RESEARCH ARTICLE

Comparative analysis of macrofaunal species richness and composition in *Posidonia oceanica*, *Cymodocea nodosa* and leaf litter beds

S. Como · P. Magni · M. Baroli · D. Casu · G. De Falco · A. Floris

Abstract We investigated macrofaunal species richness and composition in *Posidonia oceanica, Cymodocea nodosa* and *Leaf litter* beds within a coastal area of the Gulf of Oristano in proximity of the Cabras lagoon (western Sardinia, Italy). A total of 124 taxa were found, of which 116 were identified at the species level. They were analyzed based on both taxonomic and substrate affinity classification. Presence/absence analysis revealed that *P. oceanica, C. nodosa* and *Leaf litter* were all characterized by a conspicuous number of soft-bottom polychaetes (e.g., *Prionospio multibranchiata* and *Ampharete acutifrons*) and crustaceans (e.g., *Corophium sextonae* and *Dynamene bidentatus*), also known as detritivores. There were also major differences between the three habitats investigated. Consistent with its structural complexity,

P. oceanica showed the highest species richness $[E(S_{50})]$ and the most diversified macrofaunal assemblages, both in terms of taxonomic groups and taxa associated with different substrates. The two seagrasses, however, showed a similar species composition and differed from *Leaf litter* for the exclusive presence of hard-bottom species (e.g., the tunicate *Phallusia fumigata*) and seagrass-associated species (e.g., the polychaete *Syllis garciai* and the decapod *Paguristes syrtensis*). In contrast, *Leaf litter* showed the most differences between the habitats, and was characterized by the bivalves *Abra alba* and *Cerastoderma glaucum*, not found in seagrass beds, and by *Loripes lacteus* and *Ruditapes decussatus*. *Leaf litter* also had the highest content of organic matter (26.7% ± 1.4) and total organic carbon (10.3% ± 0.4). Our results confirmed the facilitative role of living seagrasses, in particular *P. oceanica*, as related to their structural complexity, for numerous species from different substrates (e.g., hard bottom species). This study also showed that leaf litter beds act as a particular environment where sediment instability, leaf breakdown, and organic matter enrichment and decomposition strongly influence animal distribution. Finally, our results highlighted the ecological and trophic importance of seagrass-derived detritus and the associated macroinvertebrate detritivores within seagrass-dominated systems.

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Introduction

Seagrass beds in coastal marine ecosystems are an optimal habitat for benthic fauna and vagile animals, including juvenile fish, as they increase the complexity of the space and the availability of food, provide refuge from predators, stabilize the sediment and improve water clarity (Orth et al.

1984; Mazzella et al. 1992; Boström et al. 2006). In the Mediterranean Sea, two seagrass species, the endemic *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Ascherson, develop the most common and widespread meadows and, often in association, play a central role in structuring coastal marine habitats in the region (Mazzella et al. 1993; Buia et al. 2000; Gambi et al. 2006; and references therein). Several studies indicate the facilitative role of both the seagrasses in terms of colonization and increased diversity of benthic assemblages. This facilitation is found to be species-specific as it depends on the seagrass morphology, life cycle and consequently on the capability to create habitats with different degrees of complexity (Mazzella et al. 1992, 1993; Gambi et al. 1995; Scipione et al. 1996; Sánchez-Jerez et al. 1999; Sfriso et al. 2001; Brito et al. 2005). *P. oceanica* and *C. nodosa*, in particular, have different growth rates, reproductive modes and plant sizes, and show differences in terms of size and structural complexity, as well as in temporal and spatial distribution (Mazzella et al. 1993; Marbà et al. 1996; Cancemi et al. 2002; Guidetti et al. 2002). *P. oceanica* is a large, long-lived and slow-growing seagrass species (Mazzella et al. 1993; Marbà et al. 1996; Guidetti et al. 2002). *C. nodosa* is smaller and shows faster colonization rates, as well as greater morphological and physiological plasticity in response to environmental variability (Marbà et al. 1996; Cancemi et al. 2002; Guidetti et al. 2002). *C. nodosa* often replaces *P. oceanica* in coastal areas, affected by both natural and human disturbances (Cancemi et al. 2000, 2002). *C. nodosa* also shows a lower structural complexity than *P. oceanica* (Marbà et al. 1996; Cancemi et al. 2002; Guidetti et al. 2002). This might support less diverse macrofaunal assemblages (Lanera and Gambi 1993; Terlizzi and Russo 1998; Brito et al. 2005) compared to those associated with *P. oceanica* (Giangrande 1986; Mazzella et al. 1989; Gambi et al. 1995). In spite of these evidences, however, there have been relatively few comparative studies done on macrofaunal assemblages associated with these seagrasses, most of which focus on the epifauna associated with the canopy (Scipione et al. 1996; Sánchez-Jerez et al. 1999; Cebrián et al. 2001). To our knowledge, no studies are available which compare macrofaunal assemblages associated with the rhizomes, roots and sediments of *P. oceanica* and *C. nodosa*.

