenness differed with substrate type, orientation, locality and sites. Prior to ANOVA, heterogeneity of variance was tested with Cochran's test. Since there was heteroscedasticity, Box-Cox routine was applied in order to estimate the most effective lambda (λ) for Box-Cox transformations ($x_t = (x_t^\lambda - 1)/\lambda$) (Osborne, 2010). Variances remained heterogenous ($p < 0.01$) for number of taxa, and thus, the level of significance was reduced consequently to $p < 0.01$ to reduce type I errors (Underwood, 1997). When ANOVA detected significant differences for a given factor, the source of difference was identified by applying the Student-Newman-Keuls (SNK) test (Underwood, 1981, 1997).

Since macroalgae were the main ecosystem-engineering taxon on the studied hard substrates, a two-way ANOVA was used to examine whether there were differences for Su and Or in terms of macroalgal morphological complexity. For this reason, macroalgae were assigned

to two morpho-functional groups, i.e. arborescent and non-arborescent taxa. The criterion followed to consider any given alga as arborescent was the capability of growing in the vertical axis forming three-dimensional branched canopies. Multivariate analyses were conducted with PRIMER v.6+PERMANOVA package (Clarke, 1993) and ANOVAs with GMAV5 software (Underwood *et al.*, 2002).

Results

A total of 49 taxa were identified, which belonged to 10 major taxonomic groups: Chlorophyta, Ochrophyta, Rhodophyta, Porifera, Cnidaria, Polychaeta, Gastropoda (family Vermetidae), Cirripedia (family Balanidae), Bryozoa, and Ascidiacea. Twenty-three out of 45 taxa identified in natural substrates were macroalgae. Rhodophytes were the dominant phylum with five taxa (*Lithophyllum* spp., *Jania adhaerens*, *Peyssonnelia* spp., *Laurencia obtusa* and *Amphiroa rigida*) contributing by 68.78% to the similarity in natural substrates. On the other hand, in the studied artificial substrates only 16 out of 30 identified taxa were macroalgae, with two taxa (the rhodophyte *Lithophyllum* spp. and the filamentous chlorophyte *Cladophora* spp.) contributing by more than 72% to the Bray-Curtis similarity. Regarding metazoans, 22 taxa were found in natural substrates while only 14 taxa in rip-raps, being noteworthy the absence of cnidarians and the lower diversity of sponges (7 versus 12 taxa) in the latter. Consequently, of the total taxa, 17 were found exclusively on natural substrates while only three on rip-raps (Table 1).

The three dimensional MDS showed a clear ordination of samples according to the habitat type (Fig. 2). Even though there was a high dispersion among samples between substrate types (see PERMDISP in Table 2), PERMANOVA results (Table 2) showed significant differences in assemblage structure between the two substrate types but not between orientations. Moreover, significant differences were observed for locality and two significant interactions between factors were detected, i.e. Su x Or and Su x Lo(Or). Pair-wise comparisons revealed that the interaction Su x Or was significant between substrates within each orientation but not between orientations for each level of substrate. Pair-wise comparisons for Su x Lo(Or) revealed that at each locality the assemblage differed between the two substrates except for Tsoutsouros (Supplementary Table S1). No significant differences were found for small-scale heterogeneity, i.e. among sites for each substrate within any given locality.

The results of the four-factor ANOVA for the three diversity measures are shown in Table 3. There were significant differences in number of taxa for substrate, locality and their interaction Su x Lo(Or). According to the SNK tests, number of taxa was significantly higher in natural substrates, and the interaction Su x Lo(Or) revealed that number of taxa was higher at every locality, although non-significantly at Tsoutsouros (Fig. 3A). With regard to the substrate type, the SNK test showed that number of

Table 1. Percentage cover for every taxon identified at each locality. Ka: Kato Galatas; Ba: Bali; Go: Gournes; Ho: Hora Sfaki-on; Ag: Agia Galini; Ts: Tsoutsouros.

	Natural substrate						Artificial substrate (rip-raps)					
	Ka	Ba	Go	Ho	Ag	Ts	Ka	Ba	Go	Ho	Ag	Ts
Phylum Chlorophyta												
Class Ulvophyceae												
Order Bryopsidales												
Family Halimedaceae												
<i>Halimeda tuna</i> (J.Ellis & Solander) J.V.Lamouroux	■				■							
Family Udoteaceae												
<i>Flabellia petiolata</i> (Turra) Nizamuddin	■											
Order Cladophorales												
Family Anadyomenaceae												
<i>Anadyomene stellata</i> (Wulfen) C.Agardh	■		■	■	■	■	■			■		
Family Cladophoraceae												
<i>Cladophora</i> spp.	■	■	■	■	■		■	■	■	■	■	■
Order Dasycladales												
Family Polyphysaceae												
<i>Acetabularia acetabulum</i> (Linnaeus) P.C. Silva											■	
Order Siphonocladales												
Family Valoniaceae												
<i>Valonia</i> sp.			■									
Phylum Ochrophyta												
Class Phaeophyceae												
Order Dictyotales												
Family Dictyotaceae												
<i>Dictyota</i> spp.	■		■	■	■	■						
<i>Padina pavonica</i> (Linnaeus) Thivy	■	■	■	■	■	■				■	■	■
<i>Zonaria</i> sp.					■	■						
Order Fucales												
Family Sargassaceae												
<i>Cystoseira spinosa</i> Sauvageau												
Order Sphacelariales												
Family Sphacelariaceae												
<i>Sphacelaria</i> sp.		■		■		■		■	■	■		
Family Stypocaulaceae												
<i>Halopteris scoparia</i> (Linnaeus) Sauvageau			■			■						
Phylum Rhodophyta												
Class Florideophyceae												
Order Ceramiales												
Family Rhodomelaceae												
<i>Alsidium helminthochorton</i> (Schwendimann) Kützling							■					
<i>Laurencia obtusa</i> (Hudson) J.V.Lamouroux	■	■	■	■	■	■	■			■	■	■
Order Corallinales												
Family Corallinaceae												
<i>Amphiroa cryptarthrodia</i> Zanardini	■		■	■	■		■			■	■	

