



## ORIGINAL ARTICLE

# Influence of wave climate on architecture and landscape characteristics of *Posidonia oceanica* meadows

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## Keywords

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## Abstract

Seagrass meadow characteristics, including distribution, shape, size and within-meadow architectural features, may be influenced by various physical factors, including hydrodynamic forces. However, such influences have hardly been assessed for meadows of the ecologically important and endemic Mediterranean seagrass *Posidonia oceanica*. The distribution of *P. oceanica* meadows at five sites in the Maltese Islands was mapped to a depth of c. 15 m using a combination of aerial photography and SCUBA diving surveys. Estimates of wind-generated wave energy and energy attenuated by depth were computed using the hydrodynamic model WEMo (Wave Exposure Model). Metrics for *P. oceanica* landscape features were calculated using FRAGSTATS for replicate 2500 m<sup>2</sup> subsamples taken from the seagrass habitat maps in order to explore the influence of wave dynamics at the landscape scale. Data on within-meadow architectural attributes were collected from five sites and analysed for relationships with wave energy. The results indicate that landscape and architectural features of *P. oceanica* meadows located within the 6–11 m depth range are significantly influenced by wave climate. *Posidonia oceanica* meadows tend to be patchier and have low overall cover, more complex patch shapes and reduced within-patch architectural complexity along a wave exposure gradient from low to high energy. The findings from the present study provide new insight into the influence of hydrodynamic factors on the natural dynamism of *P. oceanica* meadow landscape and architecture, which has implications for the conservation and management of the habitat.

## Introduction

Seagrasses form dynamic landscapes according to the physical setting; they typically colonize soft sediment substrata in shallow coastal waters and are of high ecological importance. Depending on the species, the morphological characteristics of seagrass meadows are influenced by numerous biological, chemical and physical factors, including light availability, hydrodynamic factors and substratum characteristics (Fonseca & Bell 1998; Koch 2001; Green & Short 2003). Seagrass habitat configuration and meadow architecture are determined by seagrass

growth and reproductive strategies, as well as by interactions with biotic and abiotic environmental factors (Duarte *et al.* 2006). Seagrass meadow landscape and architectural features are heterogeneous at various spatial levels, from the individual leaves at the centimetre scale to entire landscapes at the scale of tens of kilometres (Balestri *et al.* 2003; Frederiksen *et al.* 2004). Such variation in landscape spatial arrangement has been noted for several seagrass species, including the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile (Borg *et al.* 2005, 2006). Borg *et al.* (2009) described different *P. oceanica* bed morphologies that range from continuous

meadows, to semi-fragmented reticulate meadows to patchy meadows. However, although several studies have addressed the within-meadow architectural characteristics of meadows formed by *P. oceanica* (e.g. Balestri *et al.* 2003; Borg *et al.* 2005; Vasapollo & Gambi 2012), few works have investigated landscape aspects of this seagrass (Abadie *et al.* 2015).

The concept of landscape ecology and study tools used, although developed for terrestrial studies, are also applicable to the study of the dynamics and heterogeneity of marine habitats (Wedding *et al.* 2011). However, whereas techniques such as aerial imagery that have been extensively used to study terrestrial vegetation have also been widely used to assess the spatial distribution of seagrass meadows (e.g. Meinesz *et al.* 1988; Galdies & Borg 2006; Leriche *et al.* 2006), use of quantitative indices to assess the spatial configuration of *P. oceanica* habitat has been limited (Abadie *et al.* 2015).

Whereas seagrass propagation, through the colonization of unvegetated sea bed via seed dispersal or clonal growth, is the driving force for meadow expansion, physical disturbance is considered to have a primary influence on landscape configuration and dynamism. There is a tendency for seagrass meadow patchiness to increase along a gradient of increasing exposure to disturbance (Fonseca & Bell 1998; Fonseca *et al.* 2002; Frederiksen *et al.* 2004). Water movement may influence and modify habitat configuration through mechanical stress, alteration of sediment physiochemical characteristics, sediment movement and alteration of light availability when turbid conditions prevail. Seagrass burial resulting from sediment movement leads to shoot mortality and inhibits patch growth and meadow contiguity, whereas mechanical stress could lead to the uprooting of seagrass shoots and increased seedling mortality, hence inhibiting the formation of new patches (Marbà & Duarte 1994, 1995; Infantes *et al.* 2011).

In the absence of strong tidal forces, wind-generated wave action is the principal hydrodynamic force influencing shallow seagrass meadows (e.g. Stevens & Lacy 2012). In the Mediterranean, where tidal amplitudes are low, few authors have assessed the relationship between hydrodynamic setting and *P. oceanica* meadow landscape and architectural characteristics. This seagrass species occurs within the 0–45 m depth range, and shows resilience to sediment movement by forming extensive ‘mattes’ that stabilize the substrate and increasing vertical rhizome growth during periods of shoot burial (Boudouresque & de Grissac 1983; Mateo *et al.* 1997).

Seagrass habitats are undergoing worldwide degradation as a result of anthropogenic activities (Short *et al.* 2011). In the Mediterranean, seagrass habitat has declined as a result of increased meadow fragmentation and a

decrease in the lower depth limit of seagrass distribution (Ardizzone *et al.* 2006; Montefalcone *et al.* 2010). This causes concern given the importance of *P. oceanica* for primary productivity in the oligotrophic Mediterranean sea, and because meadow degradation may lead to potential release of large quantities of organic carbon stored above and below ground (Fourqurean *et al.* 2012; Pendleton *et al.* 2012). Natural stresses may exacerbate anthropogenically related seagrass meadow decline, which is often a self-accelerating process with long recovery times (Duarte 1995; Duarte *et al.* 2006). Hence, an understanding of seagrass dynamics in relation to natural environmental stresses is highly important for the conservation and management of seagrass habitat (Fonseca & Bell 1998).

