

Spatial variation in the composition of motile macroinvertebrate assemblages associated with two bed types of the seagrass *Posidonia oceanica*

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ABSTRACT: The influence of continuous (non-fragmented) and reticulate (fragmented) bed type and plant architecture on the species richness, abundance and assemblage composition of motile macroinvertebrates associated with the seagrass *Posidonia oceanica* was investigated at 3 different spatial scales (10s of metres ['small'], 100s of metres ['medium'] and kilometres ['large']). Univariate and multivariate analyses did not identify significant differences in the attributes of macroinvertebrate assemblages between the 2 *P. oceanica* bed types over the 3 spatial scales considered. On the other hand, significant spatial variation in macroinvertebrate attributes was detected at the large spatial scale. Results of univariate regression and multivariate correlation analysis consistently indicated significant relationships between attributes of the macroinvertebrate assemblages and epiphyte biomass at the large spatial scale. Although less consistent, significant relationships were also detected between attributes of the macroinvertebrate assemblages, and mean sediment grain size, total organic carbon in sediment and shoot biomass at the large and medium spatial scales. The findings indicate that naturally fragmented and non-fragmented *P. oceanica* beds have similar habitat characteristics for the associated macroinvertebrates and that local factors, which influence seagrass bed architecture and particularly epiphyte load, have greater influence on the seagrass fauna. Data from the present study support the notion that fragmented seagrass beds should receive the same attention as non-fragmented ones with regard to habitat conservation and protection.

KEY WORDS: Landscape ecology · Habitat fragmentation · Macroinvertebrates · *Posidonia oceanica* · Seagrass beds · Seagrass epiphytes

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INTRODUCTION

Seagrass beds differ greatly in morphology (i.e. bed type) and bed structure (i.e. plant architectural characteristics) depending on the seagrass species and on the physico-chemical and biological characteristics of the locality where they occur (Fonseca et al. 1983, Kirkman & Kuo 1990, Boström et al. 2006a). Seagrass bed morphology and within-bed architectural characteristics are influenced by various abiotic and biotic factors (see review by Boström et al. 2006a). As a result, the morphology of seagrass beds varies from small patches

(e.g. 1 to 20 m in diameter; Irlandi 1997, Frost et al. 1999, Hovel & Lipcius 2002, Johnson & Heck 2006) through reticulate beds (beds interspersed with soft sediment or other habitat types; e.g. Kirkman & Kuo 1990, Barberá Cebrián et al. 2002, Borg et al. 2005), to large continuous meadows (Fonseca et al. 1983, Fonseca & Bell 1998). Bed architecture varies with shoot density, leaf density, leaf length, leaf width and with growth pattern (e.g. simple, strap-like, or branching leaves; Orth et al. 1984).

Differences in seagrass bed type and plant architectural characteristics over large spatial scales result in

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varied landscapes and, possibly, variations in habitat characteristics, leading to differences in the species composition of the associated faunal assemblages (Robbins & Bell 1994, Hovel & Lipcius 2002). For example, predation pressure is expected to be higher in a fragmented seagrass bed, since the mobility of predators and, hence, foraging intensity, would be expected to be facilitated in such a bed type (e.g. Hovel & Lipcius 2002, Johnson & Heck 2006). Species-specific behavioural responses may differ depending on seagrass bed morphology, for example, preferential selection by some species for seagrass edges (e.g. mysids; Barberá Cebrián et al. 2002), higher larval settlement at bed borders (McNeill & Fairweather 1993, Bologna & Heck 2000) and enhanced food delivery (e.g. Irlandi 1996).

Plant architecture may influence the species richness and abundance of the associated macrofauna, both directly and indirectly. For example, differences in seagrass leaf morphology influence the abundance of associated motile epifauna (e.g. Schneider & Mann 1991, Tanner 2006). Differences in the density of plants and leaves and the total area of leaf surface available are also important in determining directly the diversity of seagrass-associated macrofauna (Orth et al. 1984, Heck et al. 1989, Hovel & Lipcius 2001), since variation of these plant attributes translates to differences in habitat structure, although this notion is not consistently supported by data (see Laurel et al. 2003, Mattila et al. 2008). The presence of macroalgae and epiphytes directly imparts additional physical complexity to the seagrass bed, which may enhance habitat space (Schneider & Mann 1991), or act as an obstacle for some macrofauna (Heck & Orth 1980). Seagrass epiphytes may also serve as food for several invertebrates and fishes (e.g. Duffy & Hay 2000, Duffy & Harvilicz 2001); hence, their presence and abundance is expected to have an indirect influence on the grazer assemblages associated with the habitat. Differences in bed type and plant architecture also have an indirect influence on the associated biota by exerting different magnitudes of influence on water movement (e.g. Worcester 1995) and on the physico-chemical properties of nearby sediments (Fonseca et al. 1983).

Increased awareness of the global decline of seagrass habitat (Duarte 2002, Green & Short 2003) has highlighted the importance of assessing whether fragmented seagrass beds support the same species richness and abundance of associated biota as non-fragmented beds, given that fragmentation may be the first step in the degradation of this habitat type. Most studies of the influence of seagrass bed morphology and architecture on the associated biota have compared the flora and fauna between continuous and patchy beds (Frost et al. 1999, Hovel & Lipcius 2001,

2002, Vega Fernández et al. 2005) and between differently sized patches (McNeill & Fairweather 1993, Bell et al. 2001, Bowden et al. 2001, Irlandi 1997, Johnson & Heck 2006). Comparisons of the macroinvertebrate assemblages associated with continuous and reticulate seagrass beds are largely unavailable (but see Hovel & Lipcius 2001, 2002), despite the probability that the latter may constitute the first stage in fragmentation of continuous beds (Fonseca & Bell 1998). Furthermore, despite the huge effort dedicated to ecological research on seagrass habitat, relatively few studies have considered spatial variation; this is particularly true in the case of the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile (but see Moranta et al. 2006). The present study was aimed at examining whether the species richness, abundance and composition of associated motile macroinvertebrates (i.e. all infaunal and epifaunal invertebrates, excluding sessile species, namely sponges, cnidarians and bryozoans, ranging in size between 0.5 mm and 4 cm), differed between naturally occurring continuous (= non-fragmented) and reticulate (= naturally fragmented) beds of *P. oceanica* over 3 spatial scales, varying from 10s of metres to kilometres. Accordingly, the hypotheses tested were that the species richness, abundance and composition of macroinvertebrates did not differ between continuous and fragmented beds of the seagrass over different spatial scales.

MATERIALS AND METHODS

Study sites and experimental design. Preliminary surveys confirmed that naturally occurring different bed types of *Posidonia oceanica*, including the continuous and reticulate beds described for other parts of the Mediterranean (e.g. Colantoni et al. 1982), occurred adjacent to each other and in a similar depth range around the Maltese islands (Borg et al. 2005). The occurrence of reticulate seagrass beds probably results from the interaction of a gradient of environmental factors, amongst which the sedimentation regime, sea currents, storms and exposure are the major factors; these act by promoting or halting the spread of the seagrass at bed boundaries, or by creating pockets within the seagrass beds that are devoid of living shoots (Kirkman & Kuo 1990).

