The dynamics of phytobenthos and its main drivers on abrasion platforms with vermetids (Alicante, Southeastern Iberian Peninsula)

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Research Article

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Abstract

Abrasion platforms with vermetids shape unique seascapes and biotic assemblages that characterize several of the warm Mediterranean coasts. The composition, structural and seasonal dynamics of the platforms' phytobenthos were examined at two Southeast Iberian locations through non-destructive sampling. The patterns observed were linked with environmental variables and grazers' coverage, and we assessed their possible influence. Structural descriptors α-diversity and β-diversity were applied, pointing that depth and season-related variables were the major influencing drivers. Higher α-diversity and β-diversity values during winter and spring coincided with the production optimum of the community. A greater average water depth influences the abundance of both midlittoral and infralittoral taxa. The strong resemblance between the phytobenthos of these vermetid platforms and that on similar platforms in the Eastern and Central Mediterranean Sea suggests that these are affected by the same structuring mechanisms.

Keywords: Seasonality, Community structure, Environmental factors, Species diversity, Benthos.

Introduction

Abrasion platforms with vermetids are characteristic seascapes of warm Mediterranean rocky coasts composed of limestone. Vermetid reefs of several decimetres wide are frequently found at their outer margin, contributing to the platform development (Lillo-Carpio, 1980; Laborel, 1987; Antonioli *et al.*, 1999) and playing an important role as habitat engineers (Milazzo *et al.*, 2016). Such reefs host a variety of species (Mannino, 1992; Donnarumma *et al.*, 2014) and buffer water movement over the platform, creating favourable conditions for the establishment of communities which are characteristic of calmer, more sheltered, conditions (Cano *et al.*, 1994), increasing thus shoreline biodiversity (Safriel, 1975; Chemello, 2009; Milazzo *et al.*, 2016).

Nonetheless, these systems have been poorly studied from an ecological and phycological perspective (Milazzo *et al.*, 2016). In the Iberian Peninsula, shallow systems with well-developed vermetid platforms are found from the north of the province of Alicante south to that of Almería (Molinier & Picard, 1956; Ramos-Esplá, 1985; Ramos-Esplá *et al.*, 2008; Templado *et al.*, 2016) (Fig. 1). Data on the structure and dynamics of the phytobenthic communities inhabiting such platforms are scarce (Soto, 1987; Pena-Martín, 2002; Terradas-Fernández, 2014).

The zonation pattern is easily recognizable in the whole platform. An initial sloping midlittoral algal belt dominated by Corallinaceae is followed by an upper infralittoral zone occupying a large portion of the platform,
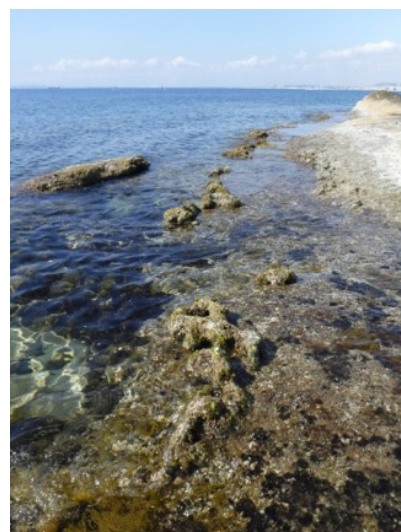

Fig. 1: Abrasion platform with vermetids at Cabo de las Huertas (Alicante). Seascapes of this type are well developed along rocky limestone shores in the Southeast Iberian Peninsula.

dominated mainly by Dictyotaceae. The exposed outer margin normally hosts Corallinaceae formations with vermetids, along with leathery algae. These platforms are very shallow in depth (≤ 40 cm), and are characterized by intermediate temperature and nutrient conditions when comparing to those found along the adjacent Iberian coasts (cooler and somewhat more eutrophic) and those in the Eastern Mediterranean (more oligotrophic and warmer) (Bosc *et al*., 2004; Coll *et al*., 2010). Such characteristics suggest that their dynamics may also be different from other comparable shallow phytobenthic assemblages, in both Iberian (Ballesteros, 1992) and Eastern Mediterranean Sea (Lipkin & Safriel, 1971; Lundberg & Olsvig-Whittaker, 1998).

The focus of this study is to explore the structure, composition and seasonal dynamics of the phytobenthic communities on abrasion platforms with vermetids and to identify the main influencing drivers of these assemblages. The results are compared with those of other analogous studies in shallow systems of the Western and Eastern Mediterranean Sea.

Material and Methods

Sampling and data collection

Two previously typified locations (Isla de Tabarca and Cabo de las Huertas) (Terradas-Fernández, 2014) were chosen. These sites present no pollution source or other visually anthropogenic disturbances. Tabarca is located at 38.16701º N, 0.48498º W and Cabo de las Huertas at 38.35340º N, 0.42053º W (Fig. 2). Three permanent transects perpendicular to the shore (3 to 6 m in long) were established at each location including: a) a proximal mid-littoral zone; b) an infralittoral zone; and c) an exposed outer margin adjoining its seaward 'wall' (Fig. 2, Electronic appendix Fig. S 1, Fig. S 2). Each transect was sampled monthly for one year (June 2015–May 2016), using contiguous 625 cm^2 pre assigned squares separated by 5 cm. Sampling squares were sampled monthly along each transect.