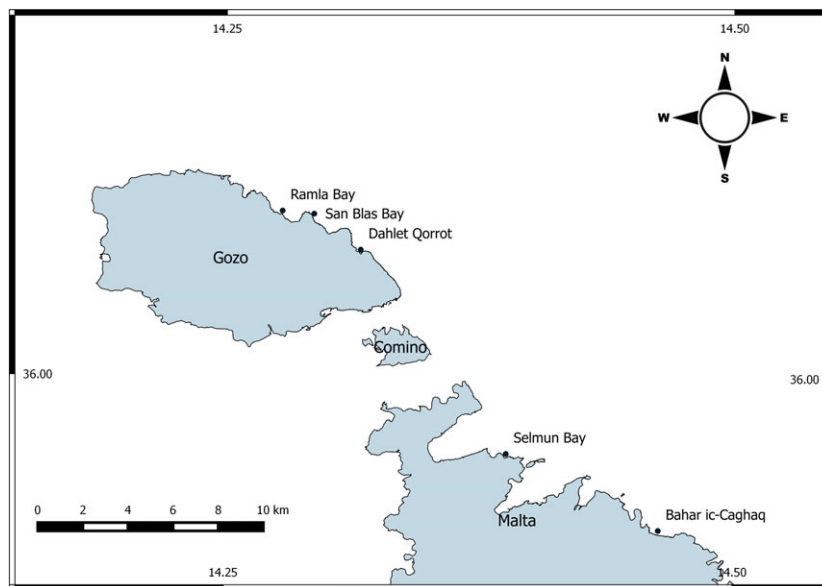
As few seagrass landscape studies have addressed the influence of wind-generated wave energy on the configuration of *P. oceanica*, there is an urgent need to understand the spatial and temporal dynamics of this relationship. Accordingly, the present study was aimed at assessing the influence of wave climate on *P. oceanica* by testing the hypothesis that exposure to wave energy influences landscape and architectural features of meadows formed by this seagrass.

## Material and Methods

### Study sites and mapping of *Posidonia oceanica* meadow distribution

Five study sites, separated from one another by at least 1.4 km and supporting extensive, healthy, monospecific meadows of *P. oceanica* located within the same depth range (5–15 m), were selected along the northeastern coast of the Maltese islands: Baħar ic-Cagħaq (BC), Selmun Bay (S), Dahlet Qorrot (DQ), San Blas Bay (SB) and Ramla Bay (RB). The sites have similar coastal geomorphological characteristics and are exposed to primarily wind-generated hydrodynamic forces (Fig. 1). As in most of the Mediterranean, Maltese coastal areas have a microtidal regime, and the northeastern coast is exposed to a wave regime that is predominantly the result of wind-generated wave action rather than long-period swell (Malta Maritime Authority 2003). The degree of coastal development in proximity to the selected sites is low and water quality is good, with relatively low levels of chlorophyll and turbidity (Axiak & Sammut 2002; MEPA 2013).

The *P. oceanica* meadows at each of the five sites were mapped for subsequent characterization of their landscape-scale spatial arrangement and canopy-scale architectural attributes. High-resolution (400 dpi) colour vertical aerial photographs, with a scale of 1:10,000, taken during an aerial survey carried out by plane in May 2008, were



**Fig. 1.** Map indicating the five study sites, located along the northeastern coast of the Maltese Islands.

acquired from the Malta Environment and Planning Authority. The aerial images were georeferenced against reference vector shoreline data provided by the hydrographic office at Transport Malta and augmented by ground control points collected adjacent to the shoreline using a handheld GPS set (Garmin eTrex H). Collinearity amongst georeferencing points was mitigated by the presence of embayments and headlands at many of the sites that allowed for a better distribution of points and a first-order polynomial rectification solution was used. A total root mean square error of better than 4 m was thus achieved for all the sites, showing that there was close positional correspondence between the georeferenced image and shoreline data.

Reference data for the corroboration of *P. oceanica* habitat spatial distribution data derived from the aerial photographs were collected through underwater surveys carried out at each study site between November 2011 and April 2012 (e.g. Borg *et al.* 2009). At each site, transects were laid underwater perpendicular to the shore and spaced approximately 100 m apart. The length of each transect ranged between 300 and 400 m, and covered a suitable depth range (c. 0–15 m) within which transitions occur between all three seagrass bed types: patchy, reticulate and continuous (Borg *et al.* 2009). The transects were traversed by SCUBA divers, and transitions between seagrass bed types and other coastal marine habitats were visually assessed and recorded to the nearest 0.1 m. Between three and four transects were surveyed within an area of approximately 90,000 m<sup>2</sup> at each of the five sites. Water depth measurements were recorded to the nearest 0.1 m at 10-m intervals along the transects using the

inbuilt electronic depth gauge in the dive computer (Suunto Vyper, Suunto Ltd, Vantaa, Finland).

SAGA GIS v. 2.0.8 (Conrad *et al.* 2015) was used to perform an unsupervised classification using the Forgy (1965) iterative optimization clustering algorithm on the aerial images for each site following normalization of the images to scale the standard deviation of each colour band in the grid to one (Olaya 2004). An unsupervised procedure was selected over supervised classification owing to the limitations in creating a training data set that is not confounded by depth-related attenuation of light (Schweizer *et al.* 2005). Normalization was found to greatly improve delineation between seagrass and macroalgal classes. Fifteen cluster classes were generated for each site and these were then merged according a classification scheme derived from the reference survey data. The principal classes that were identified at all study sites were: (i) bare soft sediment, (ii) turf algae on hard substratum, (iii) algal forests on hard substratum and (iv) *P. oceanica* meadows. The thematic accuracy of the produced maps was assessed following the recommendations of Liu *et al.* (2007). Producer's, user's and overall accuracies were calculated from an error matrix compiled from point comparisons between reference and classified map data. For a given class, the producer's and user's accuracies were respectively calculated as the proportion of correctly classified observations from the total number of observations within the reference and the classified data sets.

Overall, accuracy was high for all the maps produced (Table 1). High producer's accuracies indicate that seagrass recorded from the study sites had been correctly

**Table 1.** Summary of producer's, user's and overall accuracy scores calculated for *Posidonia oceanica* classes at each of the five study sites.

site	overall accuracy (%)	<i>Posidonia oceanica</i>	
		producer's accuracy (%)	user's accuracy (%)
Bahar ic-Caghaq	94.6	100	90.6
Selmun	95.7	100	95.6
Dahlet Qorrot	92.6	100	90.0
San Blas Bay	90.6	100	78.6
Ramla Bay	91.2	100	80.0

classified. However, although still constituting high values of accuracy, comparatively lower user's accuracy was achieved, indicating that of the mapped areas with seagrass, some areas of different habitat – particularly algal forests dominated by *Cystoseira* sp. – were incorrectly attributed to seagrass. This suggests a bias towards the identification of seagrass by the classification method resulting from some degree of overlap in macroalgal and seagrass spectral signatures. Classification errors typically occurred at the transition from extensive algal forests to *P. oceanica* meadows and, as a result of this, the boundary between these habitats was sometimes spatially displaced in relation to the recorded survey data. To mitigate the impact of classification errors, areas with *P. oceanica* habitat situated at depths <5 m, where macroalgal cover was greatest and the majority of classification errors occurred, were omitted from subsequent analyses.

