RESEARCH ARTICLE

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Wanted dead or alive: high diversity of macroinvertebrates associated with living and 'dead' *Posidonia oceanica* matte

Abstract The Mediterranean endemic seagrass *Posidonia oceanica* forms beds characterised by a dense leaf canopy and a thick root-rhizome 'matte'. Death of *P. oceanica* shoots leads to exposure of the underlying matte, which can persist for many years, and is termed 'dead' matte. Traditionally, dead matte has been regarded as a degraded habitat. To test whether this assumption was true, the motile macroinvertebrates of adjacent living (with shoots) and dead (without shoots) matte of *P. oceanica* were sampled in four different plots located at the same depth (5–6 m) in Mellieha Bay, Malta (central Mediterranean). The total number of species and abundance were significantly higher (ANOVA; $P < 0.05$ and $P < 0.01$, respectively) in the dead matte than in living *P. oceanica* matte, despite the presence of the foliar canopy in the latter. Multivariate analysis (MDS) clearly showed two main groups of assemblages, corresponding to the two matte types. The amphipods *Leptocheirus guttatus* and *Maera grossimana*, and the polychaete *Nereis rava* contributed most to the dissimilarity between the two different matte types. Several unique properties of the dead matte contributing to the unexpected higher number of species and abundance of motile macroinvertebrates associated with this habitat are discussed. The findings have important implications for the conservation of bare *P. oceanica* matte, which has been generally viewed as a habitat of low ecological value.

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Introduction

Seagrass beds consist of the foliar canopy and the root-rhizome layer (Orth et al. 1984; Mazzella et al. 1992; Buia et al. 2000), each of which varies in habitat characteristics and associated biotic assemblages (e.g. Bianchi et al. 1989). Although these different structural compartments are frequently referred to as separate sub-habitats, supporting different biotic assemblages (Kikuchi and Peres 1977; Kikuchi 1980), complex interactions occur between the associated biota, with some species migrating vertically between the two (e.g. Sánchez Jerez et al. 1999), thereby making such distinction unclear (Baden and Bostrom 2001).

Several studies have shown that the abundance of motile macrofauna associated with seagrass beds is greater than in unvegetated habitats (e.g. Virnstein et al. 1983; Lewis 1984; Curras et al. 1993; Boström and Bonsdorf 1997). This difference is more evident when the seagrass foliar canopy is compared with bare soft substrata (e.g. Howard et al. 1989; Edgar et al. 1994; Connolly 1997). However, investigations involving reduction of leaf height or complete removal of the foliar stratum have shown that the leaf canopy per se may not be of overriding importance in determining the high biodiversity recorded from seagrass beds, and that other factors may be implicated (e.g. Bell and Westoby 1986; Connoly 1995). Furthermore, few studies (Webster et al. 1998; Frost et al. 1999; Curras et al. 1993) have included the root-rhizome layer of seagrass beds in assessments of the associated macrofauna, despite indications that it may support more diverse macroinvertebrate assemblages than the foliar stratum (e.g. in *Posidonia oceanica* beds; see Harmelin 1964; Bianchi et al. 1989).

In the Mediterranean Sea, the endemic *P. oceanica* is the largest species of seagrass, with leaves sometimes

exceeding one metre in length (Drew and Jupp 1976). *P. oceanica* beds are characterised by very high shoot densities (e.g. 1,200 shoots m^{-2} at a depth of 5 m; Mazzella et al. 1992) and a root-rhizome layer consisting of tough, lignified roots and rhizomes admixed with sediment (called 'matte' by French workers) that can be several metres thick (Romero et al. 1994). *P. oceanica* beds constitute one of the most important shallow-water habitats of the Mediterranean infralittoral (Boudouresque et al. 1994). Adverse anthropogenic activities, such as pollution (e.g. resulting from discharge of sewage and harbour activities; Ramos Éspla 1984) and trawling (e.g. Ardizzone and Pelusi 1984), or disturbance from natural processes and events, such as strong currents and wave action (e.g. Blanc and Jeudy de Grissac 1984), may result in death of *P. oceanica* in parts of a bed, leading to exposure of the underlying root-rhizome layer. The remaining 'dead' root-rhizome matte (referred to as 'matte morte' by French and Italian workers) consists of the compacted remains of the seagrass root-rhizome matrix with numerous small crevices and interstices, a proportion of which are filled with sediment (see Harmelin 1964). In places, the surface of the dead *P. oceanica* matte becomes colonised by algae (Boudouresque et al. 1985; Barberi et al. 1995), and sometimes by the seagrass *Cymodocea nodosa* (Mazzella et al. 1986; Calvo and Frada-Orestanio 1984).