In the presence of *P. oceanica* and *C. nodosa* meadows, a third habitat is also commonly found. This is represented by adjacent areas of unvegetated sediments where seagrass-derived detritus accumulate. These habitats have also been shown to play an important ecological role, such as in the case of the *P. oceanica* "banquettes" (Mateo and Romero 1996). Studies on exposed beaches (Dugan et al. 2003; Ince et al. 2007) and intertidal areas (Rossi and Underwood 2002; Rossi 2007) demonstrated that the litter derived from seagrass and macroalgae promotes a distinct type of habitat for benthic invertebrates, and the leaf breakdown and organic matter decomposition significantly influence animal distribution. The influence of the litter in structuring benthic assemblages has also been demonstrated in other coastal systems such as those dominated by mangroves (Gee and Somerfield 1997; Lee 1999; Morrisey et al. 2003) and reeds (Mancinelli et al. 2005). Nevertheless, analogous observations of the infauna associated with seagrass leaf litter in near-shore, subtidal areas are relatively scarce (Vetter 1995; Norkko et al. 2000; Hyndes and Lavery 2005), especially in the Mediterranean Sea (Mancinelli and Rossi 2002; Gallmetzer et al. 2005; Dimech et al. 2006). Overall, there are no studies comparing species composition and diversity of macrofaunal assemblages in *Posidonia oceanica*, *Cymodocea nodosa* and seagrass-derived leaf litter beds.

The present study was conducted in a coastal area of the Gulf of Oristano (western Sardinia, Italy) characterized by extended patches of *P. oceanica* and *C. nodosa* meadows. The Gulf of Oristano is a highly productive and diverse system, due to the presence of extended meadows of *P. oceanica*, which covers about 70% of the total seabed surface of the gulf (150 km^2 wide) (Cancemi et al. 2000; De Falco et al. 2006). The gulf is directly connected to salt marshes and brackish lagoons, which cover an area of about 46 km^2 and represent one of the most important brackish systems in Italy. Our previous works have focused on the sediment features and benthic fauna of some of these systems (De Falco et al. 2004; Magni et al. 2004, 2005, 2006; Como et al. 2007). In this study, we focused on the belowground systems of *P. oceanica* and *C. nodosa* meadows, and seagrass-derived leaf litter beds, which were considered as three distinct habitats. We aimed to test for differences between the three habitats in terms of sediment characteristics and macrofaunal assemblages, with a special focus on macrofaunal species richness and composition.