To test for the differences in macroinvertebrate assemblages associated with continuous and reticulate *Posidonia oceanica* beds over kilometres (large spatial scale), 4 locations distributed along the north-eastern coast of the Maltese archipelago (Fig. 1a) and separated from each other by some 10 to 13 km were selected (Ramla Bay [RB], Mellieha Bay [MB], White Rocks [WR] and St Thomas Bay [STB]). The respective

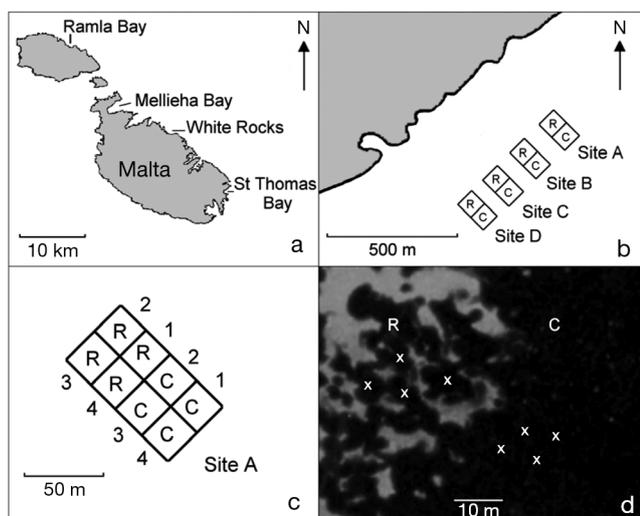


Fig. 1. Sampling localities, each with continuous (C) and reticulate (R) *Posidonia oceanica* bed types, at the 3 spatial scales: (a) 4 locations (large spatial scale), (b) 4 sites within Mellicha Bay (medium spatial scale) and (c) 4 plots within Site A at Mellicha Bay (small spatial scale). (d) Aerial photo showing typical adjacent continuous and reticulate beds at the sampled localities; crosses represent core samples collected from the 2 bed types

areas occupied by continuous and reticulate beds of *P. oceanica* at the 4 study locations were: 4.5 and 5.5 ha (RB), 12.5 and 18.2 ha (MB), 13.1 and 23.4 ha (WR) and 8.7 and 29.9 ha (STB). To test for differences in the macroinvertebrate assemblages associated with continuous and reticulate *P. oceanica* beds over a few 100s of metres (medium spatial scale), 4 sites (A, B, C and D) separated from each other by a distance of circa 150 m were selected within MB; each site measured 50 × 100 m (Fig. 1b). To test for differences over a few 10s of metres (small spatial scale), 8 plots (4 plots in the continuous and 4 in the reticulate beds), each measuring 25 × 25 m, were selected within Site A in MB (Fig. 1c). The sampling design incorporated a total of 20 sampling stations, all of which were located at a water depth of between 9 and 11 m. Ideally, to attain a fully nested design, the plot and site sampling layout should have been included in each of the other 3 locations (RB, WR and STB) (Underwood 1997). Therefore, the results obtained from the plot and site spatial scales within the chosen single location (MB) cannot be generalised to all locations.

Data collection and analyses. Sampling of *Posidonia oceanica* and associated macroinvertebrates in the 2 different bed types (Fig. 1d) was carried out using a specially designed corer with a diameter of 25 cm, to which a 400 µm mesh net was attached at its upper end (Borg et al. 2002). Using this sampler, which was

pushed into the sediment to a depth of 10 cm, 4 replicate cores were collected by SCUBA divers from adjacent continuous and reticulate beds at each of the 3 spatial scales (i.e. 20 stations × 4 replicates = 80 samples). Borg et al. (2002) showed that collecting 4 cores using this specific sampler design gave sufficient precision and accuracy estimates to ensure appropriate sampling of macroinvertebrates in *P. oceanica* beds. Cores were collected at least 2 m from the bed periphery to avoid 'edge effects' (e.g. Bowden et al. 2001) that could potentially confound the investigation. Reticulate beds had a 'branch' width of between 5 and 10 m. All sampling was carried out between 2 August and 4 September 1999. To measure seagrass architectural characteristics, 12 orthotropic (vertically growing) shoots were collected from each station, as described by Borg et al. (2005). Four replicate samples were also collected from each sampling station using a metal corer with a smaller (10 cm) diameter, to enable physico-chemical examination of the sediment and root-rhizome material.

In the laboratory, the number of shoots collected in each core was used to obtain estimates of seagrass shoot density, after which the shoots/leaves and root-rhizome matrix were separated and the macroinvertebrates removed. Estimates of total dry weight of the shoot/leaf and root-rhizome fractions (epiphyte free; see below) were obtained by drying for 24 h in an oven at 100°C. The remaining sediment and washings were passed through a 0.5 mm sieve, and the retained material was sorted in trays under a 5× magnifying lens to remove any remaining macrofauna. Macroinvertebrates were identified to the lowest taxon possible and enumerated to obtain estimates of number of species and abundance per core.

Samples collected for sediment analyses (10 cm diameter corer) were first sorted to separate the root-rhizome matrix and other plant material from the sediment. Sub-samples for the determination of sediment total organic carbon were taken and frozen at -5°C, while the remaining portions were dried in the air for granulometric analysis. Analyses to determine total organic carbon in the sediment and mean sediment grain size were carried out following Buchanan (1984).

The leaves of 12 *Posidonia oceanica* shoots from the 25 cm diameter core samples were scraped using a razor blade to remove all the epiphytes. Epiphytic material was dried for 24 h in an oven at 80°C and weighed (±0.001 g) to determine the epiphyte biomass per shoot. Estimates of epiphyte biomass per core were obtained by multiplying mean shoot epiphyte biomass by the *P. oceanica* shoot density recorded from each core sample. Estimates of leaf area per core were obtained by multiplying the mean leaf area per shoot (= total leaf length × mean leaf width per shoot; data

from Borg et al. 2005) by the *P. oceanica* shoot density recorded from each core sample.