Dead *P. oceanica* matte may persist for several years or even decades (Meinesz and Lefevre 1984) and can occur over large continuous areas, or as patches intermixed amongst 'living' matte (Augier and Boudouresque 1970; Augier 1986; Panayotidis and Simboura 1989). Dead *P. oceanica* matte has been reported from several parts of the Mediterranean, including Spain (Ramos Éspla 1984), France (Augier 1986), Italy (Vaccarella et al. 1981), Sardinia (Barberi et al. 1995), Sicily (Calvo and Frada-Orestanio 1984) and Greece (Panayotidis and Simboura 1989), showing that its occurrence is widespread in the region. This widespread occurrence is of potential concern because dead *P. oceanica* matte is generally viewed as a degraded habitat of low ecological value, however, few data of the ecology of this habitat are available (but see Harmelin 1964; De Metrio et al. 1978, 1980; Vaccarella et al. 1981; Willsie 1983; Abada Guerroui and Willsie 1984; Bellan Santini et al. 1986; Somaschini et al. 1994). Furthermore, quantitative studies designed specifically to compare the macrofauna of living and dead matte are generally lacking (Harmelin 1964) and deal only with single taxa, namely amphipods (e.g. Bellan Santini et al. 1986) and polychaetes (e.g. Somaschini et al. 1994). Therefore, data from comparative quantitative studies are required to assess the conservation value of dead *P. oceanica* matte, compared to that of living matte of the seagrass.

Sites of different matte type are likely to be characterised by different environmental conditions that could influence the composition of the associated motile macroinvertebrate assemblages. For example, rates of sediment deposition are higher in living than dead matte, since the overlying leaf canopy effectively traps suspended fine particles from the water column (Duarte et al. 1999). Dead *P. oceanica* matte lacks the foliar canopy and would therefore be more exposed to currents (Gambi et al. 1989), and hence to loss of the interstitial sediments (particularly the finer particles), which are easily resuspended by water movement and eroded from the matte (Terrados and Duarte 2000). The composition and nutritional value of detrital matter originating from the root-rhizome layer are expected to differ between the two different matte types of *P. oceanica*, since the roots and rhizomes of dead seagrass matte will be in a different state of decomposition from that of living matte (e.g. see Mfilinge et al. 2003, on nutritional quality of decomposing mangrove leaves). Furthermore, input rates of particulate matter from the *P. oceanica* leaf canopy (Duarte et al. 1999) would differ between living and dead matte of *P. oceanica*, given the absence of living shoots in dead beds of the seagrass. Therefore, one would expect differences in sediment grain size and organic matter content between living and dead *P. oceanica* matte, which in turn would affect the composition of the associated faunal assemblage.

The present study aimed to establish whether the number of species and abundance, and the species composition of motile macroinvertebrate assemblages, differed between living and dead *P. oceanica* matte. The null hypotheses tested were that the number of species, abundance and assemblage composition of associated motile macroinvertebrates did not differ between living and dead *P. oceanica* matte.

Materials and methods

Study area and sampling design

Previous surveys (Borg and Schembri 1995; Borg et al. 1997) established that areas of dead *P. oceanica* matte, interspersed amongst the living seagrass, occurred in several bays and inlets in the Maltese Islands (central Mediterranean). While in some bays and inlets, large areas of dead *P. oceanica* matte are thought to result from regression of the seagrass due to anthropogenic disturbances, in other places it appears to have resulted from natural disturbance events, including strong currents and wave action. Mellieha Bay, located on the northeastern coast of mainland Malta (Fig. 1), is one such relatively undisturbed locality where large patches of dead matte are interspersed with living matte, predominantly in the 6–8 m depth range. No information on the age of the dead matte (since loss of the foliar canopy) is available, however, surveys carried out in the same area since 1993 (Borg and Schembri 1995; Borg et al. 1997) indicate that defoliation took place more than a decade ago. The dead *P. oceanica* matte has a softer texture than its living counterpart; for example, it is penetrated easily with a diver's knife. The surface of the dead matte has numerous crevices and openings

Fig. 1 Locations of: **a** the Maltese Islands (*circle*) at the centre of the Mediterranean Sea; **b** the study area (Mellieha Bay) in the Maltese islands; **c, d** the four sampling plots in the study area where samples were taken from living (+) and dead (−) *Posidonia oceanica* matte
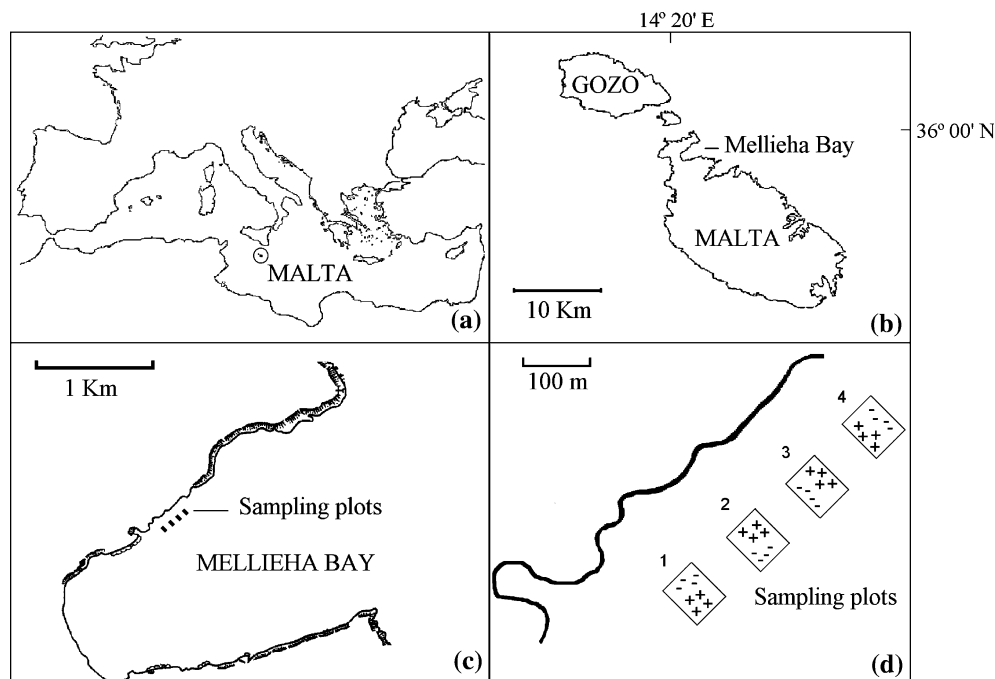
leading to channels that appear to permeate the root-rhizome lattice, giving it a spongy texture. In some places, the surface of the dead matte supports macoalgae (e.g. *Padina pavonica* and *Halopteris* spp.), or sparse stands of *C. nodosa*.