#### Computation of wave energy variables

Estimates for representative wave energy (RWE) were estimated using the model WEMo (Wave Exposure Model), which was developed for hydrodynamic modelling by the National Centers for Coastal Ocean Service (NCCOS). The model predicts locally generated wave energy by computing (via ray tracing techniques and linear wave theory) wave generation, monochromatic propagation along each fetch ray and dissipation resulting from variations in bathymetry (Malhotra & Fonseca 2007). Using the model, RWEs were calculated by the model from hourly wind speed and direction data for the years 2009–2011 measured at a meteorological station located at Selmun, which is situated within 15 km of all five study sites. The highest 5% of wind speed events from a normal frequency distribution were processed by the model (see Fonseca & Malhotra 2010). Bathymetry values

for the fetch area were extracted by the model from a grid of interpolated contour and point data derived by Transport Malta's Hydrographic Office from Admiralty Nautical Chart No. 2537 with a scale of 1:50,000, as well as by using the depth measurements collected from the field during the present study. The interpolated grid was augmented by data from the International Bathymetric Chart of the Mediterranean, available as part of the General Bathymetric Chart of the Oceans as a 30 arc-second grid (IOC *et al.* 2010). In addition to RWE, estimates of bottom shear stress (BSS) were estimated using WEMo, via the expression:

$$\tau_b = \frac{\rho f_w}{2} u_b^2 \quad (1)$$

where  $\tau_b$  is the shear stress,  $\rho$  is the water density ( $\text{kg}\cdot\text{m}^{-3}$ ),  $f_w$  is the friction factor and  $u_b$  is the orbital velocity at the sea bed (Wiberg & Sherwood 2008) calculated from an estimated surface elevation spectrum applied to significant wave height and peak wave period calculated by the model (Fonseca & Malhotra 2010).

#### *Posidonia oceanica* meadow landscape data

Metrics were used to describe numerically the geospatial configurations of the seagrass meadow landscapes studied (see Wedding *et al.* 2011). Five landscape metrics were chosen, each representing a different aspect of landscape configuration: (i) *class area*: a measure of the total area occupied by *Posidonia oceanica* within a subsample; (ii) *patch number*: the number of discrete patches of *P. oceanica* within a subsample; (iii) *patch area*: the area occupied by each patch of *P. oceanica*, (iv) *SHAPE index*: a measure of the shape complexity of each patch of *P. oceanica* (Forman & Godron 1986) given by:

$$\text{SHAPE index} = \frac{0.25p}{\sqrt{a}} \quad (2)$$

where  $p$  and  $a$  are the perimeter (m) and the area ( $\text{m}^2$ ) of the patch, respectively; and (v) *Euclidean nearest neighbour distance* (ENN): the minimum distance of a given patch to its nearest neighbour (McGarigal *et al.* 2012). Landscape metrics were calculated for replicate areal subsamples that were randomly selected and extracted from the seagrass habitat maps. In order to account for potentially unpredictable metric scaling behaviour with spatial extent, the area of extracted spatial subsamples was kept constant amongst replicates (Wu 2004). Spatial analysis was performed on data extracted from 2500  $\text{m}^2$  subsamples of the mapped *P. oceanica* seagrass landscape. This category of areal extent constituted the largest total areal extent sampled and represented the best compromise

between area sampled and predictor variable applicability, and also compared well with trends observed within other subsample areal categories. Furthermore, categories for water depth (5–7 m, 7–9 m and 9–11 m) were created to account for the marked impact that water depth variation may have on seagrass spatial pattern (see Colantoni *et al.* 1982; Borg *et al.* 2009). Four replicate subsamples were extracted from each depth category for each seagrass habitat map.

FRAGSTATS (McGarigal *et al.* 2012) was used to calculate the selected landscape metrics following resampling of the extracted subsample grids to a resolution of 0.5 m. The 8-cell neighbour rule was retained as the default setting for the duration of the analysis; hence diagonal neighbours of the same categorical value were considered to constitute part of the same patch rather than different patches.

Statistical analysis was carried out using v. 3.2.2 of the R statistical software program (R Core Team 2014). Landscape metrics are typically non-normally distributed and often display multicollinearity (Wedding *et al.* 2011). A non-parametric test, Spearman's correlation co-efficient, was therefore estimated for the landscape variables and modelled wave climate variables (RWE and BSS). Spearman's correlation co-efficients were also used to evaluate multicollinearity between landscape variables. A multivariate approach was required to explore the relationship between wave climate and the overall change in landscape configuration within seagrass meadows, and canonical correspondence analysis (CCA) was chosen to directly relate environmental variables to landscape change (Ter Braak 1986). Environmental co-variables (RWE and BSS) were rescaled and centred to a comparable range of values prior to analysis (Ter Braak 1986). Model selection was carried out via Monte Carlo permutation tests with pseudo F-ratios (Oksanen 2015). A cut-off P-value of 0.05 was applied and variance inflation factors (VIFs) were used to assess collinearity between significant variables (Oksanen 2015). VIF values for all terms in the final model were <10. CCA was performed via v. 2.2-0 of the R package 'vegan' (Oksanen *et al.* 2014).

#### *Posidonia oceanica* meadow architecture data

SCUBA diving surveys to collect data on *Posidonia oceanica* bioparameters were carried out between 14 July and 27 August 2012. Three stations, each located on a different bed type of *P. oceanica*, patchy, reticulate and continuous, were selected from within the mapped area of each study site (Baħar ic-Cagħaq, Selmun Bay, Dahlet Qorrot, San Blas Bay and Ramla Bay) within a depth range of 6.1–10.8 m. This provided a total of 15 sampling stations over the five study sites. At each station, five replicate shoot

density counts were made using a 32 × 32 cm quadrat, and 12 orthotrophic shoots collected for laboratory analysis. In the laboratory, all leaves from each shoot were counted and characterized as 'adult', 'intermediate' or 'juvenile' according to the classes proposed by Giraud (1977), and estimates of morphometric parameters made using the procedures described by Pergent *et al.* (1995). Measurements of leaf length, sheath length, shoot width and leaf necrosis were recorded to the nearest 0.1 cm. The total number of adult leaves that had a missing apex – coefficient 'A' – was recorded and expressed as a proportion for each shoot. Epiphytes were scraped off the leaves of each shoot and the removed material and leaves from each shoot were dried separately at 60 °C for 48 h in pre-weighed aluminium trays (Vasapolo & Gambi 2012), following which they were weighed to the nearest 0.0001 g using an electronic balance.