To test the hypotheses of no differences in macroinvertebrate species richness and abundance between continuous and reticulate *Posidonia oceanica* beds at each of the 3 spatial scales, 2-factor analysis of variance (ANOVA) based on an orthogonal model with 'bed type' (2 levels, fixed) and 'sampling locality' (4 levels, random) was carried out. Differences in seagrass architecture (shoot density, leaf length, number of leaves per shoot and leaf width; see Borg et al. 2005), shoot biomass, leaf area, epiphyte biomass, root-rhizome biomass and sediment (organic content and mean grain size) were tested using 2-factor ANOVA based on the same model as for the analysis of macroinvertebrate data. In view of the multiple ANOVA tests carried out on the various macroinvertebrate and seagrass bed attributes, α was set at 0.01, to reduce the possibility of Type I error. Prior to analyses, data were tested for homogeneity of variances using Cochran's test and, if necessary, appropriate transformations of data were made. When the ANOVA indicated significant differences, the source of difference was identified using Student-Neuman-Keuls (SNK) tests (Underwood 1997). Where attributes of seagrass architecture and/or sediment demonstrated the same pattern of significant differences as macroinvertebrate species richness and abundance, stepwise multiple linear regression analysis was used to investigate the corresponding relationship. Prior to carrying out the regression analysis, potential significant relationships between the independent variables (attributes of seagrass architecture and/or sediment) were investigated using Pearson's correlation coefficient. Attributes that were significantly correlated were eliminated from the analyses using a forward selection procedure. Data used in the regression analysis were checked for normality using the Shapiro-Wilk statistic (D'Agostino 1986) and transformed (\ln) if necessary.

To test for differences in the composition of macroinvertebrate assemblages associated with the 2 *Posidonia oceanica* bed types at each of the 3 spatial scales, non-metric multidimensional scaling (NMDS) using the Bray-Curtis index to construct the underlying similarity matrix was carried out on the species-abundance data (fourth-root transformed to downweigh the contribution of dominant species). The significance of differences in assemblage composition between samples grouped according to bed type and sampling locality was assessed using 2-way analysis of similarity (ANOSIM). The contribution of the different species to the observed similarity within groups of samples taken from the same bed type, and the dissimilarity between groups of samples taken from a different bed type, were determined using the similarity percentages

(SIMPER) procedure. BIOENV analysis was carried out to compare invertebrate abundance and environmental variable matrices in order to assess which variables best explained the observed multivariate patterns within the macroinvertebrate assemblage. All multivariate tests were carried out using the PRIMER V5 suite of programs.

RESULTS

Seagrass and sediment attributes

There was no consistent pattern of differences in seagrass architectural attributes between the 2 *Posidonia oceanica* bed types at any of the 3 spatial scales (see Borg et al. 2005, Fig. 2 present study). However, notable differences in leaf area, shoot biomass and epiphyte biomass were evident between sampling localities at the large (location) and medium (site) spatial scales, but not at the small spatial scale (Fig. 2). At the large spatial scale, ANOVA indicated a significant interaction for epiphyte biomass and significant differences in leaf area, shoot biomass and epiphyte biomass between locations. Epiphyte biomass differed significantly between all 4 pair comparisons of location (SNK; WR > STB > RB > MB). Leaf area was significantly higher at RB (SNK; $p < 0.01$) compared to the 3 other locations. Shoot biomass was significantly higher at WR compared to MB (SNK; $p < 0.01$) and STB (SNK; $p < 0.01$). At the medium (site) spatial scale, ANOVA indicated a significant interaction for shoot biomass, together with significant differences in shoot biomass and epiphyte biomass between sites (Tables 1 & 2). Epiphyte biomass was significantly higher at Site C compared to Sites A and B (SNK; $p < 0.01$). No significant interactions were detected by ANOVA for root-rhizome biomass (Table 2), nor were any significant differences detected in this attribute for 'bed type' or 'sampling locality' at any of the 3 spatial scales.

There were differences in sediment organic carbon content and mean grain size between continuous and reticulate *Posidonia oceanica* beds, as well as between different sampling localities at the different spatial scales (Fig. 3). At the large (location) spatial scale, ANOVA indicated significant interactions, together with significant differences in both organic carbon content and mean grain size between locations (Table 3). Organic carbon content of the sediment was significantly higher at MB compared to the other 3 locations (SNK; $p < 0.01$). Mean sediment grain size differed significantly between all pairs of locations, except between WR and STB (SNK; MB < RB < WR = STB). At the medium (site) spatial scale, ANOVA indi-