Material and methods

Study area

The study area was located in the northern sector of the Gulf of Oristano (western Sardinia, Italy), in proximity to the inlet of the Cabras lagoon (Fig. 1). This area, previously mapped by aerial photogrammetry integrated by in situ morphostructural measurements (Cancemi et al. 2000), is colonized by extended patches of *Posidonia oceanica* and *Cymodocea nodosa* meadows within a water depth of 2–8 m. The structure of *P. oceanica* was also measured during this study in eight 40 × 40 cm quadrats. Shoot

Fig. 1 Location of the study area (*square box, right panel*) in the Gulf of Oristano (western Sardinia, western Mediterranean Sea)
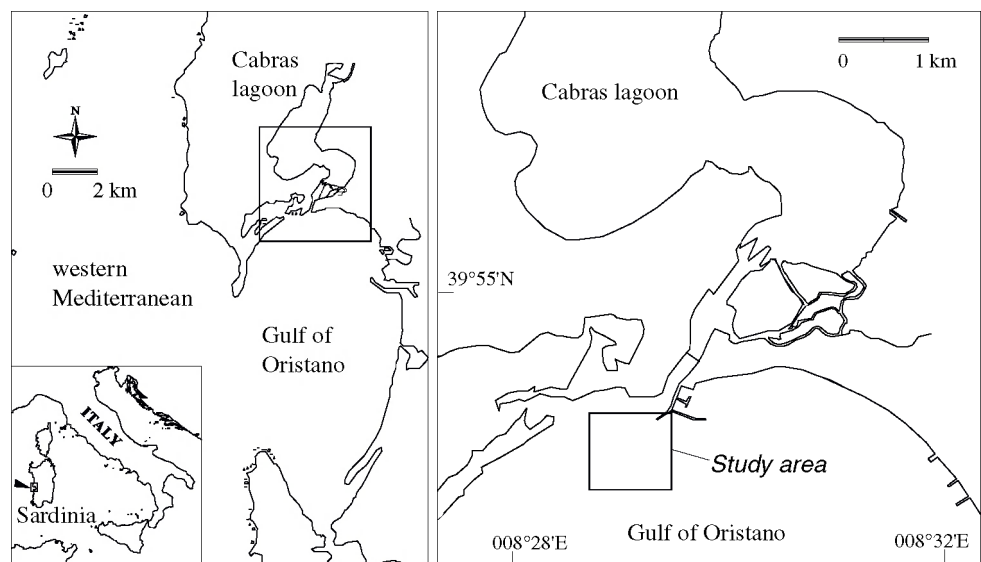
density was 298.4 ± 17.6 shoot/m², Leaf Area Index was 6.24 ± 2.42 m²/m², and total production was 2.610 ± 86 mg dry weight/year/shoot. These values are similar to those described in other parts of the Gulf of Oristano at comparable depths and seasons (Cancemi et al. 2000; De Falco et al. 2000). Within our study area, unvegetated sediments covered by exported seagrass detritus, hereafter called "*Leaf litter*", are also present.

Sample collection and laboratory analysis

Three distinct habitats were considered: *P. oceanica, C. nodosa* and *Leaf litter*. In July 2003, four plots were randomly chosen within each habitat in the study area. At each plot, one sediment sample for chemical analyses and one sediment sample for macrofauna were collected. Sediment samples for chemical analyses were taken using a manual PVC corer (5.5 cm inner diameter). In *P. oceanica* and *C. nodosa*, macrofauna samples were collected, once leaves were removed, with an airlift sampler from a 40×40 cm quadrat. In the *Leaf litter*, macrofauna samples were collected using a 216-cm⁻² Ekman-Birge grab. All macrofaunal samples were retained through a 500-μm mesh and preserved in 5% buffered formalin in seawater.

In the laboratory, sediment samples for chemical analyses were first checked visually in order to eliminate the coarsest fraction of seagrass debris. Organic matter (OM) was then determined from a sub-sample (ca. 1 g) by loss of ignition at 500°C for 3 h. Total carbon (TC), total organic carbon (TOC) and total nitrogen (TN) were determined by means of an CHNS elemental analyzer as described in Como et al. (2007). The sub-samples for TOC were decarbonated using 1 M HCl and dried at 60°C. The

reproducibility was satisfactory with an average relative standard deviation for replicate analyses of 0.5% for TC, 0.9% for TOC and 1.3% for TN. The inorganic carbon (C_{Inorg}) content was calculated as the difference between TC and TOC. Macrofauna were sorted, identified to the species level (when possible) and preserved in a solution of 70% ethanol.