Two-factor analysis of variance (ANOVA) was carried out for each measured attribute using the GMAV5 statistical package produced at the University of Sydney. The orthogonal model incorporated 'bed type' as a three-level (patchy, reticulate, continuous) fixed variable and 'site' as a five-level (BC, S, DQ, SB, RB) random variable. Evaluation of homogeneity of variance of the data was made *a priori* via Cochran's C test and appropriate transformations (see Results section) applied when the test was significant. Where the two-factor ANOVA identified a significant difference, *post hoc* Student–Neuman–Keuls (SNK) tests were performed to identify the source of difference.

Variation in *P. oceanica* architectural attributes in relation to shear stress and bed type were analysed through the fitting of generalized linear mixed models (GLMMs) using v. 1.1-10 of the 'lme4' package in R (Bates *et al.* 2015). Site was incorporated into the model *a priori* as a random effect, bottom shear stress, seagrass bed type and depth as fixed effects and architectural attributes as the response variable. Probability distributions appropriate to each architectural variable were selected, and potential interactions between each of the fixed effects were explored. Beginning with an initial maximal model, likelihood ratio tests (LRTs) were used to iteratively arrive at the final model (Zuur *et al.* 2009). The final model was validated by the evaluation of Pearson residuals for model fit.

## Results

### Landscape configuration

Despite comparable geo-morphological characteristics and depth ranges encountered at each site, clear differences in wave climate were noted amongst sites (Table 2). The

two sites most exposed to wave action are San Blas and Dahlet Qorrot, with mean values of RWE of 41.39 and 37.86  $\text{kJ}\cdot\text{m}^{-1}$ , respectively (Table 2). Mean values of near-bed shear stress indicated that San Blas remained the most exposed site ( $0.033 \text{ N}\cdot\text{m}^{-2}$ ) followed by Ramla Bay ( $0.014 \text{ N}\cdot\text{m}^{-2}$ ), whereas Baħar ic-Cagħaq, Selmun and Dahlet Qorrot had very low mean near-bed shear stress values ( $<0.01 \text{ N}\cdot\text{m}^{-2}$ ).

Results from the calculation of Spearman's correlation co-efficients (Table 3) detected monotonic relationships between *Posidonia oceanica* landscape variables and estimates for wave energy and shear stress. RWE showed weak negative correlations with SHAPE index ( $r_s = -0.091$ ,  $P < 0.01$ ), ENN distance ( $r_s = -0.191$ ,  $P < 0.01$ ) and patch area ( $r_s = -0.085$ ,  $P < 0.05$ ). Bottom shear stress showed a significant ( $P < 0.01$ ) negative correlation with class area ( $r_s = -0.509$ ), and a significant ( $P < 0.01$ ) positive correlation with number of patches per unit area ( $r_s = 0.576$ ). Significant ( $P < 0.01$ ) negative correlations were indicated between BSS and patch area ( $r_s = -0.109$ ) and ENN distance ( $r_s = -0.146$ ). However, collinearity between several landscape variables was also indicated in the results (Table 3). Strong monotonic relationships were detected between the number of *P. oceanica* patches per unit area and *P. oceanica* cover ( $r_s = -0.669$ ,  $P < 0.01$ ), and between seagrass patch area and patch shape complexity ( $r_s = 0.817$ ,  $P < 0.01$ ). The correlated metrics each measured different aspects of *P. oceanica* landscape or patch arrangement implying dependence rather than redundancy in the aspect of landscape configuration measured by the metrics (Abadie *et al.* 2015).

Dependence between patch size and shape complexity across an exposure gradient is further explored in Fig. 2. Although seagrass patches exposed to stronger near-bed shear forces tended to form more complex shapes than patches of comparable size exposed to weaker shear stress, shape complexity also scaled as a function of patch size. On average, patches tended to be smaller in more exposed areas and this contributed to high variability in patch shape complexity measurements. Given that

individual metrics often insufficiently capture the spatial variation of landscape pattern (Wedding *et al.* 2011), a multivariate approach was adopted to explore the overall variation in landscape pattern.

Canonical correspondence analysis showed that bottom shear stress had a stronger influence than RWE on the overall variation in landscape configuration. However, the impact of bottom shear stress significantly depended on depth (Monte Carlo permutation test:  $F = 24.37$ ,  $P < 0.001$ ). Overall, shear stress and depth explained 18.53% of the variation in landscape configuration, and this was mostly associated with the first CCA axis (18.21%). Across the first CCA axis, patchiness and patch shape complexity were positively associated with shear stress, whereas an inverse relationship was indicated between shear stress and patch size (Fig. 3). Closer associations with shear stress were noted for patchiness and shape complexity in deeper meadows (9–11 m). Clustering of depth centroids close to the origin of the ordination bi-plot suggests that depth does not greatly influence landscape characteristics.

#### Architectural attributes

The two-factor ANOVA detected significant differences amongst sites for all meadow architectural attributes except number of intermediate leaves per shoot (Table 4). However, although no attributes differed significantly amongst bed types, a significant interaction between site and bed type was detected for most parameters except those related to intermediate leaves (number, length, area) and shoot density. Moreover, the SNK results indicated a greater number of significantly different attributes amongst sites for shoots collected from patchy beds compared to continuous beds. Shoot biomass was significantly higher for continuous beds than for patchy beds at two of the five sites (SNK, BC:  $P < 0.05$ , RB:  $P < 0.01$ ). However, the continuous bed at Dahlet Qorrot supported significantly lower shoot biomass than the patchy bed (SNK,  $P < 0.01$ ). Epiphyte biomass was significantly lower for patchy beds than for reticulate and continuous beds at Baħar ic-Cagħaq (SNK,  $P < 0.05$ ), and the reticulate bed at Dahlet Qorrot (SNK,  $P < 0.05$ ). At Selmun, epiphyte biomass was significantly lower for the reticulate than for the continuous bed (SNK,  $P < 0.05$ ). Conversely, epiphyte biomass was significantly lower for the continuous bed than for the patchy and reticulate beds at Ramla Bay (SNK,  $P < 0.05$ ).