The coverage of visually distinguishable sessile taxa was calculated using the Braun-Blanquet scale (1979) (Díez *et al.*, 2003; Chappuis *et al.*, 2014). 6 cover-categories were used: <5% cover (1), 5–25% (2), 25–50% (3), 50–75% (4), and >75% (5). A 0.1% value (6) was used for taxa with insignificant coverage. Taxa impossible to identify *in situ* were collected for subsequent identification in the laboratory. Inconspicuous taxa with less than 0.1% coverage in all zones and seasons were excluded from the analysis (see Electronic appendix Table S 1).

For each sampled square, 6 environmental variables were measured or estimated: i) the *substrate slope*, ii) the *distance from the outer margin* (platform seaward limit), iii) the *grazers' coverage*, iv) the *sediment coverage*, v) the *topographic complexity*, and vi) the *depth*, as follows:

i) Substrate slope angle, from 0 up to 4: (0) horizontal surface; (1) 15-30º slope; (2) 30º-45º slope; (3) 45º-90º slope; (4) >90º slope.
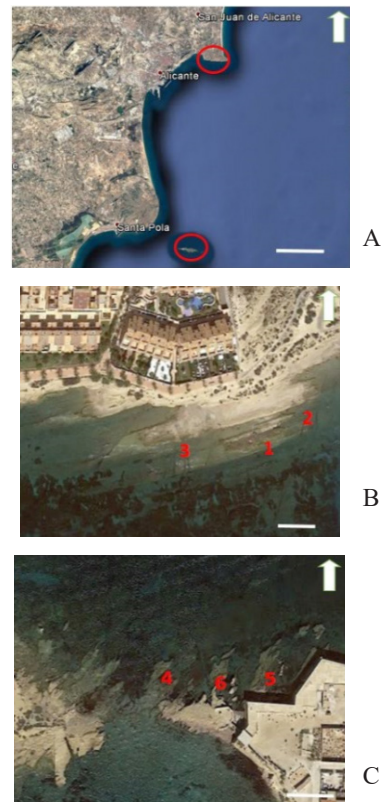

Fig. 2: Sampling locations. A. Geographic location of both areas (northern circle indicating Cabo de las Huertas, and southern circle indicating Isla de Tabarca); scale bar = 5 km. B and C. Transect locations at Cabo de las Huertas and Isla de Tabarca respectively (scale bar = 30 m). Modified from Google Earth.

ii) Distance from the outer margin in cm for each transect square (Gil *et al*., 2008; Balistreri *et al*., 2015).

iii) Grazers' coverage, using the Braun-Blanquet (1979) scale in line with Chappuis *et al*. (2014), integrating all grazers' taxa.

iv) Sediment coverage followed the criteria suggested by Díez *et al*. (2003), keeping the same Braun-Blanquet categories used for phytobenthos coverage: (1) <5% coverage, (2) 5–25%, (3) 25–50%, (4) 50–75%, and (5) >75%.

v) Topographic complexity followed the methods of Graziano *et al*. (2009) employed by Balistreri *et al*. (2015), but using the same 625 cm2 sampling squares for the calculation. Thus, the inverse ratio of the sums of the perimeter and the diagonals with regard to the measurement adjusted to the rocky substrate were calculated for each square.

vi) Depth, defined as the water-column height above each square, measured with a vertically placed ruler, resulting in an average value for each sampled square during the year. The average depth was incorporated as a variable. The reason for using the average instead of empirical value was its considerable variability even on the same day (pers. obs.).

In addition, each day's photoperiod was taken into

account based on information provided by the National Astronomical Observatory of Spain (http://www.fomento.gob.es). Finally, temperature data were obtained by CIMAR Research Station at Cabo de Santa Pola at 0.5 m depth at 9 AM over a similar abrasion platform to those studied, situated close to both sampling locations. The maximum algal canopy height of each plot was also measured with a ruler and used as a surrogate to estimate the productivity potential (Steneck & Dethier, 1994).

Data analysis

The coverage values of each phytobenthic taxon, sediment and grazers were determined by using a transformation of the Braun-Blanquet scale data, considering the median points of each interval as new values (Díez *et al.*, 2003; Guinda *et al.*, 2012). The coverage values of the taxa were square root transformed for the multivariate analyses, and a similarity matrix was generated based on them using the Bray-Curtis distance.

To assess whether there were significant differences between zones and seasons, a permutational multivariate analysis of variance (PERMANOVA) was performed (Anderson *et al.*, 2008). The analysis consisted of a two-way crossed model in which *zone* and *season* were treated as fixed factors. Sums of squares type III were employed to account for unbalanced design (Anderson *et al.*, 2008). Pairwise *post-hoc* comparisons were made to test for significant differences. The taxa that contributed most to the differences were identified using similarity percentages (SIMPER) (Clarke & Gorley, 2006).