Data analysis

Classification of macrofaunal assemblages based on substrate affinity

Each taxon collected was assigned to one or more substrates based on the substrate affinity according to the published literature. Fauvel (1923a, b), Day (1967a, b), and San Martin (1984) were used for polychaetes, Parenzan (1974, 1976) and Riedl (1986) for mollusks, and Ruffo (1982) and Riedl (1986) for crustaceans. When available, additional specific references were also used for some species, as given in Appendix A. The following seven substrates were identified: seagrass (SG), algae (AL), soft-bottom (SB), hard-bottom (HB), soft-bottom brackish (SBB), ubiquitous (UB), and not identified (NI).

Univariate analysis

Differences between habitats in OM, TOC, TN, C/N ratio, and C_{inorg} were tested using the one-way analysis of variance. Homogeneity of variances was checked using Cochran's C-test and, whenever necessary, data were log transformed and newly tested (Underwood 1997).

Significant differences between habitats detected by the analyses of variance, were further analyzed using a posteriori Student–Newman–Keuls (SNK) tests (Underwood 1997).

Species richness based on Hurlbert's $E(S_{50})$ was calculated. $E(S_n)$ is the expected number of species present in an increasingly rarefied sample of n individuals randomly selected (without replacement) from a finite collection of N individuals and S species. With this measure, meaningful comparisons of species richness can be made between the collections of different sizes by adjusting the collections to a common size (n). Thus, this measure was especially suitable for the present study in which we sought to examine species richness among the samples collected with varying types of sampling gear (Hyland et al. 2005) and in habitats with presumable varying degrees of sensitivity to disturbance (Rosenberg et al. 2004). In our study, $E(S_{50})$ was used as sample-size independent diversity measure based on the fact that N was $> n$ (where $n = 50$) in all samples. Differences in $E(S_{50})$ between the habitats were tested using one-way analysis of variance, as above.

Multivariate analyses and analyses on taxa identified by SIMPER

Due to the use of different samplers for collecting macrofauna in seagrass versus leaf litter habitats, abundances were not considered in this study, while a matrix based on the presence/absence of species was used for statistical analysis. The analysis of similarities (ANOSIM) and a non-metric multidimensional-scaling (nmMDS) ordination model based on the Bray–Curtis dissimilarity matrix (Clarke and Warwick 2001) were used. The similarity of percentages procedure (SIMPER) was conducted to identify the species that contribute most (cut-off 60%) to the dissimilarities (Clarke and Warwick 2001).

In order to characterize the macrofaunal assemblages within each habitat (i.e. P. oceanica, C. nodosa and leaf litter), the taxa identified by SIMPER analysis were clustered in two different ways: according to their taxonomic group (i.e., Polychaeta, Crustacea, Mollusca, Oligochaeta, Echinodermata, Pantopoda, and Tunicata) and their assignment to one or more substrates based on the substrate affinity according to the published literature.

Results

Sediments

Organic matter (OM) varied between $12.2\% \pm 2.2$ (*Posidonia oceanica*) and $26.7\% \pm 1.4$ (*Leaf litter*), and