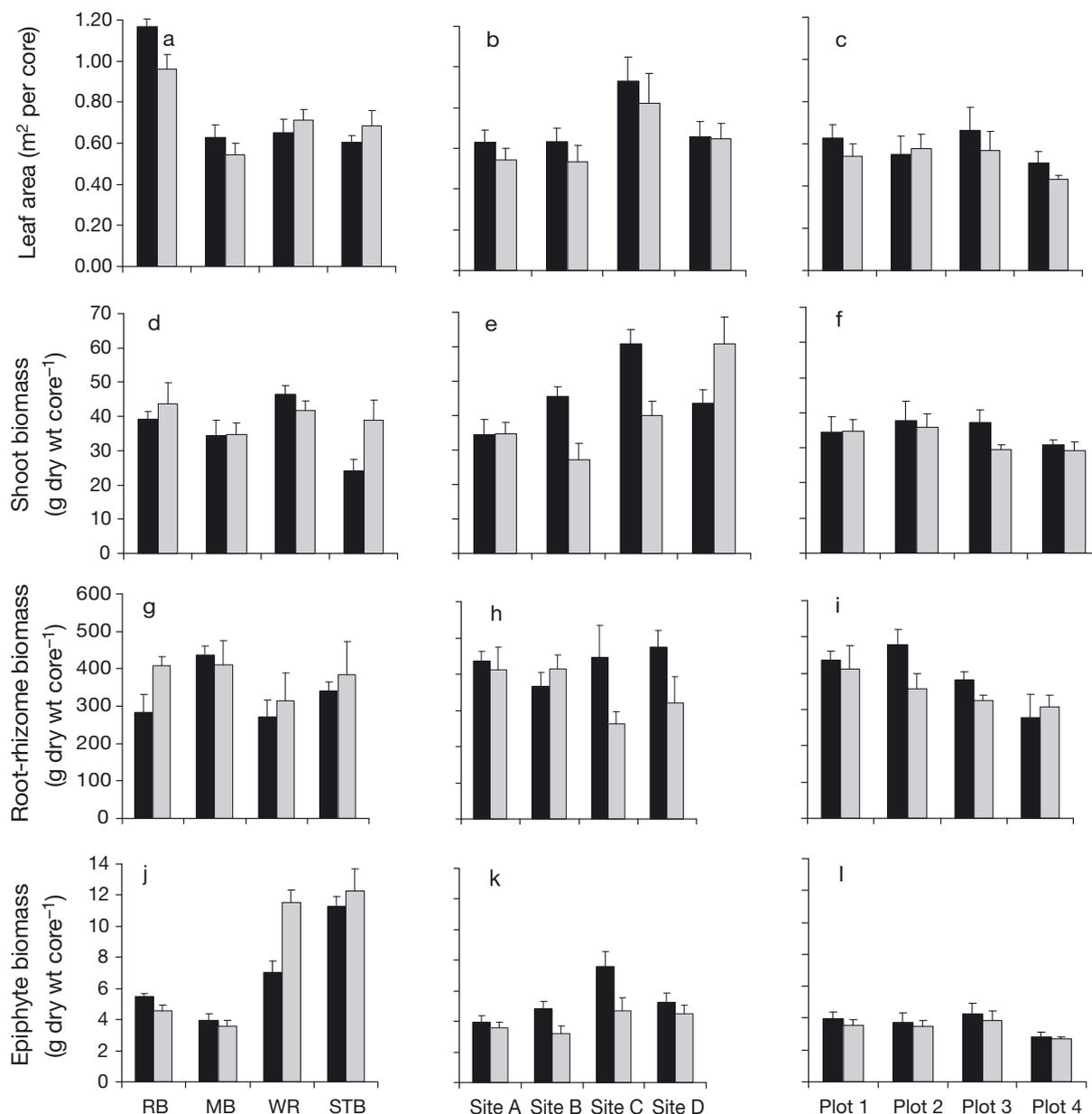


Fig. 2. *Posidonia oceanica*. Mean values (+SE) of (a–c) leaf area, (d–f) shoot biomass, (g–i) root-rhizome biomass and (j–l) epiphyte biomass for continuous (black bars) and reticulate (grey bars) *P. oceanica* beds at the 3 spatial scales: large (a, d, g, j), medium (b, e, h, k) and small (c, f, i, l). RB: Ramla Bay, MB: Mellieha Bay, WR: White Rocks, STP: St Thomas Bay

cated a significant interaction for organic carbon content of the sediment, and a significant difference in mean sediment grain size between sites (Table 3). Mean sediment grain size was significantly smaller at Site D compared to Sites A (SNK; $p < 0.01$) and C (SNK; $p < 0.05$). At the small (plot) spatial scale, ANOVA indicated significant differences in both sediment attributes between the 2 bed types and in mean sediment grain size between plots (Table 3). Organic carbon content was significantly higher in continuous beds at

all 4 plots (SNK; $p < 0.01$). Mean sediment grain size was significantly smaller in continuous beds at all 4 plots (SNK; $p < 0.01$) and at Plot 4 compared to the other 3 plots (SNK; $p < 0.01$).

Macroinvertebrate assemblages

A total of 6227 macroinvertebrates was collected. Overall, there was no trend of differences in total

Table 1. ANOVA results for leaf area ($\text{m}^2 \text{core}^{-1}$) and shoot biomass ($\text{g dry wt core}^{-1}$). Significant p-values (α set at 0.01) are shown in bold. Cochran's test was not significant

Spatial scale	Source of variation	df	Leaf area (n = 4)			Shoot biomass (n = 4)		
			Mean square	F	p	Mean square	F	p
Large	Bed type (B)	1	0.0111	0.30	0.6202	12.1525	0.04	0.8538
	Location (L)	3	0.3778	27.45	<0.0001	495.0483	6.62	0.0020
	B × L	3	0.0367	2.66	0.0708	301.8268	4.03	0.0186
	Residual	24	0.0138			74.8143		
Medium	Bed type (B)	1	0.0462	11.82	0.0413	236.2595	0.38	0.5806
	Site (S)	3	0.1529	4.58	0.0113	679.4862	8.05	0.0007
	B × S	3	0.0039	0.12	0.9492	619.5316	7.34	0.0012
	Residual	24	0.0334			84.3988		
Small	Bed type (B)	1	0.0262	3.82	0.1457	59.0241	2.55	0.2088
	Plot (P)	3	0.0316	1.50	0.2398	63.5775	1.27	0.3071
	B × P	3	0.0069	0.33	0.8067	23.1746	0.46	0.7109
	Residual	24	0.0210			50.0712		

Table 2. ANOVA results for root-rhizome biomass ($\text{g dry wt core}^{-1}$) and epiphyte biomass ($\text{g dry wt core}^{-1}$). Significant p-values (α set at 0.01) are shown in bold. Cochran's test was not significant

Spatial scale	Source of variation	df	Root-rhizome biomass (n = 4)			Epiphyte biomass (n = 4)		
			Mean square	F	p	Mean square	F	p
Large	Bed type (B)	1	17632.0726	2.39	0.2197	6.1446	0.15	0.7283
	Location (L)	3	23214.9261	1.99	0.1425	51.7436	48.21	<0.0001
	B × L	3	7373.0707	0.63	0.6016	42.2231	39.34	<0.0001
	Residual	24	11669.34			1.073		
Medium	Bed type (B)	1	49980.9440	2.12	0.2414	15.8390	6.29	0.0871
	Site (S)	3	6676.8222	0.54	0.6617	9.1927	5.85	0.0038
	B × S	3	23580.8094	1.90	0.1574	2.5181	1.60	0.2151
	Residual	24	12442.25			1.572		
Small	Bed type (B)	1	14430.4566	1.83	0.2688	0.677	13.14	0.0361
	Plot (P)	3	30168.3867	4.30	0.0146	2.474	2.81	0.0612
	B × P	3	7873.2417	1.12	0.3598	0.515	0.06	0.9810
	Residual	24	7015.9899			0.8814		

Table 3. ANOVA results for organic carbon content (%) and mean grain size (Phi) of the sediment. Significant p-values (α set at 0.01) are shown in bold. Cochran's test was not significant, except for data for organic carbon in sediment at the small spatial scale, which was consequently transformed (arcsine)

Spatial scale	Source of variation	df	Organic carbon in sediment (n = 4)			Mean sediment grain size (n = 4)		
			Mean square	F	p	Mean square	F	p
Large	Bed type (B)	1	0.1378	2.97	0.1831	0.0443	0.09	0.7894
	Location (L)	3	0.0505	12.83	<0.0001	0.4020	20.40	<0.0001
	B × L	3	0.0463	11.78	0.0001	0.5193	26.35	<0.0001
	Residual	24	0.0039			0.0197		
Medium	Bed type (B)	1	0.5778	18.86	0.0225	6.3814	22.62	0.0176
	Site (S)	3	0.0075	1.43	0.2592	0.8645	7.41	0.0011
	B × S	3	0.0306	5.87	0.0037	0.2822	2.42	0.0910
	Residual	24	0.0052			0.1166		
Small	Bed type (B)	1	22.8913	35.17	0.0096	4.1761	150.31	0.0012
	Plot (P)	3	1.5450	3.85	0.0222	0.2457	6.65	0.0020
	B × P	3	0.6509	1.62	0.2108	0.0278	0.75	0.5318
	Residual	24	0.4015			0.0369		

macroinvertebrate abundance and species richness between continuous and reticulate beds at the 3 spatial scales (Fig. 4). However, there were significant differences in macroinvertebrate abundance and species richness between different locations at the large spa-

tial scale (Table 4); values of total abundance and species richness were significantly higher for continuous and reticulate beds at WR and STB than at RB and MB (SNK; $p < 0.05$). ANOVA did not indicate any significant interactions, nor did it detect any significant dif-