To test the potential influence of each variable within the community structure, a distance-based linear model routine (DistLM) was applied to the previously generated Bray-Curtis matrix. The stepwise selection procedure was used with the R^2 criterion. Environmental variables were normalized: *grazers' coverage* was previously square-root transformed as it presented a right skewed distribution. Spearman correlations were used to test the relationship between the abundance of the algal taxa and the variables that contributed most to the DistLM analysis. Finally, a distance-based redundancy analysis (dbRDA) was performed to visualize the relationships between algal assemblages and environmental variables, based on the above multivariate regression model (DistLM analysis).

Furthermore, *α*- and *β*-diversity were used as indicators of structural complexity (Ballesteros, 1991; Simboura & Zenetos, 2002; Martí *et al.*, 2005; Mangialajo *et al.*, 2008; Balata & Piazzi, 2008; Casas-Güell, 2016). Shannon index was applied for calculating *α*-diversity, where "N" is the overall taxa coverage of a given sampled square and "ni" is the coverage of each of taxon for the same square:

$$H' = -\sum (n_i/N) \log_2 (n_i/N)$$

In order to determine whether there were significant differences between *α*-diversity values depending on the *season* and *zone*, a second PERMANOVA was applied from a similarity matrix using the Euclidean distance (Anderson *et al.*, 2008).

For calculating *β*-diversity, the criteria suggested by Anderson *et al.* (2008, 2011) were followed, here construed as the acceptance defined by the degree of variability within a community, calculated from the variability between different samples thereof. Thus, on the basis of the taxa composition in each square, a Jaccard similarity matrix was calculated and the homogeneity of the dispersions for *zone* and *season* (PERMDISP) was tested using the average distance to centroid as the measure of *β*-diversity.

All statistical analyses were performed using the PRIMER--E® v.6 + PERMANOVA package (Clarke & Gorley, 2006; Anderson *et al.*, 2008), except for the information graphics for α-diversity (Fig. 3) and Spearman correlations between taxa and environmental variables, which were performed using R software version 3.2.2 (R Development Core Team, 2011) and gggplot2 package (Wickham, 2009).

Results

Through the overall annual survey, 970 square samples were studied and over than 100 taxa were identified (see Electronic appendix Table S 1). Some commonly found species in our study areas appear to be more rare or absent in the Northeast Mediterranean Iberian Peninsula (Chappuis *et al.*, 2014), e.g. *Cladophoropsis membranacea* and *Cystoseira algeriensis*. Additionally, *Neosiphonia ferulacea* and *Chaetomorpha pachynema* were present in our infralittoral sampling squares, but neither species seems to have been reported previously in the Iberian part of the Mediterranean (Gallardo *et al.*, 2016), although C. pachynema has been reported from the Balearic Islands (Cremades, 1989).

Differences in community configuration attributable to season and zone factors

Both season and zone affiliation were significant in the configuration of the phytobenthic assemblages (Table 1). The pairwise test showed that these differences remained when comparing season effects within each zone, except the midlittoral zone between summer and autumn (P (perm) = 0.058).