continued

Table 1 continued

	Natural substrate						Artificial substrate (rip-raps)					
	Ka	Ba	Go	Ho	Ag	Ts	Ka	Ba	Go	Ho	Ag	Ts
<i>Amphiroa rigida</i> J.V.Lamouroux	■	■	■	■	■	■	■	■		■	■	■
<i>Ellisolandia elongata</i> (J.Ellis & Solander) K.R.Hind & G.W.Saunders	■		■		■	■	■					
<i>Hydrolithon farinosum</i> (J.V.Lamouroux) Penrose & Y.M.Chamberlain	■						■					
<i>Jania adhaerens</i> J.V.Lamouroux	■	■	■	■	■	■	■			■	■	■
<i>Lithophyllum</i> spp.	■	■	■	■	■	■	■	■	■	■	■	■
Order Nemaliales												
Family Galaxauraceae												
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman & R.A.Townsend					■							
Family Liagoraceae												
<i>Ganonema farinosum</i> (J.V.Lamouroux) K.C.Fan & Yung C.Wang									■	■	■	
Order Peyssonneliales												
Family Peyssonneliaceae												
<i>Peyssonnelia</i> sp.1		■	■	■		■	■	■	■	■		■
<i>Peyssonnelia</i> spp.	■	■	■	■	■	■	■	■			■	■
Turf Algae	■		■	■	■	■	■		■		■	
Phylum Porifera												
Class Demospongiae												
Order Chondrillida												
Family Chondrillidae												
<i>Chondrilla nucula</i> Schmidt, 1862	■		■				■					
Order Chondrosiida												
Family Chondrosiidae												
<i>Chondrosia reniformis</i> Nardo, 1847	■			■				■				
Order Clionaida												
Family Clionaidae												
<i>Cliona celata</i> Grant, 1826			■	■		■			■	■		
<i>Cliona schmidtii</i> (Ridley, 1881)					■	■						■
<i>Cliona</i> sp.			■	■								
<i>Cliona viridis</i> (Schmidt, 1862)	■	■	■	■	■	■	■	■		■	■	■
Family Spirastrellidae												
<i>Spirastrella cunctatrix</i> (Schmidt, 1868)		■										
Order Dictyoceratida												
Family Irciniidae												
<i>Ircinia</i> sp.	■	■		■	■	■		■	■		■	
<i>Sarcotragus spinosulus</i> (Schmidt, 1862)				■	■						■	■
Order Haplosclerida												
Family Petrosiidae												
<i>Petrosia ficiformis</i> (Poiret, 1789)		■			■	■						
Order Poecilosclerida												
Family Crambeidae												
<i>Crambe crambe</i> (Schmidt, 1862)					■	■						

continued

Table 1 continued

	Natural substrate						Artificial substrate (rip-raps)					
	Ka	Ba	Go	Ho	Ag	Ts	Ka	Ba	Go	Ho	Ag	Ts
Family Hymedesmiidae												
<i>Phorbas topsenti</i> Vacelet & Perez, 2008		■		■	■	■						
Phylum Cnidaria												
Class Anthozoa												
Order Actiniaria												
<i>Aiptasia mutabilis</i> (Gravenhorst, 1831)			■									
Order Scleractinia												
Family Dendrophylliidae												
<i>Balanophyllia</i> sp.		■										
Class Hydrozoa												
Order Anthoathecata												
Family Pennariidae												
<i>Pennaria disticha</i> Goldfuss, 1820		■										
Phylum Annelida												
Class Polychaeta												
Order Sabellida												
Family Serpulidae												
<i>Serpula</i> spp.	■	■	■	■	■	■		■	■	■	■	■
Phylum Mollusca												
Class Gastropoda												
Order Littorinimorpha												
Family Vermetidae												
<i>Dendropoma cristatum</i> (Biondi, 1859)						■		■		■		
<i>Thylacodes arenarius</i> (Linnaeus, 1758)		■		■								
Phylum Arthropoda												
Class Hexanauplia												
Order Sessilia												
Family Balanidae												
<i>Perforatus perforatus</i> (Bruguière, 1789)									■			
Phylum Bryozoa												
Class Gymnolaemata												
Order Cheilostomatida												
Family Adeonidae												
<i>Reptadeonella violacea</i> (Johnston, 1847)		■						■	■			
Family Bitectiporidae												
<i>Schizomavella</i> sp.		■						■				■
Family Schizoporellidae												
<i>Schizobrachiella sanguinea</i> (Norman, 1868)		■		■		■			■			■
Phylum Chordata												
Class Ascidiacea												
Order Aplousobranchia												
Family Didemnidae												
<i>Didemnum</i> sp.	■	■		■	■	■						■
Grades of blue represent average cover:	<div style="display: flex; justify-content: space-around; align-items: center;"> < 5% 5-10% 10-25% 25-40% > 40% </div>											

taxa was significantly higher in natural substrates of Bali compared to Gournes. In the south, natural substrates of Hora Sfakion and Agia Galini had higher number of taxa than Tsoutsouros. No differences were found in the number of taxa in artificial substrates among localities except for Kato Galatas where number of taxa was significantly higher compared to Gournes. Values of H' differed significantly for the substrate factor; SNK tests showed that H' values were higher in natural substrates. Also, a significant interaction $Su \times Lo(Or)$ was detected for H' . SNK tests (in the same way than for number of taxa) showed that H' values in natural substrates were higher at every locality except for Tsoutsouros (Fig. 3B). Regarding Pielou's evenness, communities over natural substrates

were more evenly distributed than on artificial substrates (Fig. 3C). In accordance with SNK tests results, this was explained by the significant differences found only at Bali and Gournes.

According to the SIMPER, seven species contributed to 81.12% of the similarity for natural substrates while only three species accounted for 81.78% of the similarity in artificial substrates (Fig. 4).

Ten taxa found in this study were considered as arborescent macroalgae, i.e. *Amphiroa cryptarthrodi*, *A. rigida*, *Cystoseira spinosa*, *Dictyota* spp., *Ellisolandia elongata*, *Ganonema farinosum*, *Halopteris scoparia*, *Jania adhaerens*, *Laurencia obtusa* and *Tricleocarpa fragilis*. Coralline macroalgae of the genus *Lithophyllum*

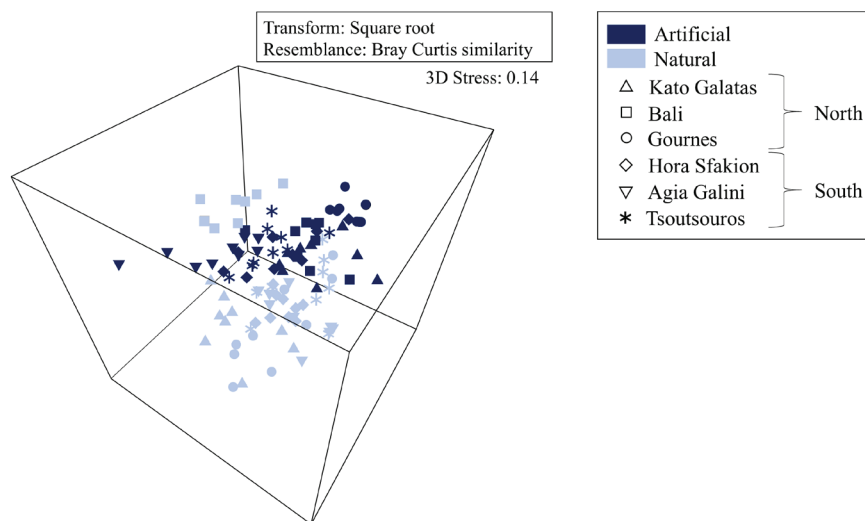


Fig. 2: Three dimensional MDS plot for sessile benthic assemblages. Each spot represents a replicate sample. Grey symbols: natural substrates; Black symbols: artificial substrates.