was significantly higher in *Leaf litter*) than in both *P. oceanica* and *Cymodocea nodosa* (OM; 1-way ANOVA, Habitat: $F_{2,9} = 6.41$, $P < 0.05$, and SNK test; $P < 0.05$; Fig. 2a). A similar pattern was described for the total organic carbon (TOC; $F_{2,9} = 8.25$, $P < 0.01$ and SNK test; $P < 0.05$) and total nitrogen (TN; $F_{2,9} = 8.33$, $P < 0.01$ and SNK test; $P < 0.05$), with the highest values in *Leaf litter* ($10.3\% \pm 0.4$ and $0.67\% \pm 0.03$, respectively). In contrast, the C/N ratio did not show significant differences ($P > 0.05$) between the habitats, as it varied between 15.2 (*P. oceanica*) and 18.1 (*Leaf litter*). Inorganic carbon (C_{inorg}) content showed an opposite pattern to that of OM, TOC and TN, being about seven times higher in *P. oceanica* and *C. nodosa* than in *Leaf litter* (1-way ANOVA: Habitat: $F_{2,9} = 18.56$, $P < 0.001$, and SNK test; $P < 0.05$; Fig. 2).
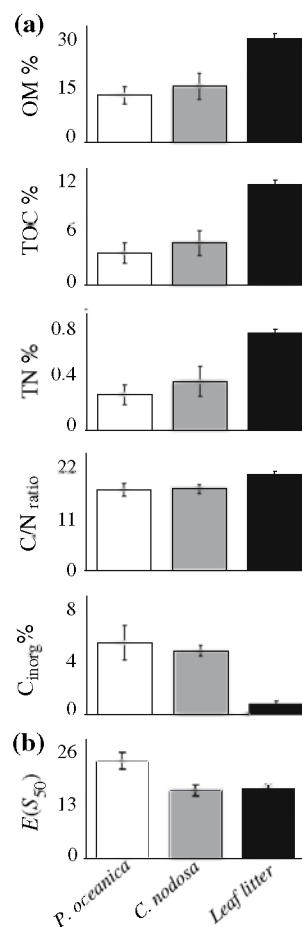

Fig. 2 a Mean ($n = 4$, ±SE) values of organic matter (*OM*), total organic carbon (*TOC*), total nitrogen (*TN*), *C/N* molar ratio, and inorganic carbon (C_{inorg}), and **b** mean ($n = 4$, ±SE) Hurlbert's species richness $E(S_{50})$ in *P. oceanica*, *C. nodosa* and *Leaf litter* within the study area

Macrofaunal assemblages

A total of 124 taxa were identified, 116 at the species level and 8 at higher taxonomic resolution. Syllidae was the family with the highest number of species (19 species, 15% of the total taxa identified). All taxa are included in Appendix A along with their ecological characterization in terms of substrate affinity.

Species richness $[E(S_{50})]$ was higher in *P. oceanica* than in both *C. nodosa* and *Leaf litter* (1-way ANOVA: Habitat: $F_{2,9} = 6.54$, $P < 0.01$; and SNK test, $P < 0.05$; Fig. 2b). The ANOSIM test also revealed differences in species composition between the three habitats (1-way ANOSIM: Global-$R = 0.889$, $P < 0.001$). As indicated by the *nm*MDS plot, macrofaunal assemblages in each habitat were clearly separated from each other (Fig. 3). Table 1 reports the mean Bray–Curtis dissimilarity values both within and between the habitats. The dissimilarities between *P. oceanica* and *C. nodosa* stations were lower than those between them and *Leaf litter*, indicating the presence of different species compositions (Table 1).