The results of the SIMPER two-way crossed analysis based on *season* and *zone* factors are shown in Table 2 with a cut-off percentage of 90% accumulated similarity. In the midlittoral zone, the major contributors to similarity were the crustose Corallinaceae, *Jania* spp., *Dendropoma lebeche,* Rivulariaceae and *Ulva* spp. In the platform's infralittoral zone, along with *Jania* spp., the role of Dictyotaceae was significant (contributions over 10%). Finally, at the outer margin, the main similarity contri-
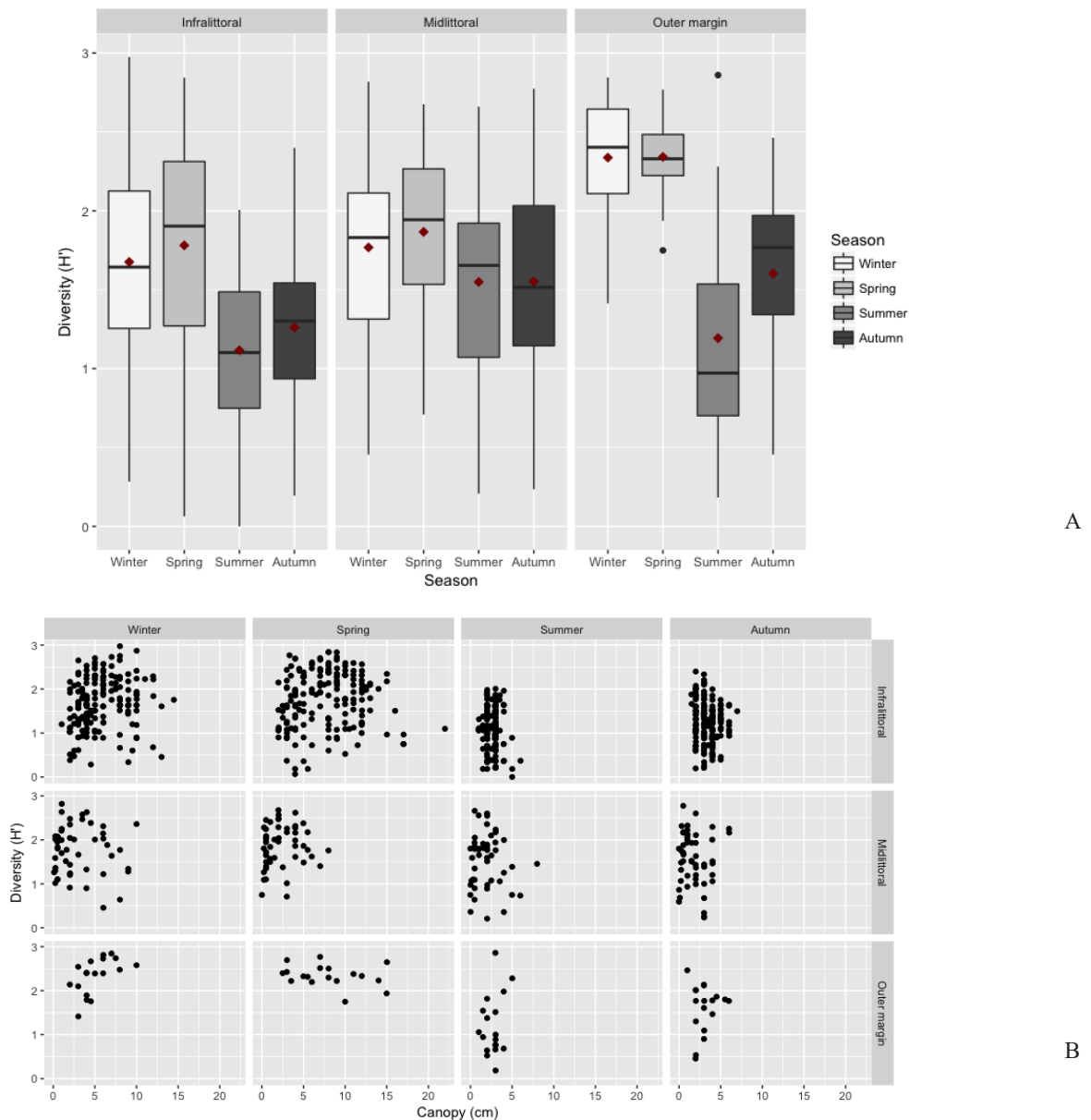
Fig. 3: A. Shannon diversity values (H') per *season* for all studied zones. B. Canopy height values per *season*, *zone* and Shannon diversity.

bution was made by a mixed group of infralittoral and midlittoral taxa. As in the infralittoral case, *Jania* spp. were the main contributors followed by *Padina pavonica* and the crustose Corallinaceae group (all with contributions above 10%). *Dictyota* spp. and *Cystoseira* spp. were found below 10%. *Ellisolandia elongata* and *Caulerpa cylindracea* contributed around 1% in the outer margin zone, while their contribution was near-zero in the midlittoral and infralittoral zones (data not shown).

The proportion of each taxon to SIMPER similarity varied highly according to season. In summer and autumn, *Jania* spp. contributed to similarity with a high percentage (over 50% in both seasons), followed by *Padina pavonica* with 34.8% in summer and 19.3% in autumn. In winter and spring, *Jania* spp. contribution progressively decreased (35% in winter and 8% in spring). On the other

hand, Dictyotaceae (*P. pavonica* and *Dictyota* spp.) showed the inverse pattern, with a total 47.2% in winter and up to 63% in spring. Other algae with strong seasonality included *Cystoseira compressa* and *Halopteris scoparia* (with spring contributions of 10.6% and 7% respectively).

α-diversity

α-diversity showed a significant seasonal pattern associated with zone (Fig. 3 and Table S 2). A greater diversity phase during winter and spring was observed, which coincided with a higher algal canopy, but a lesser diversity during summer and autumn with a lower canopy height. This pattern was observed in each zone, being greater at the outer margin and lesser in the midlittoral zone.

Table 1. Distance-based permutational two-way PERMANOVA comparing all the samples taxa inventories using *zone* and *season* as fixed factors (A). Results of pairwise analyses (B). Se, *season*; Z, *zone*; df, degrees of freedom; SS, sums of squares; MS, mean squares; Pseudo-F, pseudo-*F* ratio; t, pseudo-*t* statistic; P(perm), permutation *P*-value.