The sampling design consisted of four plots, each measuring circa 60×80 m², and located at a depth of 5–6 m in Mellieha Bay (Fig. 1). Adjacent plots were separated from each other by around 80 m, and each plot had dense and healthy *P. oceanica* beds interspersed with large patches of dead matte. Such a design ensured spatial replication and allowed detection of spatial differences, if present, between living and dead matte *P. oceanica* in the same locality (Underwood 1997).

Sampling and laboratory analyses

Living and dead *P. oceanica* matte were sampled in August 2000 using a specially designed corer having a diameter of 25 cm, to which a 0.5 mm mesh collecting bag was attached (Borg et al. 2002). Four cores were collected by SCUBA divers from each of the two matte types adjacent to each other (each matte area > 10 m²), and within each of the four plots, such that a total of 32 samples was obtained (4 replicate samples × 2 treatments × 4 plots; Fig. 1). Core samples taken on the living *P. oceanica* matte included the seagrass shoots (i.e. no in situ separation of seagrass shoots from the matte was made). Four replicate samples were also collected from each sampling station, using a smaller (10 cm) diameter metal corer, to enable physico-chemical analyses of the sediment and of the root-rhizome material. To reduce edge effects, all samples were collected at least 2 m away from the boundary between the two different matte types.

In the laboratory, samples for sediment analyses were sorted to separate the root-rhizome mesh and other plant material from the sediment. Sub-samples of the sediment were taken for the determination of total organic carbon and frozen at −25°C, while the remaining portions were dried in air for granulometric analysis. Total organic carbon in the sediment (Walkley and Black 1934) and mean sediment grain size (Folk and Ward 1957) were carried out following Buchanan (1984).

Samples collected for faunal studies were washed in seawater, and the shoots and root-rhizome matrix separated and examined carefully to remove the motile macroinvertebrates (i.e. nemerteans, polychaetes, molluscs, arthropods and echinoderms); sessile invertebrates were also separated from the plant material, but not considered in the analyses. The *P. oceanica* shoots collected in cores taken on the living matte were separated from the root-rhizome fraction and counted to obtain estimates of shoot density. The root-rhizome fraction from each sample was washed in tap water and dried at 80°C for 48 h to constant weight, to obtain estimates of dry weight. The remaining sediment and washings were passed through a 0.5 mm sieve and the retained material sorted in trays under a ×5 magnifying lens to separate the fauna. Macroinvertebrates were fixed in 10% formaldehyde in seawater and transferred to 70% ethanol prior to identification to the lowest possible taxon.

Data analyses

Differences in shoot density and leaf biomass between living *P. oceanica* matte in the four plots were tested using one-way ANOVA (with α = 0.05). Differences in

organic content and mean grain size of the sediment, and in dry weight of the root-rhizome fraction between the two different *P. oceanica* matte types in the four plots, were tested using two-way ANOVA (α = 0.05) with 'matte type' and 'plots' as main factors. Differences in the number of species and abundance of motile macro-invertebrates between the two different matte types in the four plots were also tested using two-factor ANO-VA. The ANOVA model used was orthogonal, in which 'matte type' (two levels) was a fixed factor and 'plot' (four levels) was random. Prior to analyses, all data were tested for homogeneity of variances using Cochran's test and, where necessary, appropriate transformation [ln(x)] was carried out. Analyses were carried out using the PC software package GMAV5 produced at the University of Sydney.