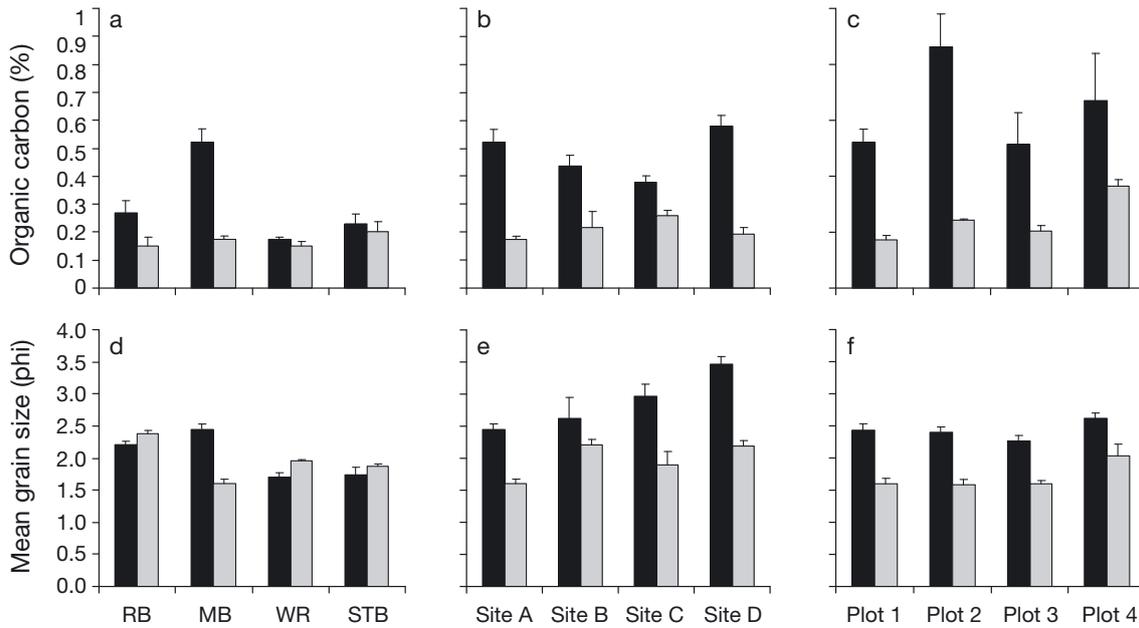


Fig. 3. Mean values (+SE) of organic carbon content in (a–c) sediment and (d–f) mean sediment grain size, for continuous (black bars) and reticulate (grey bars) *Posidonia oceanica* beds (see Fig. 2 for locations) at the 3 spatial scales: large (a,d), medium (b,e) and small (c,f)

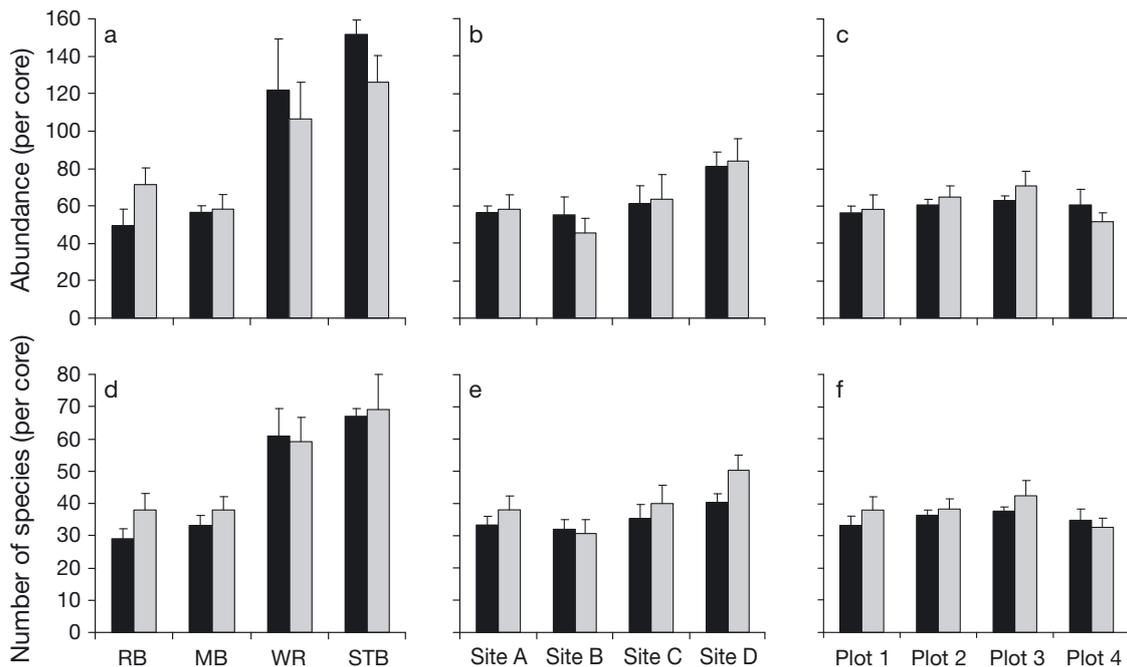


Fig. 4. Mean values (+SE) of (a–c) macroinvertebrate abundance (per core) and (d–f) number of species (per core), for continuous (black bars) and reticulate (grey bars) *Posidonia oceanica* beds (see Fig. 2 for locations) at the 3 spatial scales: large (a,d), medium (b,e) and small (c,f)

Table 4. ANOVA results for total macroinvertebrate abundance (per core) and total number of species (per core). Significant p-values (α set at 0.01) are shown in bold. Cochran's test was not significant, except for data for abundance at the large spatial scale, which was consequently transformed [$\sqrt{(x + 1)}$]

Spatial scale	Source of variation	df	Abundance (n = 4)			Number of species (n = 4)		
			Mean square	F	p	Mean square	F	p
Large	Bed type (B)	1	0.0330	0.01	0.9154	81.2813	1.75	0.2773
	Location (L)	3	34.3758	15.58	<0.0001	2382.6146	14.96	<0.0001
	B \times L	3	2.4824	1.13	0.3585	46.3646	0.29	0.8313
	Residual	24	2.2058			159.2188		
Medium	Bed type (B)	1	3.7813	0.05	0.8355	162.0000	3.83	0.1451
	Site (S)	3	1528.6146	4.42	0.0131	280.2083	4.39	0.0134
	B \times S	3	73.7813	0.21	0.8862	42.2500	0.66	0.5837
	Residual	24	345.829			63.8542		
Small	Bed type (B)	1	10.1250	0.09	0.7846	40.5000	1.84	0.2679
	Plot (P)	3	202.2083	1.45	0.2532	60.7917	1.51	0.2380
	B \times P	3	113.3750	0.81	0.4994	22.0000	0.55	0.6559
	Residual	24	139.5000			40.333		