A

Source of variation	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Se	3	102800	34267	28	0.001	996
Z	2	504190	252100	209	0.001	998
SexZ	6	52706	8784	7	0.001	999
Res	959	1155600	1205			
Total	970	1959900				

B

Pairwise analysis within levels of factor 'Z'	Midlittoral		Infralittoral		Outer margin	
Groups	t	P(perm)	t	P(perm)	t	P(perm)
Spring, Summer	2.97	0.001	12.22	0.001	3.99	0.001
Spring, Autumn	3.78	0.001	11.66	0.001	3.45	0.001
Spring, Winter	1.62	0.026	6.02	0.001	1.94	0.001
Summer, Autumn	1.48	0.058	6.16	0.001	1.82	0.004
Summer, Winter	2.79	0.001	7.75	0.001	2.69	0.001
Autumn, Winter	3.43	0.001	5.77	0.001	2.04	0.001

Table 2. Main taxa contributions to SIMPER two-way similarity (*season* and *zone*). Contrib. %: Percentage of contribution to group similarity. Cut-off for low contributions: 90%.

Species	Midlittoral Contrib%	Infralittoral Contrib%	Outer margin Contrib%
Cladophora spp.	3.38		
Corallinaceae	39.86		15.74
Cystoseira compressa / humilis		3.09	4.68
Dendropoma lebeche	10.28		1.46
Dictyota spp.		13.76	5.74
Jania spp.	16.43	43.39	46.28
Padina pavonica		31.81	17.3
Palisada spp.	2.57		
Rivulariaceae	12.91		
Ulva spp.	5.95		

Species	Spring Contrib%	Summer Contrib%	Autumn Contrib%	Winter Contrib%
Corallinaceae	4.87			5.46
Cystoseira compressa / humilis	10.56			
Dictyota spp.	21.95		11.37	21.31
Halopteris scoparia	6.95			3.03
Jania spp.	7.93	57.93	59.87	34.98
Padina pavonica	41	34.81	19.34	25.99

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β-diversity

β-diversity results can be found in Table 3. The midlittoral zone had the highest *β*-diversity, with related samples showing a Jaccard average distance to centroid of 47.46 ± 0.52%. The outer margin showed a 45.62 ± 0.79% value. Lastly, the infralittoral zone showed a value of 41.2 ± 0.35%. Based on the homogeneity of multivariate dispersions test (PERMDISP) (Table 3 A), pairwise comparisons indicated that the differences between the infralittoral and the other zones were significant. Nevertheless, the midlittoral and outer margin did not differ significantly (P (perm) = 0.09).

Comparing seasons, winter and spring had higher values of average distance from the centroid with respect to the whole platform (both slightly over 48%), while summer and autumn had lower values (40% and 42% respectively). There were no significant differences between winter and spring, or between summer and autumn, but the rest of the cross-season comparisons were significantly different (P (perm) < 0.05; Table 3 B).

The role of environmental variables

The multivariate regression model generated by the DistLM analysis showed that the matrix of environmental variables explained a significant proportion of the multivariate variation in the structure and composition of the studied communities (Table 4). On the basis of the sequential test using the step-wise selection procedure and

Table 3. *β*-diversity values and test for homogeneity of multivariate dispersions. A) Zones**;** B) Seasons (for the whole platform); t, pseudo-*t* statistic; P(perm), permutation *P*-value; Average, average Jaccard distance-to-centroid; SE, standard error.

A			
PAIRWISE COMPARISONS	**Group factor:** *Zone*		
Groups	t	P(perm)	
(Midlittoral, Infralittoral)	8.8876	0.00	
(Midlittoral, Outer margin)	1.8551	0.09	
(Infralittoral, Outer margin)	3.9516	0.00	
MEANS AND STANDARD ERRORS			
Group	Size	Average	SE
Midlittoral	204	47.46	0.51911
Infralittoral	695	41.25	0.3461
Outer margin	72	45.62	0.78543

B			
PAIRWISE COMPARISONS	**Group factor:** *Season*		
Groups	t	P(perm)	
(Spring, Summer)	8.06	0.00	
(Spring, Autumn)	6.66	0.00	
(Spring, Winter)	0.44	0.73	
(Summer, Autumn)	1.82	0.13	
(Summer, Winter)	7.78	0.00	
(Autumn, Winter)	6.35	0.00	
MEANS AND STANDARD ERRORS			
Group	Size	Average	SE
Spring	243	48.77	0.64
Summer	243	39.94	0.89
Autumn	243	42.08	0.77
Winter	242	48.37	0.62

R² criterion, *depth* was the variable explaining the greatest proportion of the variation for the model. The next-best variables to add in order to increase R² were respectively: *photoperiod*, *water temperature*, *distance from outer margin*, *topographic complexity*, *slope*, *sediment coverage* and *grazers' coverage*. Total variability, defined by the selected environmental variables, was 44%.

In the dbRDA analysis (Fig. 4), *depth* was negatively correlated with the first axis while the *distance from outer margin* was positively correlated to it, along with *topographic complexity*, *grazers' coverage* and *slope* (with a lesser correlation). The variables that correlated best with the second axis were the *photoperiod* (negatively) and *temperature* (positively). Both axes accounted for 79% of the fitted variation (35% of total variability).