The importance of wave climate varied amongst different *Posidonia oceanica* architectural attributes (Fig. 4). Although BSS negatively impacted *P. oceanica* shoot biomass overall, the degree of impact depended on the bed type (LRT:  $\chi^2 = 20.39$ ,  $df = 2$ ,  $P < 0.001$ ) and depth

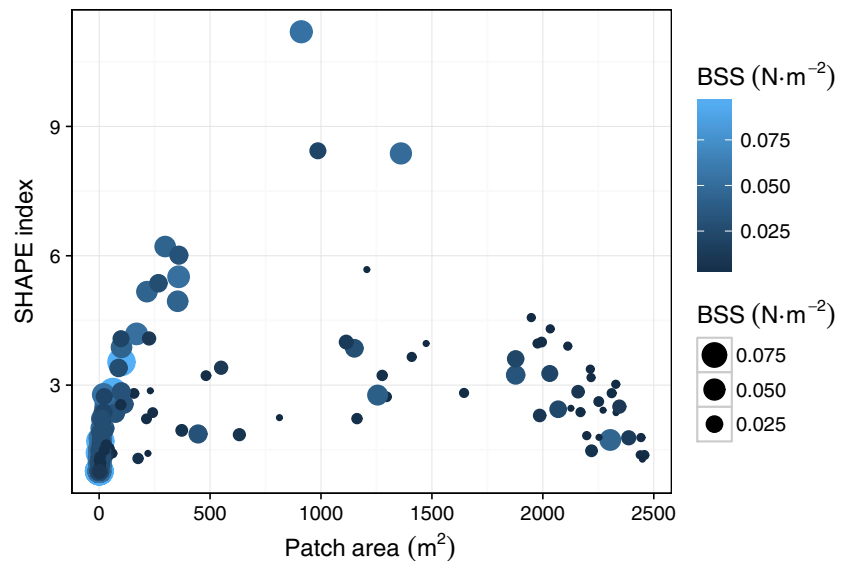
**Table 2.** Mean values ( $\pm$ SD) of depth, representative wave energy (RWE) and near-bed shear stress at each of the five study sites.

site	depth (m)	RWE ( $\text{kJ}\cdot\text{m}^{-1}$ )	shear stress ( $\text{N}\cdot\text{m}^{-2}$ )
Baħar ic-Cagħaq	10.1 $\pm$ 2.5	12.50 $\pm$ 3.82	0.003 $\pm$ 0.002
Selmun	9.7 $\pm$ 1.6	14.34 $\pm$ 6.35	0.002 $\pm$ 0.002
Dahlet Qorrot	11.1 $\pm$ 3.1	37.86 $\pm$ 18.00	0.003 $\pm$ 0.003
San Blas Bay	9.7 $\pm$ 2.4	41.39 $\pm$ 12.25	0.032 $\pm$ 0.023
Ramla Bay	8.8 $\pm$ 2.0	19.01 $\pm$ 9.81	0.014 $\pm$ 0.010

**Table 3.** Summary of statistically significant Spearman’s rank correlation co-efficients for *Posidonia oceanica* landscape characteristics calculated from 2500-m<sup>2</sup> subsamples of the seagrass meadow landscape.

landscape attributes	RWE	shear stress	class area	patch number	patch area	SHAPE index	Euclidean nearest neighbour
class area	–	–0.509**	–	–0.669**	–	0.067*	–0.134**
patch number	–	0.576**	–0.669**	–	–0.090**	–0.071*	–0.104**
patch area	–0.085*	–0.109**	–	–0.090**	–	0.817**	–0.185**
SHAPE index	–0.091**	–	0.067*	–0.071*	0.817**	–	–0.207**
Euclidean nearest neighbour	–0.191**	–0.146**	–0.134**	–0.104**	–0.185**	–0.207**	–

\* = correlation significant at 0.05 level; \*\* = correlation significant at 0.01 level; RWE = representative wave energy.



**Fig. 2.** Scatter plot of *Posidonia oceanica* patch size in m<sup>2</sup> with SHAPE index. Size and colour of an individual point corresponds to the bottom shear stress (N·m<sup>-2</sup>) experienced by the respective seagrass patch.

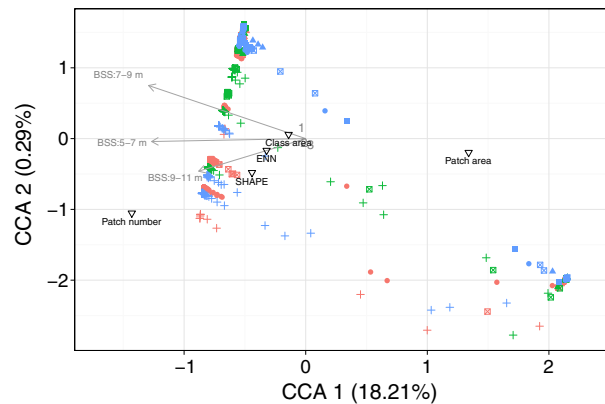
(LRT:  $\chi^2 = 18.09$ ,  $df = 1$ ,  $P < 0.001$ ) that the shoot was sampled from. However, although bed type significantly modifies the impact of BSS on leaf epiphyte biomass (LRT:  $\chi^2 = 6.2837$ ,  $df = 2$ ,  $P < 0.05$ ), water depth did not influence this relationship within the narrow depth range sampled. Conversely, the influence of BSS on leaf necrosis depended on depth (LRT:  $\chi^2 = 21.534$ ,  $df = 1$ ,  $P < 0.01$ ). The degree of leaf necrosis also differed between bed types (LRT:  $\chi^2 = 19.887$ ,  $df = 2$ ,  $P < 0.01$ ). The negative relationship between shoot width and BSS depended on bed type (LRT:  $\chi^2 = 14.583$ ,  $df = 2$ ,  $P < 0.01$ ) and depth (LRT:  $\chi^2 = 11.682$ ,  $df = 1$ ,  $P < 0.01$ ). Although the proportion of missing adult leaf apices decreased with increasing depth (LRT:  $\chi^2 = 8.594$ ,  $df = 1$ ,  $P < 0.01$ ), wave energy and shear stress did not modify this attribute. No significant relationships were indicated between any environmental predictors and

*P. oceanica* shoot density or the numbers of adult, intermediate or juvenile leaves per shoot.