Taxa accounting for the greatest dissimilarity between the three habitats (SIMPER, cut-off 60%) included 37 Polychaeta, 17 Crustacea, 5 Mollusca, 3 Echinodermata, 1 Pantopoda, and 1 Tunicata. Several of these taxa were found exclusively in *P. oceanica* and *C. nodosa*, including the polychaetes *Parapionosyllis brevicirra*, *Syllides edentatus*, *Syllis garciai*, *S. prolifera*, *S. gerlachi*, *Pista cretacea*, *P. cristata* and *Ampharete acutifrons*, the crustaceans *Phoxocephalus aquosus*, *Paguristes syrtensis*, *Dynamene bidentatus* and *Gnathia phallonajopsis*, the echinoderms *Phyllophorus urna*, *Asterina gibbosa* and
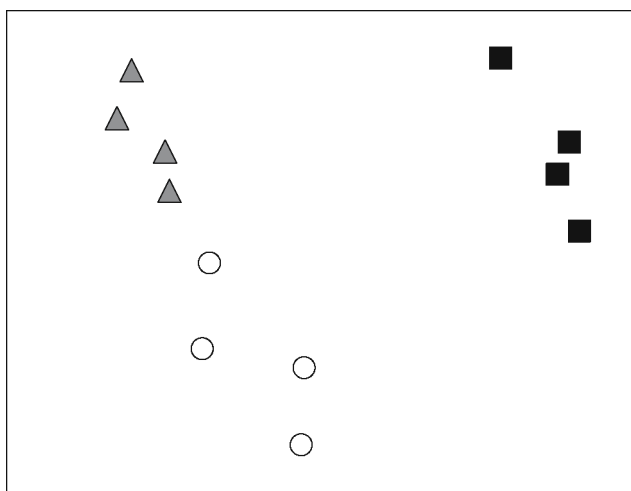
Table 1 Bray–Curtis dissimilarities (%) based on the presence/absence data of macrofaunal assemblages within and between the habitats (*P. oceanica*, *C. nodosa* and *Leaf litter*)

Dissimilarity within habitats (%)		Dissimilarity between habitats (%)	
P. oceanica	51.75	*P. oceanica* vs. *C. nodosa*	60.95
C. nodosa	42.68	*P. oceanica* vs. *Leaf litter*	74.75
Leaf litter	44.01	*C. nodosa* vs. *Leaf litter*	86.16

Amphiura chiajei, the pantopod *Achelia echinata*, and the tunicate *Phallusia fumigata* (see Appendix A). In contrast, the bivalves *Abra alba* and *Cerastoderma glaucum* and the polychaete *Prionospio multibranchiata* were exclusive to *Leaf litter* (Appendix A).

The taxa identified by SIMPER were clustered and further analyzed according to both taxonomic groups and substrate affinity. Results from these two approaches are summarized in Table 2. The analysis of taxonomic groups showed that each of the three habitats were most characterized by polychaetes and crustaceans (Table 2a). This analysis also revealed that in *Leaf litter*, the contribution of mollusks increased, while that of "Others" (including echinoderms, pantopods and tunicates) was nil. In contrast, "Others" were found in both *P. oceanica* and *C. nodosa* (Table 2a).

The analysis of taxa based on the substrate affinity provided additional insights into the ecological traits of macrofaunal assemblages in our study area. In particular, soft bottom species (SB) characterized most each of the three investigated habitats (*P. oceanica*, *C. nodosa* and leaf litter) (Table 2b). Among them, the polychaete *A. acutifrons* was exclusively found in *P. oceanica* and *C. nodosa*, while the polychaete *P. multibranchiata* was exclusively found in *Leaf litter* (Appendix A). In addition to the soft bottom species, the three habitats were also characterized by algal substrate-associated species (AL and combinations; Table 2b). These included *Corophium sextonae*, found in all three habitats, and *D. bidentatus* and *G. phallonajopsis*, found only in *P. oceanica* and *C. nodosa* (Appendix A). Brackish (SBB) and widespread distributed (UB + NI) species were also important within each habitat (Table 2b). In addition to similarities, the analysis of macrofaunal assemblages based on their substrate affinity also showed important differences between *P. oceanica*, *C. nodosa* and *Leaf litter*. In particular, only *P. oceanica* and *C. nodosa* were characterized by hard bottom species (HB), such as the pantopod *A. echinata* and the tunicate *P. fumigata*, and seagrass-associated species (SG and combinations; Table 2b), such as syllids (i.e., *S. garciai*), terebellids (i.e., *P. cretacea*), decapods (i.e. *P. syrtensis*) and echinoderms (i.e., *P. urna* and *A. gibbosa*). Finally, *P. oceanica* showed the most diverse assemblages with

Fig. 3 Non-metric multidimensional-scaling (*nm*MDS) for differences in species composition of macrofaunal assemblages. Stress = 0.05. Symbols: *white circle = P. oceanica, grey triangle = C. nodosa, black square = Leaf litter*