Crustose Corallinaceae, Rivulariaceae and *Dendropoma lebeche* were positively correlated with the first axis, while *Padina pavonica*, *Dictyota* spp. and *Cystoseira compressa* were negatively correlated to it. As for the second axis, crustose Corallinaceae and Rivulariaceae showed near-zero correlations, Jania spp. was clearly positively correlated, and the rest of the taxa showed negative correlations.

When it comes to Spearman correlations between environmental variables and taxa coverages (Table 5), it was observed that depth still showed a greater correlation with the majority of taxa. Correlation was positive with typical infralittoral species, excepting *Padina pavonica,* whereas it was negative with midlittoral taxa (Rivulariaceae, *Ulva* spp., crustose Corallinaceae).

Photoperiod only displayed a high and negative correlation value with *Jania* spp.. Crustose Corallinaceae and Rivulariaceae did not show significant correlations, while the rest of the infralittoral taxa generally showed positive correlations.

Most taxa showed negative correlations with *temperature*, coinciding with winter and spring conditions. Only *Padina pavonica*, with high coverage during summer, showed a clearly positive correlation. *Jania* spp., which develops in summer and autumn, showed a near-zero correlation.

Taxa showing a higher negative correlation with *distance from outer margin* were the *Jania* spp. and *Padina pavonica*. Conversely, Rivulariaceae was the group with the highest positive correlation.

Sediment coverage showed a moderate and positive correlation (0.3) with *Dictyota* spp., and slightly lesser with *Padina pavonica* and *Dasycladus vermicularis*. *Halopteris scoparia* presented near-zero values. The rest of the taxa displayed a negative correlation. As for the crustose Corallinaceae, their abundance in highly sediment-covered areas may have been underestimated.

Grazers' coverage, *slope* and *topographic complexity* showed a generally positive correlation with midlittoral taxa, being negative with those dominating in the other zones. Nonetheless, the midlittoral *Ulva* spp. presented a negative correlation with *slope*.

Patellidae, Trochidae, Lepidochitonidae, and Littorinidae were the main grazer families represented in the midlittoral zone. In the infralittoral, the most common visible groups were instead Columbellidae, Cerithidae, Paguroidea and Plakobranchidae, always with lower coverage values than midlittoral taxa, and barely detectable visually.

Discussion

Floristic aspects

The abrasion platforms with vermetids studied at both locations (Tabarca and Cabo de las Huertas) share the main taxa with other Mediterranean vermetid platforms (Lipkin & Safriel, 1971; Mannino, 1992; Lakkis & Novel-Lakkis, 2000). The alien alga *Caulerpa cylindracea*, despite commonly found along the entire platform, it grows better on the outer margin, generating conspicuous patches, mostly in spring. The higher coverage of this alien species on the eutrophicated Aguamarga platforms

Table 4. Results of DistLM (distance-based linear model routine). Sequential test for relationships between environmental variables and taxa coverage (considering all environmental variables and using the step-wise procedure and R² selection criterion) determining the variance explained by predictor variables when fitted sequentially.

SEQUENTIAL TEST				
Variable	**Pseudo-F**	**P**	**Prop.**	**Cumul.R²**
Depth	239.87	0.001	0.20	0.20
Photoperiod	65.39	0.001	0.05	0.25
Water temperature	118.97	0.001	0.08	0.33
Distance	48.14	0.001	0.03	0.36
Topographic complexity	51.91	0.001	0.03	0.40
Slope	32.63	0.001	0.02	0.42
Sediment	21.21	0.001	0.01	0.43
Grazers	17.49	0.001	0.01	0.44