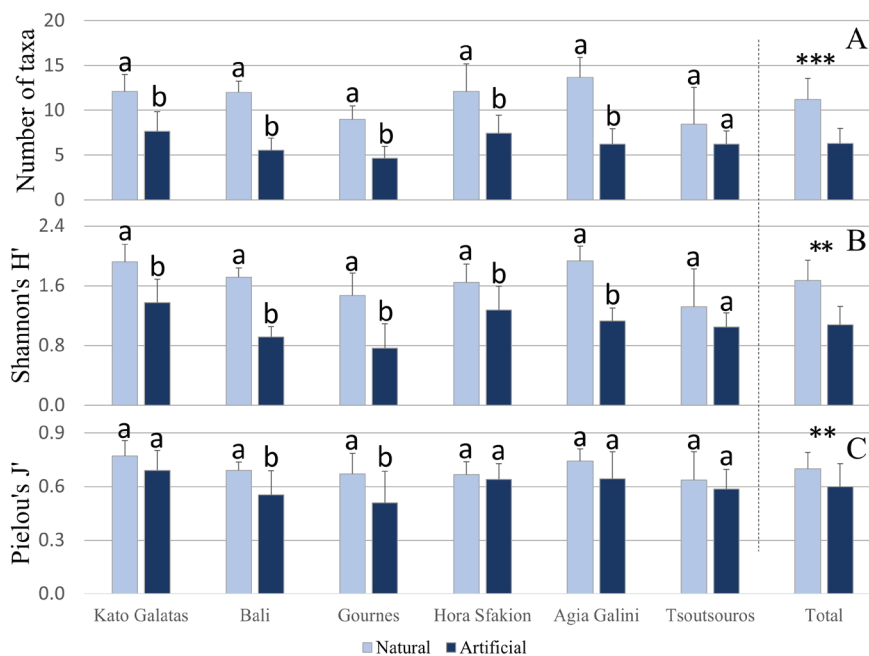


Fig. 3: Average values of three diversity indexes (A: number of taxa, B: Shannon-Wiener's diversity, C: Pielou's evenness) for artificial and natural substrates at each locality. a, b denotes significant sources of variation detected by SNK through four-factor ANOVA. ** $p < 0.01$; *** $p < 0.001$.

Table 2. Results of PERMANOVA test with Substrate (Su), Orientation (Or), Locality (Lo) and Site (St) factors for the total assemblage structure (taxa cover percentages) based on Bray-Curtis dissimilarity index of square-root transformed data. MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * p<0.05; ** p<0.01.

Source of variation	df	MS	Pseudo-F	p
Su	1	23104	5.5842	*
Or	1	9908.9	0.94008	n.s.
Lo(Or)	4	10541	10.275	**
Su x Or	1	15281	3.6934	*
Su x Lo(Or)	4	4137.4	4.0331	**
St (Su x Lo(Or))	24	1025.9	1.2002	n.s.
Residual	72	854.75		
Total	107			
PERMDISP	(Su) F = 4.42 p = 0.045*			
	(Or) F = 3.03 p = 0.115			
Pair-wise tests	Levels of factor (Or)			
Su x Or	Natural: North = South			
	Artificial: North = South			
	Levels of factor (Su)			
	North: Natural ≠ Artificial			
	South: Natural ≠ Artificial			

dominated on both artificial and natural substrates (Table 1). Consequently, average cover of non-arborescent algae was higher at every locality compared with arborescent taxa. However, average arborescent macroalgae cover was higher in natural (29.15 % ± 3.58, mean ± SE) than in artificial (12.08 % ± 2.12, mean ± SE) habitats and thus the ratio non-arborescent/arborescent algae was higher on artificial substrates (Fig. 5). ANOVA results confirmed those differences (Table 4).

Discussion

Shallow subtidal hard bottoms have been scarcely investigated in Crete, apart from some studies focusing on qualitative bionomic descriptions (Pérès & Picard, 1958), specific taxa (Poursanidis *et al.*, 2016; Katsanevakis *et al.*, 2017) or macrofaunal vagile assemblages (Chatzigeorgiou *et al.*, 2012; Poursanidis *et al.*, 2019). This work constitutes, therefore, the first quantitative comparative description of the shallow subtidal sessile benthos between artificial (rip-raps) and natural hard substrates in the area. The results supported our initial hypothesis and showed that rip-raps do not function as surrogates of natural hard substrates in the area since (1) the sessile assemblage was significantly different to that on natural rocky bottoms, (2) rip-raps supported fewer taxa and (3) had a significantly lower cover of habitat-forming arborescent macroalgae.

In shallow subtidal rocky bottoms, where light is not a limiting factor, macroalgae are expected to form a major component of sessile benthos, playing such important roles as nutrient cycling and ecosystem engineering, thus providing habitat for a broad range of organisms (e.g. Crooks, 2002; Ólafsson, 2017). Our study showed that macroalgae, and particularly rhodophytes, were the dominant taxa in natural substrates; on the contrary, macroalgae diversity was much lower on rip-raps. Indeed, rhodophytes have been previously reported as the dominant macroalgal taxon in shallow waters of Greece (Lazaridou *et al.*, 1997). The species composition of the studied natural hard substrates was similar to that described from moderately exposed subtidal hard substrates in the Aegean Sea (Orfanidis *et al.*, 2005) and light-demanding hard bottoms in the Mediterranean Sea (e.g. Boudouresque, 1971; Ballesteros, 1993).

Artificial substrates are often subjected to important levels of disturbance (Airoldi & Bulleri, 2011). These artificial habitats are usually characterized by low biodiversity (Odum, 1985), where usually a few opportunistic species thrive (Orfanidis *et al.*, 2003; Dafforn *et al.*, 2009). This is the case of *Cladophora* spp., which

Table 3. Results of the four-factor ANOVA for number of taxa (S), Shannon-Wiener's diversity (H') and Pielou's evenness (J'). MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * p<0.05; ** p<0.01; *** p<0.001.

Source of variation	df	Number of taxa (S)			Shannon-Wiener diversity (H')			Pielou's evenness (J')		
		MS	F	p	MS	F	P	MS	F	p
Su	1	36.0901	24.28	***	5.9786	27.25	**	0.5669	25.77	**
Or	1	0.9997	0.49	n.s.	0.0964	0.15	n.s.	0.0045	0.03	n.s.
Lo(Or)	4	2.0266	5.96	**	0.6289	8.84	***	0.1625	3.44	*
St (Su x Lo(Or))	24	0.3402	0.72	n.s.	0.0711	1.16	n.s.	0.0437	1.58	n.s.
Su x Or	1	0.0318	0.02	n.s.	0.2383	1.09	n.s.	0.1039	4.72	n.s.
Su x Lo(Or)	4	1.4864	4.37	**	0.2193	3.08	*	0.1039	0.47	n.s.
Residual	72	0.4705			0.0615			0.0300		
TOTAL	107									
Cochran's test		0.4085			0.0998			0.1281		
		**			n.s.			n.s.		
Transformation		Box-Cox (λ=0.3555)			Box-Cox (λ=0.2548)			Box-Cox (λ=0.2021)		

Taxa	Av. Sim. %	Contrib. %
Group Natural		
1 <i>Lithophyllum</i> spp.	16.96	39.50
2 <i>Jania adhaerens</i>	4.16	9.68
3 <i>Peyssonnelia</i> spp.	3.89	9.06
4 <i>Cladophora</i> spp.	2.70	6.30
5 <i>Cliona viridis</i>	2.59	6.04
6 <i>Laurencia obtusa</i>	2.36	5.50
7 <i>Amphiroa rigida</i>	2.17	5.04
		Total = 81.12
Group Artificial		
I <i>Lithophyllum</i> spp.	29.30	61.47
II <i>Cladophora</i> spp.	5.47	11.48
III <i>Cliona viridis</i>	4.21	8.83
IV <i>Peyssonnelia</i> spp.	3.33	7.00
		Total = 88.78