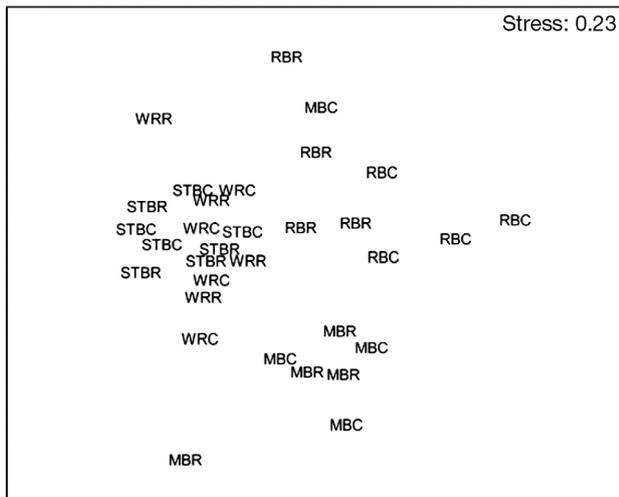


Fig. 5. NMDS plot produced from macroinvertebrate species-abundance data for core samples collected at the large spatial scales. RB: Ramla Bay; MB: Mellieha Bay; WR: White Rocks; STB: St Thomas Bay. The last letter denotes the bed type (C: continuous; R: reticulate)

ferences in total macroinvertebrate abundance and species richness for 'bed type' at the medium and small spatial scales (Table 4).

NMDS ordination plots for the species-abundance data did not show clear grouping of samples collected from continuous and reticulate *Posidonia oceanica* beds, indicating that the macroinvertebrate assemblage composition of the 2 different bed types at all 3 spatial scales was broadly similar. However, the NMDS plot for data collected at the large spatial scale (Fig. 5) indicated some degree of separation between groups of samples collected from different locations. This separation was especially evident between sam-

ples collected from RB and MB and those collected from WR and STB.

ANOSIM indicated that the composition of samples collected from the 2 different bed types did not differ significantly at any of the 3 spatial scales; however, samples differed significantly across the large (Global R = 0.526; $p < 0.01$) and small (Global R = 0.199; $p < 0.01$) spatial scales. At the large spatial scale, ANOSIM indicated significant differences between all 4 locations (R = 0.439 to 0.652; all $p < 0.01$), but not between all 4 plots at the small spatial scale.

SIMPER showed high average dissimilarity values between groups of samples collected from different locations (large spatial scale), with the minimum dissimilarity between pairs being 70.74%. However, no single species had a large contributory influence to the observed dissimilarity; the largest contribution of any one species was 3.77% (the gastropod *Alvania mamillata* Risso; Table 5). Similarly, despite the relatively high dissimilarity values between significantly different plots at the small spatial scale, no single species had a large contributory influence to the observed dissimilarity; the largest contribution of any one species being 3.47% (the sipunculid *Phascolion strombi* [Montagu]).

Relationship between macroinvertebrates and seagrass bed attributes

BIOENV indicated that the combination of environmental variables that best explained the macroinvertebrate assemblage composition observed at the large spatial scale was: epiphyte biomass, mean sediment grain size and total organic carbon in the sediment ($\rho_w = 0.34$). Spearman's rank correlation coeffi-

Table 5. Results of SIMPER analysis for species contributing most to dissimilarity between groups of samples taken from the 4 different locations (large spatial scale): RB: Ramla Bay; MB: Mellieha Bay; WR: White Rocks; STB: St Thomas Bay. AA: average abundance (number of individuals per core); AD: average dissimilarity; AD/SD: ratio of the average dissimilarity to the standard deviation of dissimilarity for the particular species

Species	Locations compared		AA		AD	AD/SD	Contribution (%)
	x	y	x	y			
<i>Alvania mamillata</i>	RB	MB	3.88	0.50	3.07	1.08	3.77
<i>Pagurus chevreuxi</i>	RB	MB	3.75	0.00	3.00	1.14	3.68
<i>Amphicteis midas</i>	RB	MB	0.13	2.75	2.41	1.25	2.96
<i>Piromis eruca</i>	RB	MB	0.75	2.38	2.04	1.00	2.50
<i>Elasmopus brasiliensis</i>	RB	STB	0.00	5.13	2.25	1.83	2.78
<i>Maera inaequipes</i>	RB	STB	1.25	5.50	1.96	0.85	2.42
<i>Alvania mamillata</i>	RB	STB	3.88	0.75	1.70	1.06	2.10
<i>Pagurus chevreuxi</i>	RB	STB	3.75	2.75	1.61	1.27	1.99
<i>Maera inaequipes</i>	MB	STB	0.50	5.50	2.03	0.83	2.48
<i>Elasmopus brasiliensis</i>	MB	STB	1.00	5.13	1.90	1.55	2.32
<i>Amphicteis midas</i>	MB	STB	2.75	0.25	1.28	1.21	1.56
<i>Piromis eruca</i>	MB	STB	1.75	0.00	0.80	0.70	0.98
<i>Cestopagurus timidus</i>	RB	WR	1.13	5.50	2.56	1.05	3.29
<i>Alvania mamillata</i>	RB	WR	3.88	1.88	2.20	1.00	2.83
<i>Pagurus chevreuxi</i>	RB	WR	3.75	0.38	2.09	1.09	2.68
<i>Galathea bolivari</i>	RB	WR	0.00	2.75	1.52	1.26	1.95
<i>Cestopagurus timidus</i>	MB	WR	0.00	5.50	2.86	1.15	3.56
<i>Amphicteis midas</i>	MB	WR	2.75	0.38	1.62	1.10	2.02
<i>Galathea bolivari</i>	MB	WR	0.13	2.75	1.47	1.21	1.83
<i>Piromis eruca</i>	MB	WR	2.38	0.00	1.46	0.84	1.82
<i>Maera inaequipes</i>	STB	WR	5.50	4.00	1.84	1.10	2.60
<i>Cestopagurus timidus</i>	STB	WR	2.38	5.50	1.61	1.01	2.27
<i>Elasmopus brasiliensis</i>	STB	WR	5.13	2.13	1.45	1.28	2.05
<i>Galathea bolivari</i>	STB	WR	2.00	2.75	0.78	1.21	1.10

Table 6. Results of multiple linear regression A: abundance; SR: species richness; EB: epiphyte biomass; G: mean sediment grain size; SB: shoot biomass. Units are per core (n = 32) for all attributes. Values of the coefficient standard error (CSE) are indicated for the respective term (EB, G, SB) in the model. The critical value for the Shapiro-Wilk (SW) test for normality in regression residuals (n = 32) = 0.927 at p < 0.05

Spatial scale	Model	CSE	R ²	F	p	SW
Large	$\ln(A) = 0.745 \ln(EB) + 3.011$	0.12	0.55	37.48	<0.001	0.933
	$SR = 0.73 \ln(EB) + 0.22 (G) + 7.07$	3.98,				
Medium	$A = 0.58 (SB) + 4.98$	6.18	0.72	23.68	<0.001	0.976
	$SR = 0.510 (SB) + 23.00$	0.22	0.35	7.83	0.002	0.961
		0.10	0.26	10.57	0.003	0.975

cients were low (<0.26) for each of the environmental attributes considered individually; the highest value was for epiphyte biomass. At the medium spatial scale, a combination of leaf area, root-rhizome biomass, mean sediment grain size and total organic carbon in the sediment best explained the macroinvertebrate assemblage composition ($\rho_w = 0.264$). Values of Spearman's rank correlation coefficient were very low (<0.15) for each of the single environmental variables. At the small spatial scale, relationships between biotic and environmental variables were weak, the highest correlation being for a combination of shoot biomass and sediment grain size ($\rho_w =$

0.096). Like the combined variables, values of Spearman's rank correlation coefficients were very low (<0.085) for each environmental variable considered individually.