## Discussion

### Landscape configuration

Numerous studies have identified differences in landscape and meadow architectural characteristics of seagrass habitat according to the hydrodynamic setting at spatial scales ranging from shoot to landscape (e.g. Fonseca & Bell 1998; Fonseca *et al.* 2002, 2007; Frederiksen *et al.* 2004). The present results indicate: (i) that patchiness in *Posidonia oceanica* meadows is significantly increased with exposure near-bed shear forces, (ii) that seagrass patch size and shape complexity show strong inter-dependence in their relationship with wave climate, and (iii) an



**Fig. 3.** Canonical correspondence analysis ordination biplot showing variation in *Posidonia oceanica* landscape variables ( $\nabla$ ; Class area, Patch number, Patch area, SHAPE index and Euclidean Nearest Neighbour) in relation to bottom shear stress (arrows) at three depth categories: 5–7 m (red), 7–9 m (green), and 9–11 m (blue). Sites: BC ( $\bullet$ ), S ( $\Delta$ ), DQ ( $\blacksquare$ ), SB ( $+$ ), and RB ( $\boxtimes$ ). Depth centroids: 5–7 m (1), 7–9 m (2), and 9–11 m (3).

overall shift in landscape configuration, involving co-variation of all the measured aspects of landscape spatial arrangement, across a gradient of near-bed shear stress.

The scale-dependence of several landscape metrics underscores the importance of interpreting landscape data with due consideration of the sampled area Wu (2004). On the basis that small spatial levels may be insufficient to describe landscape pattern (Fonseca *et al.* 2002; Bell *et al.* 2006), the 2500-m<sup>2</sup> landscapes used in the present study were a suitable compromise between the need to analyse a sufficiently large area within each replicate while maintaining a narrow depth range within the area sampled. Therefore, this scale may be suitable for further landscape studies of *P. oceanica* meadows.

*Posidonia oceanica* meadow patchiness increased and seagrass cover decreased significantly from low- to high-energy environments, suggesting a pattern of increasing spatial fragmentation of *P. oceanica* meadows and larger areas of unvegetated sediment as a result of exposure to wave forces. This relationship is described for greater water depth in the present study compared to previous works and, given the narrow range of modelled near-bed shear stress experienced by the *P. oceanica* patches (0.001–0.05 N·m<sup>-2</sup>), implies that deeper meadows of this seagrass may be more sensitive to changes in hydrodynamic forces. Although other studies have noted increased fragmentation of seagrass meadows situated in high-energy sites relative to those located in low-energy sites, as well as significant relationship between seagrass cover and hydrodynamic setting (Fonseca & Bell 1998; Fonseca *et al.* 2002; Frederiksen *et al.* 2004), the seagrass meadows considered in these studies were located in

shallow water depths (<6 m). Hence, although the lower limit of seagrass vertical distribution in exposed sites may be determined by light availability, the present results suggest that landscape configuration could also be a product of wave climate throughout the vertical distribution of *P. oceanica* meadows (Vacchi *et al.* 2012). This would corroborate observations of increased patchiness at the lower seagrass limit in meadows exposed to strong water movement but needs to be verified through further studies (Colantoni *et al.* 1982).

In the present study, light attenuation with depth prevented accurate classification beyond 15 m and this prevented exploration of the relationship beyond the considered depth categories; however, this is an inherent limitation of the use of aerial imagery. In addition, wave energy is attenuated by *P. oceanica* meadows in shallow water (Folkard 2005; Koftis *et al.* 2013). As the canopy height of the meadows studied occupied a small fraction of the water depth, dampening of the propagating wave is not expected to be significant. Nevertheless, because the model does not account for attenuation of energy by seagrass meadows, the local dampening of flow near the canopy is not quantified. Thus, the modelled energy and bottom stress values provide a quantitative and comparable estimation of wave climate and are indicative of the mean energy experienced in different parts of the meadows, but do not represent absolute values of near-bottom shear stress.

There are very few comparable studies on *P. oceanica* landscape pattern in relation to the physical setting. One such study found no relationship between meadow fragmentation and wave exposure (Borg *et al.* 2009). However, that study did not take into consideration the effect of water depth attenuation on wave energy, and used the ‘relative exposure index’, which is a unitless index. In the Mediterranean Sea, Infantes *et al.* (2009) identified an inverse relationship between near-bottom orbital velocity and *P. oceanica* cover. In the present study, bottom shear stress was a better predictor of *P. oceanica* cover and patchiness than surface wave energy, which highlights the importance of depth attenuation on wave energy, and implies that future *P. oceanica* landscape studies should assess wave climate using near-bed estimates of wave energy.

Borg *et al.* (2009) found that at water depths of approximately 5–10 m, transitions from discrete patches of *P. oceanica* to reticulate meadows of the seagrass occur. The findings of the multivariate analysis conducted here generally corroborate this trend, and indicate that water depth has a primarily modulating effect on the factors influencing seagrass landscape configuration (Boström *et al.* 2006; Koch *et al.* 2006). However, the relatively low predictive value of depth indicated by the multivariate analysis suggests that other unidentified



**Table 4.** Summary of ANOVA results comparing *Posidonia oceanica* architectural features amongst three bed types (patchy, reticulate and continuous) at five sites. Architectural features tested are shoot biomass, epiphyte biomass, shoot density, number of adult leaves per shoot, number of intermediate leaves per shoot, number of juvenile leaves per shoot, shoot width (cm), % necrosis per shoot and co-efficient 'A' per shoot.

source of variation	shoot biomass (g DW·shoot <sup>-1</sup> )				epiphyte biomass (g DW·shoot <sup>-1</sup> )				shoot density (m <sup>-2</sup> )			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
bed type	2	0.0701	0.16	0.8561	2	0.1567	0.17	0.8400	2	13.66	1.203	0.307
site	4	1.3771	21.32	<0.0001	4	6.8390	29.17	<0.0001	4	92.41	8.136	<0.0001
site × bed type	8	0.4424	7.95	<0.0001	8	0.9055	3.86	0.0004	8	10.23	0.901	0.522
residual	150	0.0803			150	0.2345			60	11.36		
transform:					arcsin (%)				sqrt(X + 1)			
Cochran's C:	0.1514				0.1645				0.2177			

source of variation	number of adult leaves (shoot <sup>-1</sup> )				number of intermediate leaves (shoot <sup>-1</sup> )				number of juvenile leaves (shoot <sup>-1</sup> )			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
bed type	2	0.7818	0.63	0.5578	2	2.2545	4.40	0.0514	2	2.7455	1.08	0.3842
site	4	2.6121	6.30	0.0001	4	0.6758	1.96	0.1041	4	5.6909	7.92	<0.0001
site × bed type	8	1.2439	3.00	0.0038	8	0.5121	1.48	0.1680	8	2.5409	3.53	0.0009
residual	150	0.4145			150	0.3455			150			
transform:												
Cochran's C:	0.1374				0.1474				0.1315			