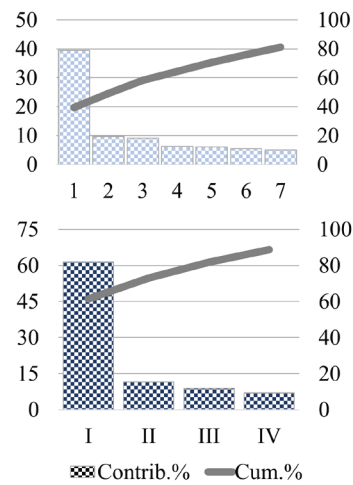


Fig. 4: Results of SIMPER analysis. Taxa that contributed less than 5% to the total similarity are not shown. Histograms represent contributions (bars, left axis) and cumulative contributions (grey line, right axis) for the taxa indicated with natural numbers (Group Natural) or Roman numerals (Group Artificial).

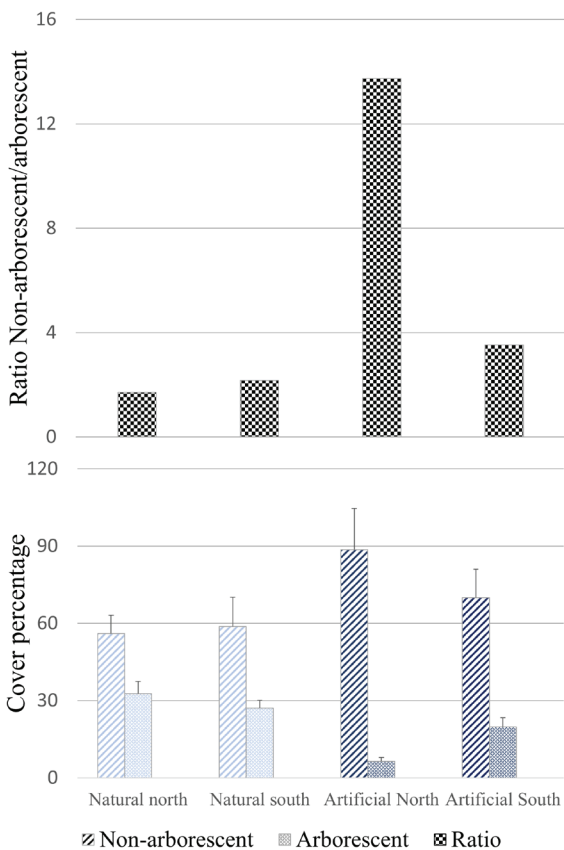


Fig. 5: Average cover (%) of arborescent and non-arborescent algae on artificial and natural substrates. The ratio non-arborescent/arborescent is also shown. Error bars represent standard deviation (SD).

show tolerance to environmental disturbances (e.g. Peckol & Rivers, 1995; Orfanidis *et al.*, 2001; Salomidi *et al.*, 2016), and presented higher cover percentages on the studied rip-raps compared to natural substrates. In fact, opportunistic species could outcompete other species on hard substrates, thus resulting in fewer number of species

Table 4. ANOVA test with Substrate (Su) and Orientation (Or) factors for arborescent algae cover percentages. Due to heteroscedasticity, level of significance was reduced to $p < 0.01$ to reduce type I error. MS: mean square; p: level of significance; df: degrees of freedom; n.s.: not significant; * $p < 0.01$.

Source of variation	df	MS	Pseudo-F	p
Su	1	7862.6134	19.098	*
Or	1	368.5208	0.522	n.s.
Su x Or	1	1629.4468	3.56	n.s.
Residual	104	458.0262		
Total	107			
Cochran's-test				*

than in natural habitats (Bacchiocchi & Airoidi, 2003).

It is noteworthy that 17 taxa were exclusively found on natural hard substrates while only three were found as exclusive on artificial ones (Table 1), including the cryptogenic species *Ganonema farinosum* (Verlaque *et al.*, 2015; Zenetos *et al.*, 2018) that was recently reported to be widely distributed in Crete Island (Gerovasileiou *et al.*, 2017). Moreover, some species found exclusively on natural hard substrates in the study area (e.g. *Thylacodes arenarius* and *Cystoseira spinosa*) have been proposed as bioindicators of good environmental status within monitoring schemes under the Marine Strategy Framework Directive (MSFD) (WoRMS Editorial Board, 2018). They are also considered in some ecological indices, such as CARLIT (Ballesteros *et al.*, 2007). In addition, *C. spinosa* is included in the list of endangered or threatened species (Annex II) of the Barcelona Convention (1996).

The sessile benthic assemblage on rip-raps had fewer taxa and lower values of diversity (H'), suggesting that those support a poorer and more homogeneous assemblage than natural rocky reefs. The construction of coastal defense infrastructures (e.g. rip-raps and seawalls) has

been previously identified as a “driver of global biotic homogenization” (see review in Firth *et al.*, 2016a) which is defined as the process under which communities become more uniform in terms of number of taxa, similarity of functions and genetic diversity (McKinney, 2006).

Differences in assemblage structure between natural and artificial substrates were clearly portrayed by the MDS ordination. In fact, natural substrates were pooled together and separated from artificial ones indicating that the substrate type has a major role in structuring sessile benthos. Multivariate analyses (Supplementary Table S1) highlighted higher variability among localities than among sites within a given locality, indicating that local populations could have been established depending on the local variability of environmental conditions (e.g. Tofts & Silvertown, 2000). Although variability is usually larger at small spatial scales in shallow rocky coasts (Fraschetti *et al.*, 2005), our results suggest higher variability at a broader scale (among different localities, tens of kilometers away); this contrasts with other studies for Mediterranean rocky beds with canopy-forming macroalgae (Dal Bello *et al.*, 2016). Our results might be explained because depth, wave exposure, age and inclination of hard substrates was similar in all sites within localities in an effort to ensure comparability. Nevertheless, statistically significant differences were still found between artificial and natural substrates.

Differences of artificial versus natural hard substrate assemblages are mainly related to habitat complexity, wave exposure, age of the substratum, dispersal potential of propagules and larvae, substrate inclination and orientation (e.g. Glasby & Connell, 2001; Firth *et al.*, 2016b; Ushiyama *et al.*, 2016), herbivory (Forrest *et al.*, 2013; Ferrario *et al.*, 2016), roughness and nature of building materials (e.g. Coombes *et al.*, 2015; Cacabelos *et al.*, 2016; Sempere-Valverde *et al.*, 2018). The sampling design considered in our study eliminated potential confounding effects due to some factors (e.g. wave exposure, inclination and dispersal of propagules and larvae), thus allowing more rigorous conclusions with regard to the examined factors.