To examine for differences in the composition of assemblages associated with the two different *P. oceanica* matte types, multivariate analysis was carried out on the species-abundance data (4th root transformed, to downweigh the contribution of dominant species) using the PRIMER v5 suite of programs (Clarke and Gorley 2001). A ranked triangular similarity matrix was constructed using the Bray-Curtis similarity measure. Subsequent ordination from the similarity matrix consisted of non-metric multidimensional scaling (MDS). The species abundance data from the two different matte types were tested for differences in assemblage composition using two-way crossed analysis of similarity (ANOSIM). The contribution of the different species to the observed similarity within groups of samples taken from the same type of matte, and the dissimilarity between groups of samples taken from different matte types, were determined using the similarity percentages (SIMPER) procedure (Clarke 1993). SIMPER identifies and ranks species according to their overall contribution to dissimilarity between the various groups of samples and helps identify the species that are good discriminators. Species are good discriminators when they show large differences in their respective average abundances (between different sample groups), and have a high average dissimilarity value and ratio of average dissimilarity to standard deviation of dissimilarity (Clarke 1993). BIOENV analysis (using Spearman's rank correlation coefficient ρ_w) was carried out to examine the relationships between macroinvertebrate assemblage composition and environmental variables measured (Clarke and Ainsworth 1993). The environmental variables included in the analysis were the same as those included in the ANOVA analysis.

Results

One-factor ANOVA indicated that values of shoot density and leaf biomass were not significantly different between living *P. oceanica* matte in the four plots. The two-factor ANOVA did not indicate any significant differences in organic carbon content and mean grain

size of the sediment between living and dead *P. oceanica* matte, and among different plots (Fig. 2a, b, Table 1). Values of dry weight of the root-rhizome fraction from the dead matte were higher (Fig. 2c), but this difference was not significant (two-factor ANOVA; Table 1).

A total of 5,695 individuals comprising 215 species were collected, of which 39 were exclusively collected from dead matte and 32 were collected exclusively from living matte (Appendix). The two-factor ANOVA indicated that both mean total abundance and number of species were significantly higher in samples collected from dead *P. oceanica* matte than from living matte (which included the shoots), but no significant differences were indicated among different plots for the same matte type (Fig. 3, Table 2).

The MDS plot indicated a clear separation between the samples collected from living and dead *P. oceanica* matte, except for a single sample taken from living
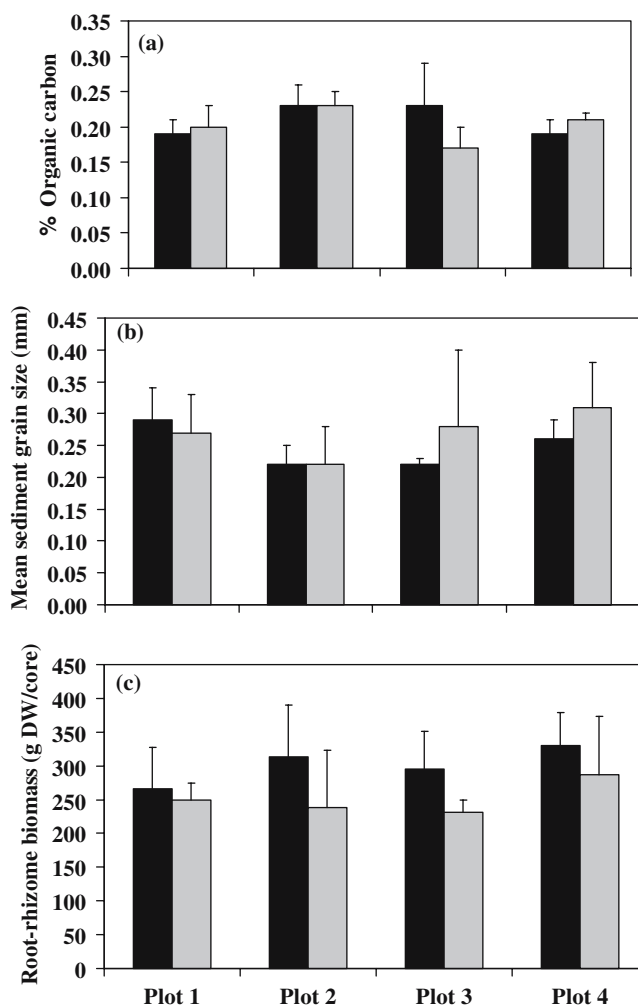

Fig. 2 Mean values (+ 1SD) of **a** % organic carbon in sediment, **b** sediment grain size and **c** dry weight of root-rhizomes, recorded for living and dead *Posidonia oceanica* matte from the four sampling plots. *Black bars* show dead matte and *grey bars* show living matte

Table 1 ANOVA results for total percentage organic carbon in the sediment, mean sediment grain size and root-rhizome biomass

Source of variation	df	% Organic carbon (n=4)			Mean sediment grain size (mm) (n=4)			Root-rhizome biomass (g) (n=4)		
		Mean square	F	P	Mean square	F	P	Mean square	F	P
Matte type	1	0.151	0.21	NS	0.048	1.73	NS	20034.21	15.30	NS
Plot	3	0.052	2.01	NS	0.007	1.40	NS	4194.55	0.82	NS
Interaction	3	0.070	2.73	NS	0.003	0.54	NS	1309.24	0.26	NS
Residual	24	0.026			0.005			5106.46		