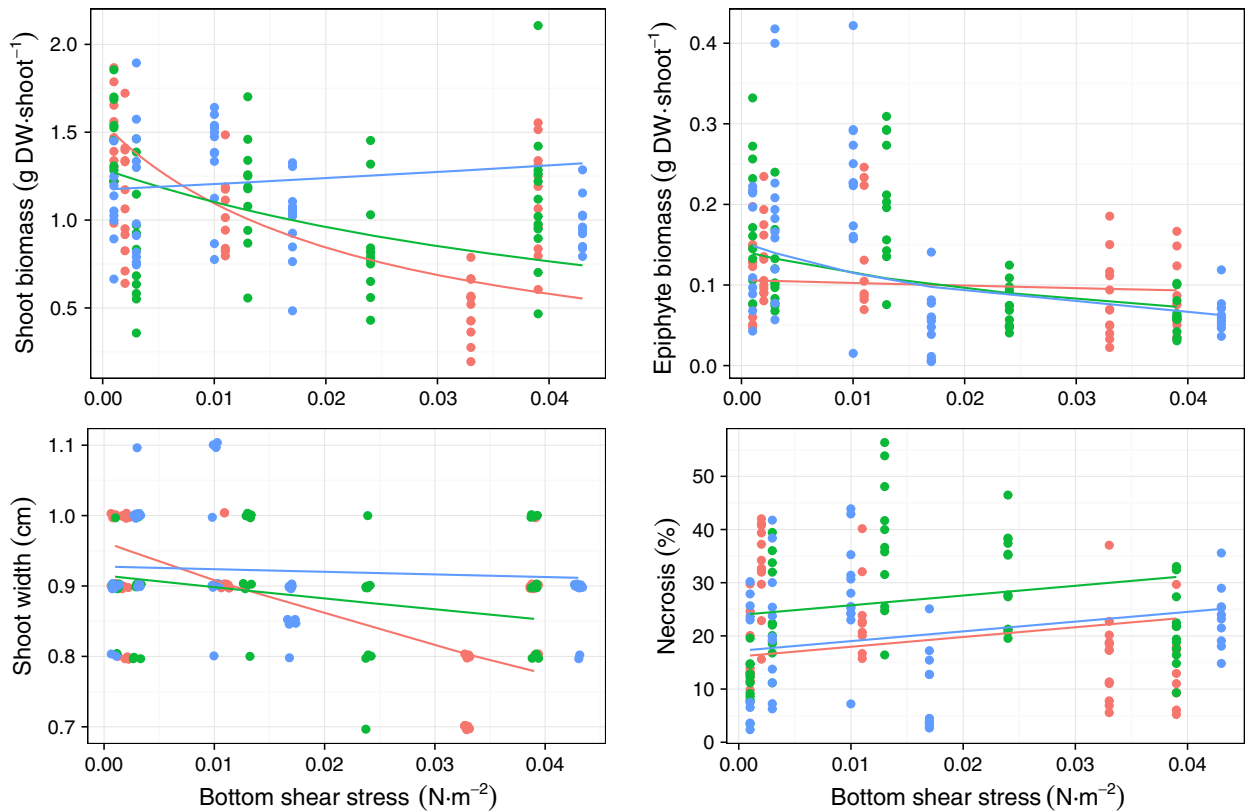
  

source of variation	shoot width (cm shoot <sup>-1</sup> )				% necrosis (shoot <sup>-1</sup> )				co-efficient 'A' (shoot <sup>-1</sup> )			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
bed type	2	0.0201	1.03	0.4008	2	493.18	0.91	0.4403	2	1.8728	0.25	0.7845
site	4	0.0595	13.82	<0.0001	4	1190.75	15.88	<0.0001	4	41.7688	5.21	0.0006
site × bed type	8	0.0195	4.54	0.0001	8	541.71	7.22	<0.0001	8	7.4829	0.93	0.4914
residual	150	0.0043			150	75.01			150	8.0223		
transform:									sqrt(X + 1)			
Cochran's C:	0.1662				0.1376				0.1451			

DW = dry weight; MS = mean square; sqrt = square root.

factors that vary with depth may contribute to a modifying effect on this relationship. For instance, it was noted that at many of the study sites the near-shore environment was dominated by hard substratum, which would be expected to have limited colonization opportunities for *P. oceanica*. This would be expected to be an important limiting factor for seagrass cover, as such restriction is reduced in deeper areas where soft sediment substratum is more prevalent. Thus, substratum characteristics could contribute to the relatively poor predictions of *P. oceanica* cover and, to a far lesser extent, patchiness in shallow areas. Such an inference, however, would need to be substantiated by further studies incorporating substratum type as a potential influencing variable.

Strong grouping of patch characteristics in the CCA bi-plot indicated an overall shift in the landscape configuration of *P. oceanica* meadows along a gradient of near-bed shear stress. Similarly, Fonseca & Bell (1998) noted particular 'threshold' values for measures of seagrass habitat complexity, cover and other landscape attributes in relation to hydrodynamic flow, and postulated sediment movement and direct mechanical stress as possible links for the observed trends in landscape configuration. Exploration of the dependency between patch size and shape complexity showed that high-energy meadows were characterized by fewer patches with an area greater than 100 m<sup>2</sup> and a greater number of small patches. Patch shape complexity was greatest where meadows were



**Fig. 4.** Scatter plots showing observed (points) and GLMM predicted (lines) values for the relationships between bottom shear stress ( $\text{N}\cdot\text{m}^{-2}$ ) and: (top row from left) *Posidonia oceanica* shoot biomass (g), epiphyte biomass (g); (bottom row from left) shoot width (cm), and % necrosis per shoot. For models incorporating depth as a covariate, mean values were used (7.9 m). DW = dry weight.

exposed to relatively high wave energy. This situation corroborates the results from other studies in which workers found increased seagrass patch shape complexity from low- to high-energy environments (Fonseca & Bell 1998; Frederiksen *et al.* 2004).

The landscape spatial arrangement data indicate that patches in spatially fragmented *P. oceanica* meadows are closely clustered and, therefore, there is no indication of reduction in meadow connectivity from low-energy to high-energy sites. Overall, this supports a hypothesis of *P. oceanica* meadow expansion in sites exposed to high wave energy whereby high seedling mortality inhibits the formation of new patches and hydrodynamic stress prevents the expansion of established patches (Kendrick *et al.* 2005; Fonseca *et al.* 2007; Infantes *et al.* 2011). This inhibits the coalescing of patches to create a contiguous meadow and contributes to a naturally heterogeneous, spatially fragmented seagrass landscape (Kendrick *et al.* 2005). Complex patch shapes in sites exposed to moderately high energy are therefore formed by the coalescing of adjacent patches and patch shape complexity thus has an inverse relationship with the distance between neighbouring patches (Frederiksen *et al.* 2004). This interpretation could

account for the strong observed relationship between seagrass meadow patchiness and wave energy regime.