So far, it is uncertain how many years are needed for artificial structures to hold a “climax community” or to determine if that is even possible. Some authors have estimated that it takes between 5 and 20 years for artificial structures to reach climax communities (Hawkins *et al.*, 1983; Pinn *et al.*, 2005; Coombes, 2011) while others suggest that low crested structures (like the ones studied here) never become natural climax communities (Gacia *et al.*, 2007) or that incomplete succession could be a persistent stable state (Ferrario *et al.*, 2016 and references therein). The taxa which were exclusively found on natural substrates in the study area reproduce by releasing spores or larvae to the water column, being capable of colonising nearby hard substrates within the immersion time of the studied artificial substrates (>10 years). Thus, we believe that the immersion time of the artificial substrates was not a major factor structuring the communities in the present study.

Different substrate inclination (i.e. vertical versus

horizontal surfaces) has been shown to affect small-scale variability on artificial substrates (Glasby, 2000; Ushiyama *et al.*, 2016). In this study, all examined surfaces were vertical in order to minimize heterogeneity linked to different surface inclination. Exposure to sunlight has been found to have more determinant effects on epibiotic assemblages compared to surface inclination (see Glasby & Connell, 2001). Nevertheless, in our study there were no significant differences between northern and southern localities. In addition, the entire coastline of Crete belongs to the same biogeographical area (the South Aegean ecoregion) and there is high connectivity between the north and south sides due to the interconnection of cyclonic and anticyclonic gyres by currents and jets (Theocharis *et al.*, 1999). All in all, and given that the sampled artificial structures in our study were adjacent to natural hard substrates, thus facilitating the potential nourishment of rip-raps (Gacia *et al.*, 2007), it is improbable that poor larval or propagules dispersal limits the establishment of assemblages on rip-raps. On the other hand, their settlement could be affected by other factors such as nature of building materials and roughness (Coombes *et al.*, 2015; Ido & Shimrit, 2015; Sempere-Valverde *et al.*, 2018) or ecological processes, such as grazing, predation and competition (Foster *et al.*, 2003; Bulleri, 2005; Marzinelli *et al.*, 2011; Ferrario *et al.*, 2017).

Besides the differences in assemblage composition and diversity, the cover of habitat-forming arborescent macroalgae was significantly lower in rip-raps, thus potentially generating differences in ecosystem functioning. These species can modify the community structure (Benedetti-Cecchi *et al.*, 2001; Maggi *et al.*, 2009) by providing new habitat and shelter (Boudouresque, 1971; Cheminée *et al.*, 2017) and facilitating the establishment of propagules and larvae (Arenas *et al.*, 2006; Bulleri, *et al.*, 2009). In addition to the increase of habitat complexity, they constitute an important source of primary production, supporting rich vagile biota, such as fish (Thiriet *et al.*, 2016; Cheminée *et al.*, 2017).

In natural habitats, coexistence of arborescent and encrusting taxa on macroalgal communities is common since encrusting species are usually tolerant to overgrowth (Airoldi, 2000; Bulleri, 2006); this coexistence was observed in the studied natural substrates while rip-raps exhibited a shift towards non-arborescent algae. This might be explained by different grazing pressures between habitats. Indeed, grazing has been identified as relevant in shaping macroalgal assemblages (Underwood & Jernakoff, 1984; Coleman *et al.*, 2006; Tsirintanis *et al.*, 2018). For instance, Ferrario *et al.* (2016) reported higher grazing pressure in artificial structures in comparison to natural ones in the North Adriatic Sea. First, isolated artificial structures over soft bottoms would probably be subjected to higher grazing pressure compared to large rocky reefs due to the greater concentration of potential grazers in the only available, artificial rocky substrates (Ferrario *et al.*, 2016). In our case, Gournes had rip-raps settled over soft bottoms approximately 1 km away from the nearest natural rocky shore. Second, the higher diversity and abundance of palatable algae in natural habitats results in

a share-out of grazing pressure among targeted algae species. In accordance with this hypothesis, the most abundant arborescent species of the study area (*Jania adhaerens*, *Laurencia obtusa* and *Amphiroa rigida*) were absent from rip-raps. However, apart from Gournes, rip-raps in other localities were adjacent to natural hard substrates. Therefore, a different grazing pressure across localities from highly motile herbivores such as certain fishes is rather unlikely. Nevertheless, the invasive crab *Percnon gibbesi* (H. Milne Edwards, 1853) was abundant in all sampling localities in the boulder-like rip-raps (authors' personal observations, Fig. 6). *Percnon gibbesi* has been described as a herbivorous species, mostly feeding on articulated Corallinaceae and Sphacelariaceae (Deudero *et al.*, 2005; Puccio *et al.*, 2006), possibly exerting this way a differential grazing pressure. Katsanevakis *et al.* (2010) also measured higher densities of this crab in boulder-like habitats near marinas. Therefore, it is likely that the introduction of highly heterogeneous artificial structures for coastal defense purposes could facilitate the establishment of some non-indigenous species. The potential impact of such introductions should be considered in future management practices for deployment of coastal defense structures, especially in marine areas highly susceptible to biological invasions.

In conclusion, the composition and diversity of shallow subtidal sessile assemblages on rip-raps suggest that these artificial structures do not function as surrogates of natural hard substrates in the study area, considering both a taxonomic and a functional approach. The deficient performance of this artificial habitat could be attributed to a combination of co-occurring abiotic and biotic factors such as the nature and roughness of the building material as well as differential grazing pressure. We suggest that future constructions should apply ecological criteria considering various materials (e.g. Sempere-Valverde *et al.*, 2018) and novel designs (Ostalé-Valriberas *et al.*, 2018) which could match the particular scenario of the Cretan coast. Further research for the ecological characterization of these structures is critical in order to improve our knowledge in support of better management practices, under the framework of green engineering, in coastal and marine infrastructure of the Eastern Mediterranean Sea.

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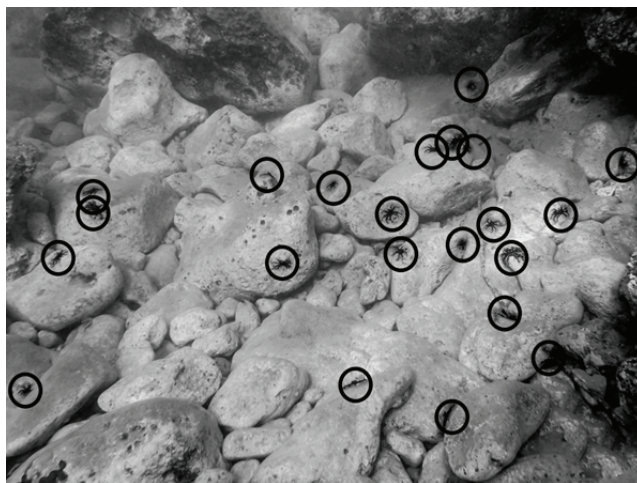


Fig. 6: Specimens of the invasive crab *Percnon gibbesi* (encircled) inhabiting a boulder-like rip-rap in one the sampling locations (July 2017, Kato Galatas, Crete).