NS Not significant ($P > 0.05$)

matte, which was an outlier (Fig. 4). The separate grouping of samples was corroborated by the two-way crossed ANOSIM, which indicated that assemblages sampled from the two matte types were significantly different (Global $R = 0.911$; $P < 0.05$). Samples collected from the same type of matte did not, however, differ significantly between the four different plots, for both living and dead *P. oceanica* matte (ANOSIM; Global $R = 0.029$; $P > 0.05$; see also the lack of sample grouping by plot on the MDS plot). SIMPER analysis (Table 3) showed that the average dissimilarity value between the two groups of samples taken from the two different matte types was 80%, while the three species which contributed most to dissimilarity were the amphipods *Leptocheirus guttatus* and *Maera inaequipes*, and the polychaete *Nereis rava*. The amphipod *L. guttatus* alone

contributed 12% to the dissimilarity, being found only in samples from dead matte. Overall, the observed differences were due to: (1) species that were recorded only from one of the two *P. oceanica* matte types, for example, the amphipods *L. guttatus* and *Lysianassa costae*, and the decapod *Galathea bolivari* (dead matte) and the amphipod *Ampelisca* cf. *rubella* (living matte); or (2) large differences in abundance of species between the two matte types, for example, the amphipods *M. inaequipes* and *Maera. grossimana*, the decapod *Athanas nitescens* and the polychaete *N. rava* (dead matte), and the amphipods *Elasmopus pocillimanus* and *Aora* sp. (living matte) (see Table 3 for further detail). BIOENV indicated that the environmental attribute that best explained the macroinvertebrate composition was mean sediment grain size ($\rho_w = 0.136$); however, the value of the correlation coefficient was very low (and no combination of the three variables achieved a greater correlation).
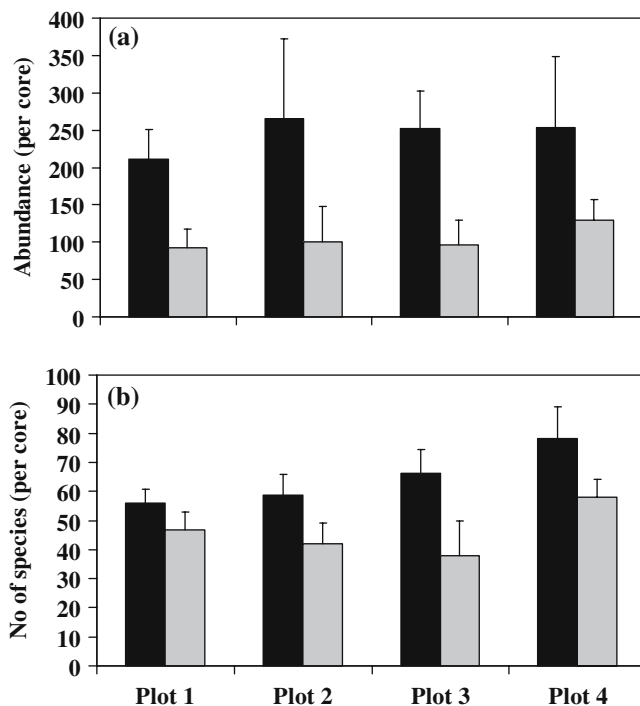
Discussion

The present study demonstrated that, in the study area, dead *P. oceanica* matte supported a significantly higher number of species and abundance of motile macroinvertebrates than living matte, and this was consistent across the spatial scale considered. Multivariate analysis indicated that the composition of the associated motile macroinvertebrate assemblages differed significantly between the two matte types, such that many species were recorded exclusively from each of the two sub-habitats. Based on these results, the null hypotheses of no difference in the number of species and abundance, and in the assemblage composition between living and dead matte of *P. oceanica*, were rejected.

Previous studies on the macroinvertebrate assemblages of dead *P. oceanica* matte (Harmelin 1964; Abada Guerroui and Willsie 1984; Somaschini et al. 1994) indicated that this habitat supports a rich macrofauna, in terms of number of species and abundance. Some of these investigations indicated also that the species composition and structure of the biotic assemblages associated with dead *P. oceanica* matte may vary, depending on matte type and structure (Harmelin 1964; De Metrio et al. 1978, 1980). For example, De Metrio et al. (1978, 1980) noted differences in the

Fig. 3 Mean values (+1SD) of **a** total abundance and **b** total number of species recorded for the living and dead *Posidonia oceanica* matte from the four sampling plots. *Black bars* show dead matte and *grey bars* show living matte

Table 2 ANOVA results for total abundance (per core) and total number of species (per core)

Source of variation	df	Abundance (per core) (n = 4)			df	Number of species (per core)(n = 4)		
		Mean square	F	P		Mean square	F	P
Matte type	1	146746.53	70.04	**	1	1875.78	10.22	*
Plot	3	1109.86	0.32	NS	3	202.44	2.55	NS
Interaction	3	2095.20	0.60	NS	3	183.53	2.31	NS
Residual	24	3470.38			24	79.406		

*$P < 0.05$
**$P < 0.01$
NS Not significant

assemblage structure of associated macroinvertebrates between two dead mattes of *P. oceanica* that had different elevation (i.e. the two matte surfaces were located at different water depths), while Harmelin (1964) and Abada Guerroui and Willsie (1984) also noted differences in the associated macroinvertebrate assemblages between dead matte located in different water quality regimes.

Univariate analyses indicated that the physical properties of the matte substratum, namely organic content, grain size and root-rhizome biomass, were not significantly different between the two matte types, nor were these variables correlated strongly with the assemblage composition of macroinvertebrates associated with living and dead matte. Thus, other factors not measured in the present study must be considered to explain the observed difference in the motile macroinvertebrate assemblages of living and dead matte.