Results of multiple linear regression (Table 6) indicated that macroinvertebrate abundance was significantly related to epiphyte biomass at the large spatial scale (Fig. 6a) and to shoot biomass (Fig. 6b) at the medium spatial scale, while macroinvertebrate species richness was related to epiphyte biomass and mean sediment grain size at the large spatial scale (Fig. 7a,b) and to shoot biomass at the medium spatial scale (Fig. 7c).

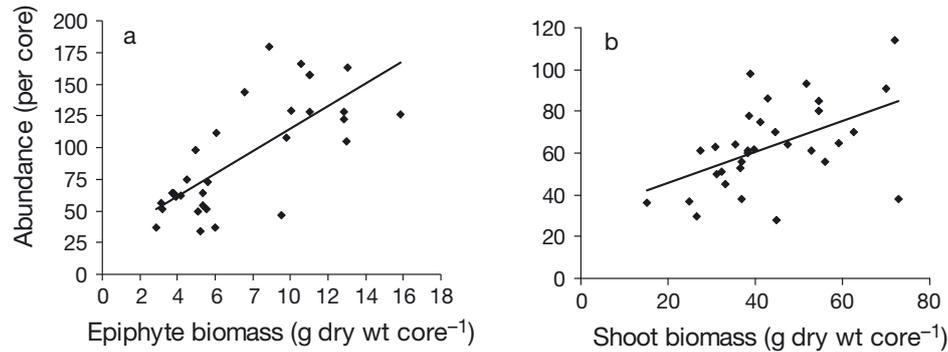


Fig. 6. Macroinvertebrate abundance with (a) epiphyte biomass at the large spatial scale and (b) shoot biomass at the medium spatial scale

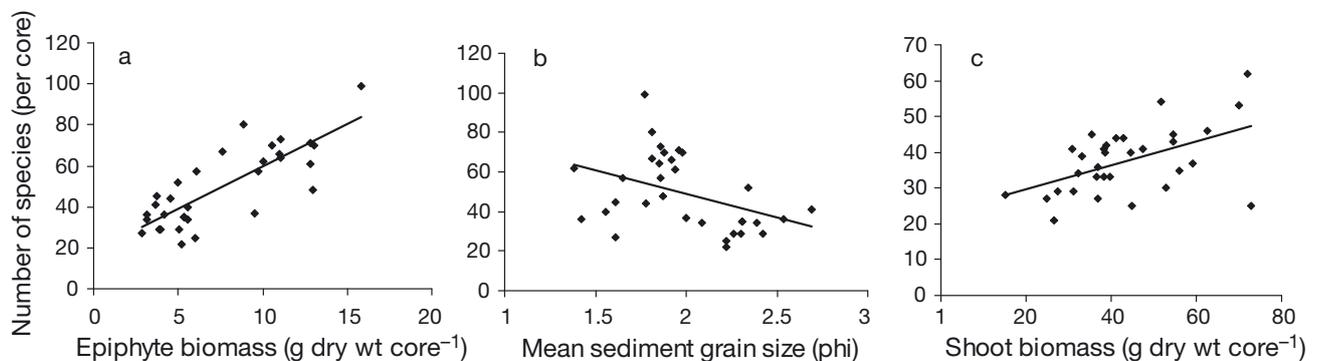


Fig. 7. Macroinvertebrate species richness with (a) epiphyte biomass and (b) mean sediment grain size, both at the large spatial scale, and (c) shoot biomass at the medium spatial scale

DISCUSSION

Results of both univariate and multivariate analyses indicated that the species richness, abundance and assemblage composition of macroinvertebrates did not differ significantly between non-fragmented and fragmented beds of *Posidonia oceanica*, across 3 spatial scales. On the other hand, significant differences in macroinvertebrate attributes were detected between different sampling localities, namely across the large (location) spatial scale, thereby highlighting the importance of local factors over bed type in influencing the invertebrate assemblages associated with *P. oceanica*. At the medium (site) and small (plot) spatial scales, univariate and multivariate analyses did not indicate consistent significant differences in attributes of the macroinvertebrates associated with *P. oceanica* beds.

Posidonia oceanica architectural features were, overall, similar between continuous and reticulate beds at all 3 spatial scales, as shown by the lack of significant differences in seagrass attributes between the 2 bed types. Significant interactions were detected by ANOVA for epiphyte biomass at the large spatial scale and for shoot biomass at the medium scale, which indicate site-specific influences of both bed type and sam-

pling locality for some of the sampled localities. On the other hand, significant differences in leaf area, shoot biomass and epiphyte biomass were detected by ANOVA at the large (location) spatial scale and in epiphyte biomass and shoot biomass at the medium (site) spatial scale, indicating significant variation in these seagrass attributes at both large and medium spatial scales. No significant interactions were detected by ANOVA at the small (plot) spatial scale, nor did it detect significant differences for any of the seagrass attributes at this spatial level. In contrast with the findings for seagrass attributes, there were differences in the organic carbon content and mean sediment grain size of the sediment between the 2 *P. oceanica* bed types, as well as differences between different sampling localities, at the different spatial scales. This is highlighted by the significant interactions detected by ANOVA at the large (location) and medium (site) spatial scales and by significant differences in the 2 sediment attributes between the 2 bed types and between different sampling localities.

While there were differences in sediment attributes between continuous and reticulate *Posidonia oceanica* bed types, the overall similarity in plant architectural features (see also Borg et al. 2005) may account for the

observed lack of significant differences in macroinvertebrate species richness, abundance and assemblage composition between the 2 seagrass bed types, given that within-bed architecture may be important in influencing macrofaunal species richness and abundance (e.g. Heck & Orth 1980, Orth et al. 1984, Tolan et al. 1997, Hovel & Lipcius 2001). Boström et al. (2006b) noted that sediment organic carbon and grain size were amongst the most important factors in determining the diversity of infauna associated with *Zostera marina* beds. Differences in sediment organic carbon and grain size between continuous and reticulate *P. oceanica* bed types were noted in the present study. However, these did not result in significant differences in the attributes of the macroinvertebrates associated with the 2 different bed types. A possible reason for this is the large size of *P. oceanica*, which contributes to very high architectural complexity, with the consequence that shoot canopy architecture has an overriding influence over sediment attributes, especially when considering both the infauna and epifauna, as was the case in the present study. On the other hand, in the light of the significant relationships obtained from linear regression between attributes of the macroinvertebrate assemblages and sediment variables (see below), the potential influence of sediment organic carbon content and sediment grain size on macroinvertebrates associated with *P. oceanica* should not be ignored.