References

- Airoidi, L., 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology*, 81 (3), 798-814.
- Airoidi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology: An Annual Review*, 45, 345-405.
- Airoidi, L., Bulleri, F., 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *PLoS ONE*, 6 (8), e22985.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. *PERMANOVA for PRIMER: guide to software and statistical methods*. PRIMER-E, Plymouth, 214 pp.
- Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83 (4), 557-574.
- Arenas, F., Sánchez, I., Hawkins, S.J., Jenkins, S.R., 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology*, 87 (11), 2851-2861.
- Bacchiocchi, F., Airoidi, L., 2003. Distribution and dynamics of epibiota on hard structures for coastal protection. *Estuarine Coastal and Shelf Science*, 56, 1157-1166.
- Ballesteros, E., 1993. Species composition and structure of a photophilic algal community dominated by *Halopteris scoparia* (L.) Sauvageau from the North-Western Mediterranean. *Collectanea Botanica*, 22, 5-24.
- Ballesteros, E., Torras, X., Pinedo, S., García, M., Mangialajo, L. *et al.*, 2007. A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive. *Marine Pollution Bulletin*, 55 (1-6), 172-180.
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoidi, L. *et al.*, 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology Progress Series*, 214, 137-150.
- Bianchi, C.N., Pronzato, R., Cattaneo-Vietti, R., Benedetti Cecchi, L., Morri, C. *et al.*, 2004. Hard bottoms. p. 185-215. In:

- Mediterranean marine benthos: a manual of methods for its sampling and study*. Gambi, M.C., Dappiano, M. (Eds.). *Biologia Marina Mediterranea*, 11 (Suppl. 1). SIBM, Genoa.
- Boetius, A., Scheibe, S., Tselepidis, A., Thiel, H., 1996. Microbial biomass and activities in deep-sea sediments of the Eastern Mediterranean: trenches and benthic hotspots. *Deep-Sea Research*, 43 (9), 1439-1460.
- Boudouresque, C.F., 1971. Contribution à l'étude phytosociologique des peuplements algaux des côtes varoises. *Végétatio*, 22 (1-3), 83-184.
- Bulleri, F., 2005. Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. *Marine Environmental Research*, 60 (3), 355-374.
- Bulleri, F., 2006. Duration of overgrowth affects survival of encrusting coralline algae. *Marine Ecology Progress Series*, 321, 79-85.
- Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology*, 47 (1), 26-35.
- Bulleri, F., Tamburello, L., Benedetti-Cecchi, L., 2009. Loss of consumers alters the effects of resident assemblages on the local spread of an introduced macroalga. *Oikos*, 118 (2), 269-279.
- Cacabelos, E., Martins, G.M., Thompson, R., Prestes, A.C., Azevedo, J.M.N. *et al.*, 2016. Material type and roughness influence structure of inter-tidal communities on coastal defenses. *Marine Ecology*, 37 (4), 801-812.
- Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. *Journal of Experimental Marine Biology and Ecology*, 400 (1-2), 302-313.
- Chatzigeorgiou, G., Faulwetter, S., López, E., Sardá, R., Arvanitidis, C., 2012. Can coastal biodiversity measured in four Mediterranean sites be representative of the region? A test for the robustness of the NaGISA protocol by using the hard substrate syllid (Annelida, Polychaeta) taxo-communities as a surrogate. *Hydrobiologia*, 691, 147-156.
- Chatzinikolaou, E., Arvanitidis, C., 2016. Status, values and present threats in Heraklion harbour (Crete, Greece). *Regional Studies in Marine Science*, 8, 252-258.
- Chatzinikolaou, E., Mandalakis, M., Damianidis, P., Dailianis, T., Gambineri, S. *et al.*, 2018. Spatio-temporal benthic biodiversity patterns and pollution pressure in three Mediterranean touristic ports. *Science of The Total Environment*, 624, 648-660.
- Cheminée, A., Pastor, J., Bianchimani, O., Thiriet, P., Sala, E. *et al.*, 2017. Juvenile fish assemblages in temperate rocky reefs are shaped by the presence of macro-algae canopy and its three-dimensional structure. *Scientific Reports*, 7 (1), 14638.
- Chintiroglou, C.C., Antoniadou, C., Baxevanis, A., Damianidis, P., Karalis, P. *et al.*, 2004. Peracarida populations of hard substrate assemblages in ports of the NW Aegean Sea (eastern Mediterranean). *Helgoland Marine Research*, 58 (1), 54-61.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 17-143.
- Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Åberg, P., Arenas, F. *et al.*, 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia*, 147 (3), 556-564.
- Coombes M.A., 2011. *Biogeomorphology of coastal structures: Understanding interactions between hard substrata and colonising organisms as a tool for ecological enhancement*. PhD dissertation. University of Exeter, UK, 592pp.
- Coombes, M.A., La Marca, E.C., Naylor, L.A., Thompson, R.C., 2015. Getting into the groove: opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale surface textures. *Ecological Engineering*, 77, 314-323.
- Corsini-Foka, M., Zenetos, A., Crocetta, F., Çinar, M.E., Koçak, F. *et al.*, 2015. Inventory of alien and cryptogenic species of the Dodecanese (Aegean Sea, Greece): collaboration through COST action training school. *Management of Biological Invasions*, 6 (4), 351-366.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97, 153-166.
- Dafforn, K.A., Glasby, T.M., Airoidi, L., Rivero, N.K., Mayer-Pinto, M. *et al.*, 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. *Frontiers in Ecology and the Environment*, 13 (2), 82-90.
- Dafforn, K.A., Johnston, E.L., Glasby, T.M., 2009. Shallow moving structures promote marine invader dominance. *Biofouling*, 25 (3), 277-287.
- Dal Bello, M., Leclerc, J.C., Benedetti-Cecchi, L., De Lucia, G.A., Arvanitidis, C. *et al.*, 2016. Consistent patterns of spatial variability between NE Atlantic and Mediterranean rocky shores. *Journal of the Marine Biological Association of the United Kingdom*, 97 (3), 539-547.
- Deudero, S., Frau, A., Cerda, M., Hampel, H., 2005. Distribution and densities of the decapod crab *Percnon gibbesi*, an invasive Grapsidae, in western Mediterranean waters. *Marine Ecology Progress Series*, 285, 151-156.
- Fabi, G., Spagnolo, A., Bellan-Santini, D., Charbonnel, E., Çiçek, B.A. *et al.*, 2011. Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography*, 59 (SPE1), 155-166.
- Fernández-González, V., Sánchez-Jerez, P., 2017. Fouling assemblages associated with off-coast aquaculture facilities: an overall assessment of the Mediterranean Sea. *Mediterranean Marine Science*, 18 (1), 87-96.
- Ferrario, F., Iveša, L., Jaklin, A., Perkol-Finkel, S., Airoidi, L., 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. *Journal of Applied Ecology*, 53 (1), 16-24.
- Ferrario, J., Caronni, S., Occhipinti-Ambrogi, A., Marchini, A., 2017. Role of commercial harbours and recreational marinas in the spread of non-indigenous fouling species. *Biofouling*, 33 (8), 651-660.
- Firth, L.B., Knights, A.M., Bridger, D., Evans, A., Mieskowska, N. *et al.*, 2016a. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanography and Marine Biology: An Annual Review*, 54, 193-269.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoidi, L. *et al.*, 2014. Between a rock and a hard place: environmental and engineering considerations when designing coastal