The less compact and spongy texture of dead *P. oceanica* matte apparently offers less resistance to burrowing by macroinvertebrates compared to living matte. Burrowing decapods, which were much more

Fig. 4 MDS plot for the species-abundance data from the 32 samples collected from living and dead *Posidonia oceanica* matte in the four sampling plots. *D* samples collected on dead matte, *L* samples collected on living matte; the *number* indicates the plot from where the respective sample was collected

abundant in dead *P. oceanica* matte (e.g. the shrimp *Alpheus dentipes*), may play an important role in increasing the amount of detrital matter available for consumption by other macroinvertebrates, through harvesting detritus and root-rhizome material and reworking of sediment (e.g. Stapel and Erftemeijer 2000). Since these and other shrimps found in greater abundance, or exclusively, in dead matte (e.g. *Upogebia mediterranea*) ventilate their burrows, they help create an environment rich in organic matter and oxygen, which favours bacterial growth (e.g. Branch and Pringle 1987). This, in turn, may lead to more rapid decomposition of seagrass (leaf and root-rhizome) tissue (e.g. Harrison 1989; Enríquez et al. 1993) to a detrital form that is more palatable and has a higher energy yield for the consumers (the macrofauna of dead matte) (e.g. Edgar et al. 1994). Thus, it is possible (as observed in the present study) that there would be no difference in the amount of organic matter between the living and dead matte habitat, nor any relationship between the associated macroinvertebrate composition and the organic matter content, but the dead *P. oceanica* matte habitat may be supplying larger amounts of detritus in a form that is more readily available as food (e.g. Mfilinge et al. 2003). Most of the macroinvertebrates recorded in higher abundance from dead *P. oceanica* matte, and which were identified by the SIMPER analysis to contribute most to the dissimilarity between samples collected from dead and living matte, were predominantly detritivores, for example, the amphipods *L. guttatus*, *M. inaequipes*, *M. grossimana* and *Leptocheirus bispinosus*; the polychaetes *N. rava*, Amphinomidae sp. and Terebellidae sp.; the isopod *Cyathura carinata* and the tanaid *Leptochelia savignyi* (Wittmann et al. 1981; Scipione 1999; Gambi et al. 1992). This observation supports the contention that the dead *P. oceanica* matte provides a rich source of detritus. On the other hand, species identified by the SIMPER analysis as high contributors to the similarity between samples taken from living *P. oceanica* matte included herbivores, for example, the amphipods *E. pocillimanus*, *Aora* sp., *Liljeborgia dellavallei* and *Microjassa cumbrensis* (Wittmann et al. 1981; Scipione 1999). This observation indicates that the living *P. oceanica* beds provide a rich source of algal epiphytes as food, thereby influencing the macroinver-

Table 3 Results of the SIMPER analysis for species having the highest dissimilarity values between the two groups of samples taken from different *Posidonia oceanica* matte types

Species	AA Dead matte	AA Living matte	AD	AD/SD	Contribution (%)
Leptocheirus guttatus	34.63	0.00	9.56	3.30	11.98
Maera inaequipes	14.50	2.00	3.46	1.46	4.33
Nereis rava	12.88	1.13	3.27	1.89	4.09
Maera grossimana	11.50	2.25	2.63	1.61	3.30
Elasmopus pocillimanus	2.44	8.63	2.31	0.90	2.90
Athanas nitescens	8.94	3.38	1.91	1.08	2.39
Lysianassa costae	6.56	0.00	1.90	1.04	2.38
Amphinomidae sp.	6.69	0.13	1.89	1.88	2.36
Galathea bolivari	5.81	0.00	1.62	1.95	2.03
Syllidae sp. B	7.50	2.25	1.62	1.38	2.03
Aoridae sp.	6.63	8.88	1.58	1.41	1.98
Terebellidae sp.A	5.38	0.25	1.56	1.07	1.95
Cyathura carinata	5.31	0.31	1.39	1.59	1.75
Leptochelia savignyi	5.25	0.50	1.33	1.45	1.67
Leptocheirus bispinosus	5.00	0.38	1.29	1.13	1.61
Alpheus dentipes	5.25	1.00	1.28	1.62	1.60
Liljeborgia dellavallei	0.06	4.13	1.18	1.23	1.48
Pontogenia chrysoscoma	4.63	0.63	1.14	1.47	1.43
Piromis eruca	4.06	0.50	1.09	1.20	1.37
Ampelisca cf *rubella*	0.00	3.75	1.05	1.35	1.32
Amphithoe ramondi	4.13	0.44	1.02	1.34	1.28
Notomastus latericeus	4.13	1.38	0.94	1.01	1.18
Microjassa cumbrensis	1.31	3.69	0.94	1.38	1.18
Cestopagurus timidus	0.44	3.31	0.88	1.17	1.10

AA average abundance (number of individuals per core), *AD* average dissimilarity between the two locations being compared; *AD/SD* ratio of the average dissimilarity to the standard deviation of dissimilarity for the particular species

tebrates associated with this particular sub-habitat, hence the differences observed between the assemblage composition of the two matte types.