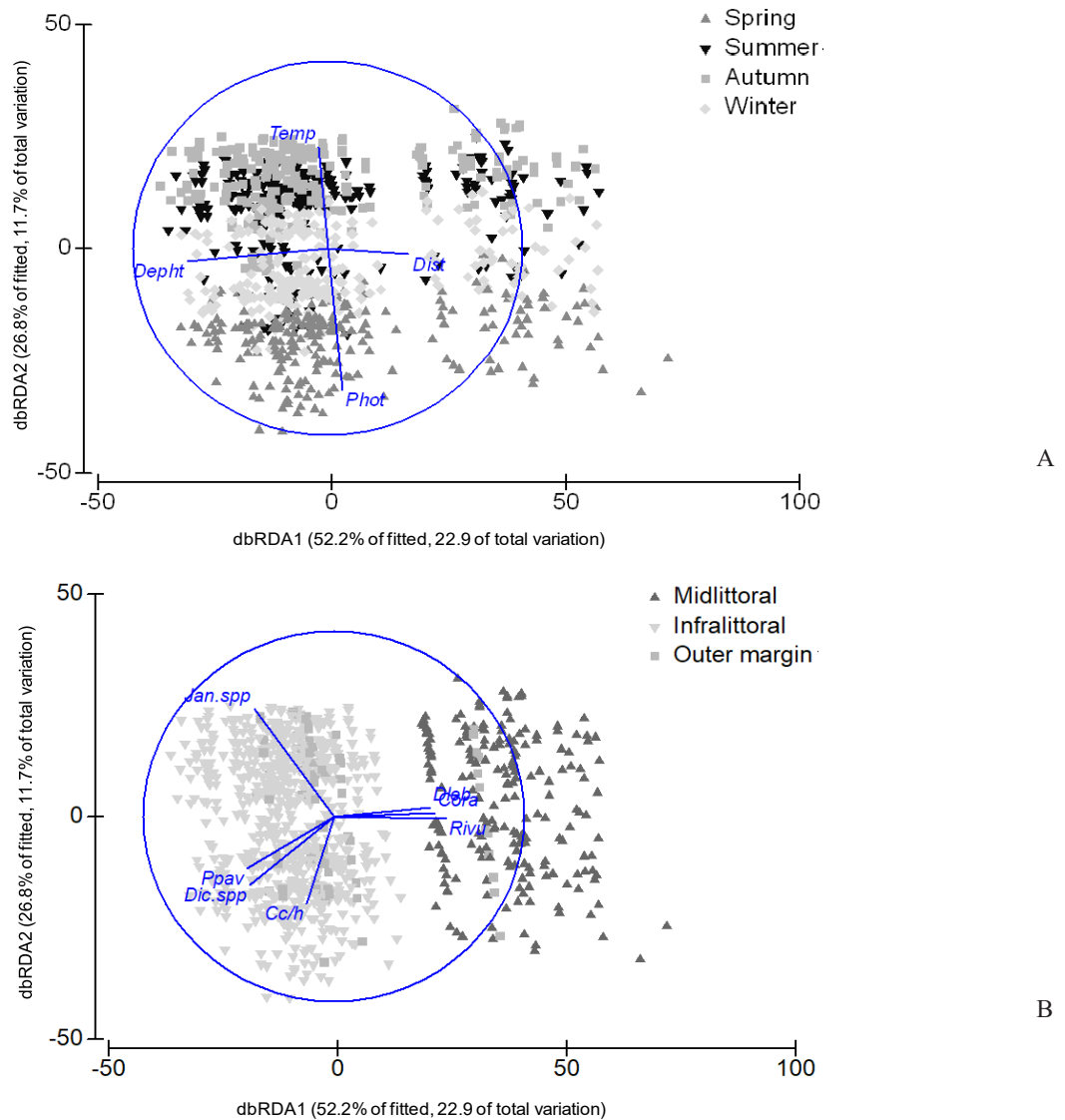*Medit. Mar. Sci.*, 19/1, 2018, 58-68

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Fig. 4: Distance-based redundancy analysis (dbRDA). A. Relationships between the ordination of samples, based on taxa coverage and environmental variables (four variables that explain most of the variability in the data cloud are shown, according to the stepwise procedure and R2 criterion). Abbreviations: Temp = water temperature, Dist = Distance from outer margin, Phot = photoperiod. B. Direction of increasing coverage of the most abundant taxa with Spearman correlations over 0.4. Abbreviations: Cora = Corallinaceae, *Cc/h* = *Cystoseira compressa/humilis*, *Dleb* = *Dendropoma lebeche, Dic*.spp = *Dictyota* spp., *Jan*.spp = *Jania* spp., *Ppav* = *Padina pavonica*, *Rivu* = *Rivulariaceae*.

(a place close to Alicante, being under the influence of sewage), could indicate that this alien species thrives better in the most productive locations along these platforms, with the increased water motion and/or eutrophication being the two important factors enforcing its growth. Similarly, experimental studies indicate that this alga is favoured by eutrophic conditions (Gennaro & Piazzi, 2011).

The role of resource availability in the phytobenthos structure of the platform

The variables determining productivity potential, i.e. contributing to the maximum possible rate of biomass production (Steneck & Dethier, 1994), appear to exert the major role as drivers of the phytobenthic communities growing on vermetid platforms. Some of these variables are non-seasonal (*depth* and *distance from outer margin*), while others show a seasonal variability (*photoperiod, temperature*).

Low-canopy taxa (such as encrusting calcareous algae and *Padina* taxa) are followed by larger-sized taxa (such as *Dictyota* and *Cystoseira* taxa) according to the increase in depth and/or water motion, the latter variable being more important when the distance from the outer margin diminishes.

Regarding the seasonal cycle, the canopy height rises during winter and spring, coinciding with the photoperiod increase. This is because larger erect algae (*Dictyota*

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Table 5. Spearman correlations between the coverage of the most abundant taxa and the environmental variables studied. Shaded results indicate correlations over 0.3. Significant results (P < 0.05) were marked with an asterisk (*). Abbreviations: *Top.comp = Topographic complexity*.