- defence structures. *Coastal Engineering*, 87, 122-135.
- Firth, L.B., White, F.J., Schofield, M., Hanley, M.E., Burrows, M.T. *et al.*, 2016b. Facing the future: the importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. *Marine and Freshwater Research*, 67 (1), 131-143.
- Forrest, B.M., Fletcher, L.M., Atalah, J., Piola, R.F., Hopkins, G.A., 2013. Predation limits spread of *Didemnum vexillum* into natural habitats from refuges on anthropogenic structures. *PLoS ONE*, 8 (12), e82229.
- Foster, M.S., Nigg, E.W., Kiguchi, L.M., Hardin, D.D., Pearse, J.S., 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *Journal of Experimental Marine Biology and Ecology*, 289 (1), 15-39.
- Fraschetti, S., Terlizzi, A., Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, 296, 13-29.
- Gacia, E., Satta, M.P., Martín, D., 2007. Low crested coastal defence structures on the Catalan coast of the Mediterranean Sea: how they compare with natural rocky shores. *Scientia Marina*, 71 (2), 259-267.
- García-Gómez, J.C., Guerra-García, J.M., Espinosa, F., Maestre, M.J., Rivera-Ingraham, G. *et al.*, 2015. Artificial marine micro-reserves networks (AMMRNs): an innovative approach to conserve marine littoral biodiversity and protect endangered species. *Marine Ecology*, 36 (3), 259-277.
- Gerovasileiou, V., Akel, E.H.KH., Akyol, O., Alongi, G., Azevedo, F. *et al.*, 2017. New Mediterranean biodiversity records (July 2017). *Mediterranean Marine Science*, 18 (2), 355-384.
- Glasby, T.M., 2000. Surface composition and orientation interact to affect subtidal epibiota. *Journal of Experimental Marine Biology and Ecology*, 248 (2), 177-190.
- Glasby, T.M., Connell, S.D., 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Marine Ecology Progress Series*, 214, 127-135.
- Hawkins, S.J., Southward, A.J., Barrett, R.L., 1983. Population structure of *Patella vulgata* L. during succession on rocky shores in Southwest England. *Oceanologica Acta*, Special issue, 103-107.
- Ido, S., Shimrit, P.F., 2015. Blue is the new green—ecological enhancement of concrete based coastal and marine infrastructure. *Ecological Engineering*, 84, 260-272.
- Karalis, P., Antoniadou, C., Chintiroglou, C.C., 2003. Structure of the artificial hard substrate assemblages in ports in Thermaikos Gulf (North Aegean Sea). *Oceanologica Acta*, 26 (3), 215-224.
- Katsanevakis, S., Poursanidis, D., Issaris, Y., Tsiamis, K., Salomidi, M. *et al.*, 2010. The invasive crab *Percnon gibbesi* (Crustacea: Decapoda: Plagusidae) is spreading in the Aegean and Ionian Seas. *Marine Biodiversity Records*, 3, e53.
- Katsanevakis, S., Sini, M., Dailianis, T., Gerovasileiou, V., Koukouroufli, N. *et al.*, 2017. Identifying where vulnerable species occur in a data-poor context: combining satellite imaging and underwater occupancy surveys. *Marine Ecology Progress Series*, 577, 17-32.
- Klaoudatos, D.S., Anastasopoulou, A., Papaconstantinou, C., Conides, A.I., 2012. The Greek experience of artificial reef construction and management. *Journal of Environmental Protection and Ecology*, 13 (3A), 1647-1655.
- Kruskal, J.B., Wish, M., 1978. *Multidimensional Scaling. Series on Quantitative Applications in the Social Sciences*, 07-011. Sage Publications, Beverly Hills and London, 98 pp.
- Lam, N.W., Huang, R., Chan, B.K., 2009. Variations in intertidal assemblages and zonation patterns between vertical artificial seawalls and natural rocky shores: A case study from Victoria Harbour, Hong Kong. *Zoological Studies*, 48 (2), 184-195.
- Lazaridou, E., Orfanidis, S., Haritonidis, S., Seferlis, M., 1997. Impact of eutrophication on species composition and diversity of macrophytes in the gulf of Thessaloniki, Macedonia, Greece: first evaluation of the results of one year study. *Fredericus Environmental Bulletin*, 6, 54-59.
- Lök, A., Gül, B., Ulas, A., Düzbastılar, F.O., Metin, C., 2008. Diel variations on the fish assemblages at artificial reefs in two different environments of the Aegean Sea (Western Coast of Turkey). *Turkish Journal of Fisheries and Aquatic Sciences*, 8, 79-85.
- Loke, L.H., Ladle, R.J., Bouma, T.J., Todd, P.A., 2015. Creating complex habitats for restoration and reconciliation. *Ecological Engineering*, 77, 307-313.
- López, I., Tinoco, H., Aragonés, L., García-Barba, J., 2016. The multifunctional artificial reef and its role in the defence of the Mediterranean coast. *Science of the Total Environment*, 550, 910-923.
- Maggi, E., Bertocci, I., Vaselli, S., Benedetti-Cecchi, L., 2009. Effects of changes in number, identity and abundance of habitat-forming species on assemblages of rocky seashores. *Marine Ecology Progress Series*, 381, 39-49.
- Martínez-Laiz, G., Ros, M., Guerra-García, J.M., 2018. Marine exotic isopods from the Iberian Peninsula and nearby waters. *PeerJ*, 6, e4408.
- Marzinelli, E.M., Underwood, A.J., Coleman, R.A., 2011. Modified habitats influence kelp epibiota via direct and indirect effects. *PLoS ONE*, 6 (7), e21936.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247-260.
- Mercader, M., Mercière, A., Saragoni, G., Cheminée, A., Crec'hriou, R. *et al.*, 2017. Small artificial habitats to enhance the nursery function for juvenile fish in a large commercial port of the Mediterranean. *Ecological Engineering*, 105, 78-86.
- Moreira, J., Chapman, M.G., Underwood, A.J., 2006. Seawalls do not sustain viable populations of limpets. *Marine Ecology Progress Series*, 322, 179-188.
- Moschella, P.S., Abbiati, M., Åberg, P., Airoidi, L., Anderson, J.M. *et al.*, 2005. Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coastal Engineering*, 52 (10-11), 1053-1071.
- Odum, E.P., 1985. Trends Expected in Stressed Ecosystems. *BioScience*, 35 (7), 419-422.
- Ólafsson, E. (Ed.), 2017. *Marine Macrophytes as Foundation Species*. CRC Press, USA, 285 pp.
- Orfanidis, S., Panayotidis, P., Siakavara, A., 2005. Benthic macrophytes: main trends in diversity and distribution. p. 226-235. In: *State of the Hellenic Marine Environment (SoHelME)*. Papathanassiou, E., Zenetos, A. (Eds). HCMR Publication, Athens.
- Orfanidis, S., Panayotidis, P., Stamatis, N., 2001. Ecological