The surface of the dead *P. oceanica* matte also serves as a hard substratum, enabling colonisation by algae and other sessile epibiota, whose associated species composition would be expected to resemble that of the photophilic assemblages on hard substrata at similar depths (e.g. Vaccarella et al. 1981). The epibiota of living *P. oceanica* matte receives less light, being shaded by the overlying leaf canopy, and is therefore sciaphilic (e.g. García Raso et al. 1996). Such differences in the species composition of associated epiphytic assemblages between living and dead matte of *P. oceanica* are likely to influence the species composition of the motile macro-invertebrate assemblages that feed on them (Jernakoff et al. 1996; Jernakoff and Nielsen 1997).

Several workers have emphasised the important role of the physical complexity of the seagrass foliar stratum in enhancing the diversity of associated macrofauna by providing refugia against predation, habitat for larval settlement and growth, and food (see reviews by Heck and Wetstone 1977; Orth et al. 1984; Virnstein 1987; Heck and Crowder 1991; Jernakoff et al. 1996). Therefore, it is also likely that the physical complexity of dead matte plays an equally important role in promoting diversity and influencing the composition of associated macroinvertebrate assemblages. The presence of more hollow spaces and crevices in the dead matte (compared to its living counterpart) will increase microhabitats available to cryptic fauna. Again, the results of the SIMPER analysis support this contention. For example, the galatheid *G. bolivari*, the

shrimps *Alpheus dentipes* and *A. nitescens*, the isopod *C. carinata* and the tanaid *L. savignyi* often occupy hollows and crevices in substrata (Harmelin 1964; García Raso 1990; García Raso et al. 1996). These species were more abundant in dead matte and contributed most to the observed dissimilarity between the motile macroinvertebrate assemblage compositions of the two sub-habitats.

Present results, that dead *P. oceanica* matte resulting from natural disturbance supports a distinct and richer motile macroinvertebrate assemblage than living matte, cannot be generalised to other dead matte habitats in different environmental conditions (e.g. at different water depths Harmelin 1964; De Metrio et al. 1978, 1980), or resulting from death of the seagrass due to pollution (Bellan Santini et al. 1986). Present findings do, however, highlight the importance of the matte habitat in its own right (Harmelin 1964; Vaccarella et al. 1981) and indicate the need for further study. On the other hand, dead *P. oceanica* matte can never be considered as an acceptable substitute for living matte, since the high ecological value of the foliar canopy (e.g. as a nursery, feeding ground and refuge against predation for many commercially important fishes; see Bell and Harmelin-Vivien 1982; Harmelin-Vivien 1982; Harmelin-Vivien 1984) is well established. Indeed, the only source of dead *P. oceanica* matte is the living matte itself! Furthermore, unless recolonised by seagrass shoots, dead *P. oceanica* matte is a habitat that is slowly moving toward bare sand through gradual decomposition, and is therefore in a state of slow 'regression', while living matte is a habitat under gradual construction, and is therefore in a state of 'progression'.

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The unfortunate labelling of unvegetated *P. oceanica* matte that does not possess living shoots as 'dead' could easily lead to general acceptance that this habitat type supports a lower biodiversity and is of low conservation importance. Clearly, the data from the present study indicate otherwise. Indeed, the importance of dead *P. oceanica* matte in supporting a high diversity of associated biota was recognized by Harmelin ([1964]) over four decades ago. Furthermore, present results and other studies (e.g. Harmelin [1964]; De Metrio et al. [1980]) show that some of the species that occur in dead *P. oceanica* matte are generally rare, making this habitat of potentially high conservation value. For example, De Metrio et al. ([1978], [1980]) recorded a number of species from this habitat (e.g. the serpulid polychaete *Hydroides helmatus* and the gastropod *Tectonatica filosa*), which were considered very rare. We propose, therefore, that the term 'dead' should be replaced by 'bare' when referring to *P. oceanica* matte that lacks living shoots. However, present results should not, in any way, be interpreted to imply that bare *P. oceanica* matte has a higher ecological value than the living matte of the same seagrass. The high ecological value of living *P. oceanica* beds is overwhelmingly supported by data from all over the Mediterranean (e.g. Boudouresque et al. [1994]; Buia et al. [2000]); the habitat fulfils many ecological functions that cannot be sustained by bare matte, such as its primary productivity (Ott [1980]; Pergent-Martini et al. [1984]), its role as a nursery habitat for many faunal species (e.g. Mazzella et al. [1992]) and its interactions with the physical environment (den Hartog [1970]; Jeudy de Grissac [1984]; Granata et al. [2001]). Furthermore, several species that occur exclusively in living *P. oceanica* beds (see Procaccini et al. [2003]) are not present in bare matte of the seagrass. Rather, results from this study highlight the peculiar characteristics of *P. oceanica* beds and their highly dynamic and plastic nature in undergoing structural changes to produce different habitats, including bare matte, which support macrofaunal assemblages having a high diversity, and that may differ in species composition.

Appendix

Motile macroinvertebrates recorded exclusively from either dead or living *Posidonia oceanica* matte. The total number of individuals (from all 16 cores) for species collected on the respective matte type is indicated. Sp. 'A' and 'B' refer to unidentified species of the respective family.