Variables	Depth	Distance	Grazers	Photoperiod	Sediment	Slope	Top.complexity	T°
Corallinaceae	-0.43*	0.14*	0.31*	-0.06	-0.24*	0.29*	0.40*	0.11*
C. compressa/ humilis	0.10*	-0.24*	-0.14*	0.28*	0.13*	-0.09*	-0.095 *	-0.16*
D. vermicu- laris	0.50*	-0.07*	-0.09*	-0.09*	0.17*	-0.16*	-0.16*	-0.13*
Dictyota spp.	0.57*	-0.21*	-0.10*	-0.11*	0.31*	-0.17*	-0.09*	-0.38*
H. scoparia	0.32*	-0.09*	-0.14*	0.25*	0.02	-0.06	-0.17*	-0.02
Jania spp.	0.23*	-0.33*	-0.32*	-0.40*	-0.27*	-0.04	-0.21*	0.03
P. pavonica	-0.32*	-0.42*	-0.30*	0.27*	0.29*	-0.29*	0.11*	0.11*
Rivulariaceae	-0.54*	0.49*	0.41*	0.06	-0.24*	0.22*	0.28*	-0.05
Ulva spp.	-0.32*	0.27*	0.05	0.07*	-0.18*	-0.01	-0.11*	-0.11*

and *Cystoseira* taxa) increase in coverage. On the other hand, articulated calcareous algae (*Jania* spp.) are more abundant during summer and autumn when photoperiod shortens. This pattern fits with the productive cycle observed in shallow Northwest Mediterranean phytobenthic communities, where the production phase coincides with high nutrient concentrations (Ballesteros, 1989).

The scarcity of grazers' coverage in the outer margin and infralittoral platform zone suggests that their impact is limited as drivers of the macroalgae thriving in these zones. This suggests that bottom-up processes seem to be the main structuring mechanisms of at least a large portion of these shallow platforms. The importance of bottom-up processes and disturbances has already been examined in other works related to Mediterranean vermetid platforms; radiation intensity, wave strength, emersion periods and temperature appeared to be significant drivers for macroalgae thriving in these systems (Lundberg & Olsvig-Whittaker, 1998; Einav *et al.*, 1998; Einav & Israel, 2007; Gil *et al.*, 2008; Chemello, 2009).

The response found in several studies performed on Mediterranean infralittoral bottoms, where grazing pressure was experimentally modified (Verlaque, 1987; Sala, 1996; Hereu *et al.*, 2008), is similar to that found with increasing depth in our grazer-deficient system. In the first case, larger algae tend to thrive more as grazing decreases. In the second case, larger algae tend to thrive more in line with the rise in water depth. Both responses fit with Steneck & Dethier (1994) predictions on the dominance of different morphological groups according to their production potential and degree of disturbance. Crustose and calcified thalli withstand the disturbances and stress better, while the more complex thalli (large and rather internally complex) are more developed in situations showing greater productivity potential and stability.

Diversity pattern

A positive correlation between α-diversity and β-diversity was found for the production phases (winter and spring). The α-diversity shows the opposite pattern compared to that of several Mediterranean littoral rocky benthic communities (Soto, 1987; Rull-Lluch & Gómez-Garreta, 1990; Ballesteros, 1991; Rodríguez-Prieto *et al.*, 2013), where production phases are accompanied by a lower α-diversity. Instead, our observed α-diversity pattern is similar to that of other infralittoral rocky shallow systems, where diversity values may be uncorrelated or positively correlated with the production phases (Garrabou *et al.*, 2002; Martí *et al.*, 2005). These differences appear to be caused by the dominance of relatively persistent habitat engineering species, which thrive in disturbance-free systems in high productivity conditions. The quantitative importance of these species affects the diversity values of the whole community (Wernberg & Goldberg, 2008). On the other hand, under stress conditions (whether by lack of water movement or light), or under a high disturbance degree (herbivory), the persistent species dominance seems to be hindered. In such cases, the seasonal production peak may not coincide with a diversity decrease, but rather the opposite (Martí *et al.*, 2005). This would be the case of the majority of the communities on the surveyed platforms. Thus, their relatively buffered hydrodynamics and especially the lack of enough depth would limit the community's productivity, hindering the establishment of persistent taxa with high coverages, such as Cystoseira taxa, which may lower the α-diversity values during the productive phase.

The lower annual α-diversity fluctuations in our midlittoral zone platform could be caused by a lesser fluctuation in taxa coverage due to stress caused by low aver-

age depth and water motion deficit. In contrast, the wide environmental variation in this midlittoral zone results in a relatively high heterogeneity between midlittoral sampling squares, making for maximum β-diversity values, although close to those observed on the platform's outer margin.

In conclusion, the main drivers of the studied vermetid abrasion platforms seem to be bottom-up in their influence, water availability (depth) and seasonal factors being the most important. These results contrast with those obtained in other infralittoral systems, which are apparently under more intense grazing pressure (Verlaque, 1987; Hereu *et al.*, 2008). Diversity is positively linked to the production cycle of the phytobenthos inhabiting these platforms, due to the lack of a persistent dominant group able to reduce diversity at its peak productivity.

Eutrophication and extreme climatic events (Sanz-Lázaro, 2016), such as unusual long emersion periods or strong storms, are other important factors not directly considered in this study. They should be taken into account in future research in order to widen our knowledge of these scarcely studied seascapes, typically found in the warm parts of the Mediterranean, along with their possible interaction with the current global warming scenario.

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