Several workers have noted differences in faunal assemblages between different seagrass bed types (e.g. Hovel & Lipcius 2001, Vega Fernández et al. 2005) or between seagrass patches of different sizes (e.g. Bowden et al. 2001, Laurel et al. 2003), which would seem to indicate that fragmentation of seagrass beds may influence the diversity of associated biota. On the other hand, seagrass bed size has a relatively minor role in influencing the diversity of associated fauna and local factors such as sediment attributes, amongst others, have a more important influence (e.g. Boström et al. 2006b). Despite the large number of available studies, there is no general agreement on whether fragmentation of seagrass beds influences the diversity of associated fauna. Possible reasons for this include the different spatial scales considered in the different studies, which would lead to differences in the interpretation of obtained results (McNeill & Fairweather 1993, Bell et al. 2001, Hovel & Lipcius 2002), as well as to factors related to aspects of the sampling design (see review by Connolly & Hindell 2006).

At the large spatial scale, linear regression indicated that macroinvertebrate species richness and abundance were significantly related to epiphyte biomass, while species richness was also inversely related to mean sediment grain size. At the medium (site) spatial

scale, macroinvertebrate species richness and abundance were related to shoot biomass. These results were corroborated by BIOENV, which indicated that epiphyte biomass and mean sediment grain size were amongst the environmental variables that best explained the assemblage composition at the large spatial scale. However, BIOENV did not include shoot biomass in the set of environmental variables that best explained the assemblage composition at the medium spatial scale. Attrill et al. (2000) cautioned against conclusions reached from significant relationships detected between shoot biomass and attributes of seagrass-associated macroinvertebrate assemblages, as these could result from species–area relationships. Nevertheless, the present findings highlight the important influence of spatial variation in plant biomass (be it seagrass, epiphyte, or other) on the macroinvertebrate assemblages associated with seagrass.

Taken together, the present results indicate that, at the large spatial scale, epiphytes appear to constitute an important factor in influencing the species richness, abundance and assemblage composition of macroinvertebrates associated with *Posidonia oceanica* beds, while mean sediment grain size also exerts an influence on species richness. The significantly higher values of shoot epiphyte weight recorded from the *P. oceanica* beds at WR and STB (large spatial scale) may be attributed to higher nutrient loading of coastal waters in the southern half of the Maltese Islands (Axiak et al. 2000) (see Fig. 1), resulting from a higher human population density and more intense coastal use (Mallia et al. 2002) compared to the northern half of the islands.

Seagrass epiphytes are an important food supply (Jernakoff & Nielsen 1997, Bologna & Heck 1999, Moncreiff & Sullivan 2001) and microhabitat (Heck & Orth 1980, Kitting 1984, Leber 1985, Worthington et al. 1991) for a variety of macroinvertebrate species (see also review by Valentine & Duffy 2006). Epiphytes may also facilitate the passive settlement of the larvae of some organisms, while tube-building amphipods use them for support (Coen et al. 1981, Worthington et al. 1991). The importance of epiphytes in influencing the diversity of macroinvertebrate assemblages associated with marine macroalgae and seagrasses has been emphasised in the literature (e.g. Kitting 1984, Schneider & Mann 1991, Gambi et al. 1992), but relatively few authors (Hall & Bell 1988, Edgar & Robertson 1992, Saunders et al. 2003, Tomas et al. 2005, Prado et al. 2007) have given it due consideration in ecological studies of seagrass habitat.

No studies are yet available which quantitatively show a significant relationship between the epiphyte biomass of *Posidonia oceanica* beds and the diversity of associated macroinvertebrates, although some authors

(e.g. Gambi et al. 1992) have noted it, while recent studies (e.g. Tomas et al. 2005, Prado et al. 2007) have emphasised the important role of epiphytes on the fauna associated with this habitat. For example, the species that contributed most to the observed differences and were good discriminators between samples taken from the *P. oceanica* beds at WR and STB (the 2 locations having the highest seagrass epiphyte biomass) and those taken at the other 2 locations, included the amphipods *Maera inaequipes* and *Elasmopus brasiliensis*. These species could be utilising the shoot epiphytes as microhabitat and may also be feeding on epiphytes, or on particulate organic matter deposited on their surface (e.g. Gambi et al. 1992, Scipione 1999).

In conclusion, the present findings suggest that environmental factors operating at local spatial scales are more important than bed type in influencing attributes of the macroinvertebrate assemblages associated with *Posidonia oceanica* habitat and that naturally occurring continuous and fragmented seagrass beds appear to have broadly similar habitat 'value' for macroinvertebrates. A similar assertion has been made by other workers (e.g. Bell et al. 2001, Healy & Hovel 2004, Boström et al. 2006b). However, given that sampling at the medium and small spatial levels was only undertaken at a single location (MB), caution should be adopted in generalising results from the plot and site scales to all locations. Certainly, the present results do not provide evidence that fragmentation of continuous seagrass beds should be considered as an 'acceptable' change and, hence, a pretext for allowing anthropogenic activities to modify continuous beds to reticulate ones, particularly since naturally occurring fragmented seagrass beds may not be useful proxies for fragmented beds that result from anthropogenic disturbance. It should be remembered that fragmentation of seagrass habitat leads not only to a change in bed configuration, but also to reduced coverage and thus to loss in habitat area (Hemminga & Duarte 2000). Furthermore, fragmentation of continuous seagrass beds to very small-sized patches (e.g. 1 to 10 m across) leads to bed types that essentially consist of edge habitat, which would have implications for the associated macrofauna (Irlandi 1997, Bowden et al. 2001, Johnson & Heck 2006). Additionally, fragmentation of seagrass beds increases their exposure to colonisation by opportunistic species, such as the alien *Caulerpa* spp. (e.g. Ceccherelli et al. 2000). Hence, fragmented beds should receive the same attention as non-fragmented ones when considering conservation and protection issues (McNeill & Fairweather 1993, Healy & Hovel 2004, Hirst & Attrill 2008). Further work involving comparisons of the biotic assemblage composition between bed types of the same seagrass, other than the assem-

blage component considered in the present study, is necessary to understand *P. oceanica* landscape ecological processes, especially given the large variation in bed morphology of this seagrass (e.g. Colantoni et al. 1982, Borg et al. 2005, Vega Fernández et al. 2005), while investigations that incorporate sampling across different seasons will also be very useful in assessing the influence of temporal factors on this important Mediterranean marine habitat.

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