Taxon	Dead matte	Living matte
Polychaeta		
Aphroditidae sp.		2
Arabella sp.	4	
Capitellidae sp.		1
Diopatra sp.		7
Eunice sp.	3	
Glycera sp.	8	
Goniada emerita Audouin & Milne-Edwards, 1833	2	
Lepidonotus squamatus (Linnaeus, 1758)	2	
Lumbriclymene cf *minor* Arwidsson, 1907	2	
Lysidice ninetta Audouin & Milne-Edwards, 1833		1
Marphysa sanguinea (Montagu, 1815)	1	
Nepthys sp.	3	
Nepthydae sp. A		1
Nereidae sp. B	1	
Polyopthalmus sp.	1	
Phyllodocidae sp. A	1	
Phyllodocidae sp. B	1	
Serpulidae sp.		2
Total	29	14
Mollusca		
Leptochiton cancellatus (Sowerby, 1840)		1
Lepidopleurus cajetanus (Poli, 1791)		1
Aclis ascaris (Turton, 1819)	3	
Alvania discors (Allan, 1818)		25
Berthella sp.		1
Bittium latreillii (Payraudeau, 1826)	1	
Bulla striata Bruguière, 1792	1	
Cerithium vulgatum Bruguière, 1792	4	
Colubraria reticulata (de Blainville, 1826)	1	
Emarginula octaviana Coen, 1939	1	
Gibbula guttadauri (Philippi, 1836)	2	
Gibbula umbilicaris (Linnaeus, 1758)		3
Haminoea hydatis (Linnaeus, 1758)	23	
Hexaplex trunculus (Linnaeus, 1758)		2
Mangelia sp.	1	
Mangiliella taeniata (Deshayes, 1835)	5	
Mitra corniculum (Linnaeus, 1758)	1	
Mitrella minor (Scacchi, 1836)	6	
Ocinebrina edwardsi (Payraudeau, 1826)	1	
Odostomia conoidea (Brocchi, 1814)	1	
Parvioris anderswareni Van Artsen & Savelli, 1991		1
Philine aperta (Linnaeus, 1767)	2	
Raphitoma codieri (Payraudeau, 1826)	1	
Raphitoma philberti (Michaud, 1829)	1	
Thracia papyracea (Poli, 1791)	1	
Tricolia speciosa (Von Mühlfeldt, 1824)		11
Trivia pulex (Solander in J. E. Gray, 1828)	1	
Turbonilla jeffreysii (Jeffreys, 1848)	1	
Turbonilla lactea (Linnaeus, 1758)		1
Vitreolina philippi (Rayneval & Ponzi, 1854)		1
Ascobulla fragilis (Jeffreys, 1856)	1	
Glans aculeata (Poli, 1795)	3	
Lima hians (Gmelin, 1791)	6	
Loripes lucinalis (Lamarck, 1818)		2
Modiolus barbatus (Linnaeus, 1758)	1	
Tellina balaustina (Linnaeus, 1758)	1	
Sepia sp.		1
Total	70	50
Crustacea		
Cumacea sp.		2
Nebalia bipes (O. Fabricius, 1780)		8
Ampelisca cf *rubella* A. Costa, 1864		60
Amphithoe helleri G. Karaman, 1975	11	
Atylus guttatus (A. Costa, 1851)		5
Atylus vedlomensis (Bate & Westwood, 1862)		3
Caprella acanthifera Leach, 1814	45	

Appendix Table (Contd.)

Dexamine cf *spiniventris* (A. Costa, 1853)	1	
Harpinia sp.	1	
Iphimedia minuta G.O. Sars, 1864		3
Leptocheirus guttatus (Grube, 1864)	554	
Lysianassa costae Milne Edwards, 1830	105	
Lysianassa longicornis Lucas, 1849	46	
Melita hergensis Reid, 1939		
Pereionotus testudo (Montagu, 1808)	3	1
Phoxocephalidae sp.	2	
Stenothoe sp.	3	
Urothoe cf *intermedia* Bellan Santini & Ruffo, 1986	2	
Dynamene tubicauda Holdich, 1968	1	
Eurydice sp.		2
Gnathia sp.	13	
Idotea cf *emarginata* (Fabricius, 1793)		1
Synisoma cf *lancifer* (Miers, 1881)		1
Zenobiana prismatica (Risso, 1826)		2
Alpheus macrocheles (Hailstone, 1835)	4	
Anapagurus sp.	4	
Galathea bolivari Zariquiey Alvarez, 1950	93	
Gourretia denticulata (Lütze, 1937)	3	
Ilia nucleus (Linnaeus, 1758)	1	
Paguristes cf *eremita* (Linnaeus, 1767)	1	
Palaemon xiphias Risso, 1816		2
Philocheras fasciatus (Risso, 1816)		4
Thoralus cranchii (Leach, 1817)	14	
Upogebia mediterranea Noël, 1992	15	
Total:	1062	194
Echinodermata		
Ophiomyxa pentagona (lamarck, 1816)	5	
Asterina gibbosa (Pennant, 1777)		9
Total	5	9

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