- evaluation of transitional and coastal waters: A marine benthic macrophytes-based model. *Mediterranean Marine Science*, 2 (2), 45-65.
- Orfanidis, S., Panayotidis, P., Stamatis, N., 2003. An insight to the ecological evaluation index (EEI). *Ecological Indicators*, 3 (1), 27-33.
- Osborne, J.W., 2010. Improving your data transformations: Applying the Box-Cox transformation. *Practical Assessment, Research & Evaluation*, 15 (12), 1-9.
- Ostalé-Valriberas, E., Sempere-Valverde, J., Coppa, S., García-Gómez, J.C., Espinosa, F., 2018. Creation of microhabitats (tidepools) in ripraps with climax communities as a way to mitigate negative effects of artificial substrate on marine biodiversity. *Ecological Engineering*, 120, 522-531.
- Peckol, P., Rivers, J.S., 1995. Physiological responses of the opportunistic macroalgae *Cladophora vagabunda* (L.) van den Hoek and *Gracilaria tikvahiae* (McLachlan) to environmental disturbances associated with eutrophication. *Journal of Experimental Marine Biology and Ecology*, 190 (1), 1-16.
- Pérès, J.M., Picard, J., 1958. Recherches sur les peuplements benthiques de la Méditerranée nord-orientale. *Annales de l'Institut Oceanographique*, 34, 213-291.
- Perkins, M.J., Ng, T.P., Dudgeon, D., Bonebrake, T.C., Leung, K.M., 2015. Conserving intertidal habitats: what is the potential of ecological engineering to mitigate impacts of coastal structures? *Estuarine, Coastal and Shelf Science*, 167, 504-515.
- Perkol-Finkel, S., Benayahu, Y., 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. *Coral reefs*, 23 (2), 195-205.
- Pinn, E.H., Mitchell, K., Corkill, J., 2005. The assemblages of groynes in relation to substratum age, aspect and microhabitat. *Estuarine, Coastal and Shelf Science*, 62 (1-2), 271-282
- Poursanidis, D., Chatzigeorgiou, G., Dimitriadis, C., Koutsoubas, D., Arvanitidis, C., 2019. Testing the robustness of a coastal biodiversity data protocol in the Mediterranean: insights from the molluscan assemblages from the sublittoral macroalgae communities. *Hydrobiologia*, 826 (1), 159-172.
- Poursanidis, D., Koutsoubas, D., Arvanitidis, C., Chatzigeorgiou, G., 2016. ReefMedMol: Mollusca from the infralittoral rocky shores - the biocoenosis of photophilic algae - in the Mediterranean Sea. *Biodiversity Data Journal*, 4, e7516.
- Puccio, V., Relini, M., Azzurro, E., Relini, L.O., 2006. Feeding habits of *Percnon gibbesi* (H. Milne Edwards, 1853) in the Sicily Strait. *Hydrobiologia*, 557, 79.
- Rilov, G., Galil, B., 2009. Marine Bioinvasions in the Mediterranean Sea – History, Distribution and Ecology. p. 549-575. In: *Biological Invasions in Marine Ecosystems: Ecological, Management, and Geographic Perspectives*. Rilov, G., Crooks, J.A. (Eds). Springer, Berlin.
- Ros, M., Guerra-García, J.M., Navarro-Barranco, C., Cabezas, M.P., Vázquez-Luis, M., 2014. The spreading of the non-native caprellid (Crustacea: Amphipoda) *Caprella scaura* Templeton, 1836 into southern Europe and northern Africa: a complicated taxonomic history. *Mediterranean Marine Science*, 15 (1), 145-155.
- Salomidi, M., Giakoumi, S., Gerakaris, V., Issaris, Y., Sini, M. et al., 2016. Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini Island, Aegean Sea. *Mediterranean Marine Science*, 17 (3), 720-737.
- Salomidi, M., Katsanevakis, S., Issaris, Y., Tsiamis, K., Katsiaras, N., 2013. Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. *Biological Invasions*, 15 (9), 1961-1971.
- Sempere-Valverde, J., Ostalé-Valriberas, E., Farfán, G.M., Espinosa, F., 2018. Substratum type affects recruitment and development of marine assemblages over artificial substrata: A case study in the Alboran Sea. *Estuarine, Coastal and Shelf Science*, 204, 56-65.
- Sinis, A.I., Chintiroglou, C.C., Stergiou, K.I., 2000. Preliminary results from the establishment of experimental artificial reefs in the N. Aegean Sea (Chalkidiki, Greece). *Belgian Journal of Zoology*, 130 (Supplement), 143-147.
- Strain, E.M., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L. et al., 2018. Eco-engineering urban infrastructure for marine and coastal biodiversity: Which interventions have the greatest ecological benefit? *Journal of Applied Ecology*, 55 (1), 426-441.
- Theocharis, A., Balopoulos, E., Kioroglou, S., Kontoyianis, H., Iona, A., 1999. A synthesis of the circulation and hydrography of the South Aegean Sea and the Straits of the Cretan Arc (March 1994–January 1995). *Progress in Oceanography*, 44 (4), 469-509.
- Thiriet, P.D., Di Franco, A., Cheminée, A., Guidetti, P., Bianchimani, O. et al., 2016. Abundance and diversity of crypto- and necto-benthic coastal fish are higher in marine forests than in structurally less complex macroalgal assemblages. *PLoS ONE*, 11 (10), e0164121.
- Tofts, R., Silvertown, J., 2000. A phylogenetic approach to community assembly from a local species pool. *Proceedings of the Royal Society B*, 267, 363-369.
- Trygonis, V., Sini, M., 2012. PhotoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine Biology and Ecology*, 424-425, 99-108.
- Tsirintanis, K., Sini, M., Doumas, O., Trygonis, V., Katsanevakis, S., 2018. Assessment of grazing effects on phyto-benthic community structure at shallow rocky reefs: An experimental field study in the North Aegean Sea. *Journal of Experimental Marine Biology and Ecology*, 503, 31-40.
- Ulman, A., Ferrario, J., Occhpinti-Ambrogi, A., Arvanitidis, C., Bandi, A. et al., 2017. A massive update of non-indigenous species records in Mediterranean marinas. *PeerJ*, 5, e3954.
- Underwood, A.J., 1981. Techniques of analysis of variance in experimental biology and ecology. *Oceanography and Marine Biology: An Annual Review*, 19, 513-605.
- Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, 504 pp.
- Underwood, A.J., Chapman, M.G., Richards, S.A., 2002. *GMAV-5 for Windows. An Analysis of Variance Programme*. University of Sydney, Australia.
- Underwood, A.J., Jernakoff, P., 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on graz-

- ing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology*, 75 (1), 71-96.
- Ushiyama, S., Smith, J.A., Suthers, I.M., Lowry, M., Johnston, E.L., 2016. The effects of substratum material and surface orientation on the developing epibenthic community on a designed artificial reef. *Biofouling*, 32 (9), 1049-1060.
- Verlaque, M., Ruitton, S., Mineur, F., Boudouresque, C.F., 2015. Vol.4. Macrophytes. In: *CIESM Atlas of exotic species in the Mediterranean*. Briand, F. (Ed.). CIESM Publishers, Monaco, 360 pp.
- WoRMS Editorial Board, 2018. *World Register of Marine Species*. <http://www.marinespecies.org> (Accessed 28 June 2018).
- Zenetos, A., Corsini-Foka, M., Crocetta, F., Gerovasileiou, V., Karachle, P.K. *et al.*, 2018. Deep cleaning of alien species records in the Greek Seas (2018 update). *Management of Biological Invasions*, 9 (3), 209-226.