Increased seagrass patchiness, owing to anthropogenic pressure or acute stress, could reduce the ability of a seagrass meadow to attenuate wave energy or stabilize sediments (Fonseca & Bell 1998; Fonseca & Koehl 2006). This could lead to a reduction in sedimentation and changes in sediment characteristics. A reduced sediment stabilization capability and increased habitat edge owing to patchiness may mean that the ability of a seagrass landscape to withstand physical stress such as that resulting from water movement is reduced relative to continuous meadows and decline in seagrass cover may occur (Frederiksen *et al.* 2004).

#### Architectural attributes

The present assessment of seagrass bed architectural attributes in relation to the modelled wave energy climate indicated that: (i) shoot biomass, epiphyte biomass, leaf width and total leaf length and area were negatively correlated with shear stress, (ii) leaf necrosis was positively correlated with shear stress, (iii) shoot density, the

number of leaves per shoot and co-efficient 'A' showed inconsistent trends in relation to modelled wave energy, and (iv) the large variance in the data indicated that architectural complexity is influenced to a greater extent by local-scale factors than by the wave energy regime. GLMM results for the present study suggest that bed type plays a significant role in modifying the impact of wave climate on *Posidonia oceanica* architectural attributes. However, differences in patterns amongst different attributes meant that the mechanism was not evident. The results of the two-factor ANOVA detected no consistent pattern amongst bed types or across sites, and therefore corroborate the findings of other researchers. Borg *et al.* (2005) tested for differences in a number of architectural characteristics between reticulate and continuous beds over a range of spatial scales (m – km) and found no consistent trends for shoot density, shoot biomass or leaf morphometry. Similarly, Hovel & Lipcius (2001) found no relationship between seagrass meadow patchiness and shoot density.

The present findings generally corroborate the hypothesis that *P. oceanica* meadow architectural features are influenced by the wave climate but inconsistent trends and high variability in the data indicate that this influence is low and modification by additional untested factors, including water movement over smaller spatial and temporal scales, may be more important. To date, very few studies have investigated the relationship between *P. oceanica* meadow architectural features and water movement; the works published to date have focussed on meadows located at shallow water depths (<6 m) and involved estimates of exposure to surface wave energy. In one of the few studies to explore the relationship with seagrass attributes, Rubegni *et al.* (2013) applied WEMo to a shallow non-tidal lagoon; however, no *P. oceanica* was recorded in this study. The present study therefore seems to be one of the first assessments of the influence of wave dynamics on the architectural characteristics of relatively deep (>6 m) *P. oceanica* meadows. Bottom shear stress was found to be a better estimate of the energy impacting seagrass habitats than RWE. Bottom shear stress was also significantly correlated to more architectural attributes than RWE. It is therefore recommended that similar quantitative estimates of depth-attenuated wave energy be used in similar future studies. The methods used in the present study could not account for any further attenuation or modification of the energy experienced by a given seagrass shoot by surrounding shoots in the seagrass canopy and this may have contributed to the poor precision of the significant relationships noted (see Fonseca *et al.* 2007).

Shoot biomass, epiphyte biomass, leaf width, total leaf length and shoot area were consistently shown to have a significant negative relationship with wave energy.

However, the high variance shown in the data for these relationships indicates that local-scale variables have a greater influence on these attributes (*sensu* Boström *et al.* 2006). Future studies could reduce such small-scale variability by increasing sampling effort over a wider range of energy exposure. The importance of factors that vary over a small scale (metres) and that influence the dynamics of seagrass meadow architectural characteristics has been noted by other researchers (Wittmann 1984; Borg *et al.* 2005). The findings from the present study also complement the low prediction strengths noted by Fonseca *et al.* (2002) for regressed seagrass structural attributes; namely percentage of organic matter, shoot density, and above- and below-ground biomass. The inverse relationship between wave energy and seagrass biomass has been corroborated in subsequent studies (Rubegni *et al.* 2013). Although the relationship between epiphytic growth and nutrient availability has been characterized in seagrasses, the effect of water flow is poorly known and few studies have addressed the relationship of epiphyte loading with hydrodynamic energy (Koch *et al.* 2006). Nonetheless, Bridgwood (2006) observed a trend for lower epiphyte loading in high-energy environments, although this was not quantified. The relationship between epiphytic growth and exposure to wave energy described in the present study is of significance to the photosynthetic capability of the plant and productivity of the seagrass ecosystem. It is possible that the impact on epiphytic loading may be more profound in seagrass meadows at shallower depths by virtue of the greater near-bed energy that is experienced by the canopy. However, this would have to be substantiated through further study.

Values of shoot density were not clearly related to exposure, despite the positive relationships between shoot density and exposure to wave energy noted by Fonseca & Bell (1998) and Fonseca *et al.* (2002). Although a clear relationship between co-efficient 'A' and wind-wave energy was expected (Pergent *et al.* 1995; Fonseca *et al.* 2007), this was not observed in the present study. This may suggest that the loss of leaf apices owing to mechanical stress is a result of acute physical disturbance that was not reflected by the broad temporal and spatial scale of the modelled hydrodynamic patterns. Furthermore, the results obtained in the present study may have been influenced by factors that were not accounted for, such as substratum type and characteristics; hence, further studies are required to test this relationship (Pergent *et al.* 1995).

## Summary

Overall, the present results show that, although other factors that were unaccounted for influence seagrass

meadow spatial arrangement and architectural attributes, exposure to wind-wave energy modifies seagrass habitat meadow landscape and architectural features. High-energy environments support patchier *Posidonia oceanica* meadow landscapes with lower seagrass cover, more complex patch shapes and lower intra-patch architectural complexity relative to sites exposed to low wave energy. This supports the general view that water movement serves to modify seagrass meadows within the 6–11 m depth range (e.g. Colantoni *et al.* 1982). The impact of wave climate on *P. oceanica* architecture differs amongst bed types. Near-bed shear forces were able to better account for variation in landscape and architectural features than surface estimates of wave energy. This underscores the importance of using near-bed wave variables in future studies of this seagrass.

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