Table 2 Contribution, in percentage (%), of the groups obtained from the presence/absence data of the macrofaunal taxa, which contribute to dissimilarities (cut-off 60%) between the three investigated habitats, *P. oceanica*, *C. nodosa* and *Leaf litter* (SIMPER)

	P. oceanica	*C. nodosa*	*Leaf litter*
(a) Taxonomic groups			
Polychaeta	60.0 (36)	53.3 (16)	50.0 (13)
Crustacea	26.7 (16)	23.3 (7)	34.6 (9)
Mollusca	5.0 (3)	6.7 (2)	15.4 (4)
Others[a]	8.3 (5)	16.7 (5)	0.0 (0)
(b) Substrate(s)			
SB	36.7 (22)	43.4 (13)	46.2 (12)
AL/SB	10.0 (6)	10.0 (3)	15.4 (4)
AL/HB	13.3 (8)	10.0 (3)	7.7 (2)
AL	6.7 (4)	6.7 (2)	3.8 (1)
SBB	3.3 (2)	3.3 (1)	15.4 (4)
UB + NI	10.0 (6)	3.3 (1)	7.7 (2)
HB	1.7 (1)	3.3 (1)	0.0 (0)
SG	5.0 (3)	6.7 (2)	0.0 (0)
SG/SB	8.3 (5)	10.0 (3)	0.0 (0)
SG/HB	1.7 (1)	3.3 (1)	0.0 (0)
SG/AL	1.7 (1)	0.0 (0)	3.8 (1)
SG/AL/HB	1.7 (1)	0.0 (0)	0.0 (0)

Presence/absence data clustered based on (a) taxonomic groups and (b) substrate affinity according to the published literature (see "Materials and Methods"). Substrate: soft-bottom (*SB*), algae (*AL*), hard-bottom (*HB*), soft-bottom brackish (*SBB*), ubiquitous and not identified (*UB + NI*), seagrass (*SG*). In parentheses: number of taxa

[a] This group includes echinoderms, pantopods, and tunicates

taxa belonging to all different substrates [(SG), (AL), (SB), (HB), (SBB), and (UB + NI)] and their possible combinations [(AL/SB), (AL/HB), (SG/SB), (SG/HB), (SG/AL), and (SG/AL/HB)]. In contrast, *C. nodosa* and *Leaf litter* were represented only by taxa belonging to 10 and 7 of the above 12 categories, respectively (Table 2b).

Discussion

Sediment characteristics

A comparison of sediment composition between the three investigated habitats indicated a major organic enrichment in *Leaf litter*, with OM and TOC contents similar to those commonly reported for seagrass detritus (Enríquez et al. 1993 and references therein) and in leaf litter beds of both *Posidonia oceanica* (Cebrian and Duarte 2001) and *Cymodocea nodosa* (Perez et al. 2001). In contrast, inorganic carbon was higher in *P. oceanica* and *C. nodosa* than in *Leaf litter*, which is consistent with the presence of large

amounts of carbonates and biogenic sediments in living seagrass beds (De Falco et al. 2000, 2003). In spite of these differences, the C/N ratio did not vary significantly between the three habitats. While C/N values of about 8–12 are common in estuarine and coastal marine sediments, values above this range tend to occur when the refractory portion of organic matter increases, e.g. in the presence of seagrass and its detritus (Tyson 1995 and references therein). The C/N ratio found in our study area was 17 on average, which is consistent with the presence of *P. oceanica*, *C. nodosa* and seagrass-derived detritus. On the other hand, these values are much lower that those described in other leaf litter beds in the Mediterranean Sea, with averages ranging from about 35 to 48 (Enríquez et al. 1993; Mateo and Romero 1996; Mateo et al. 2003). These differences can be related to the total carbon and nitrogen budget contributed in each system by additional autochthonous and/or allochthonous nitrogen-enriched sources. For instance, it has been shown that bacteria and fungi can grow easily in leaf litter beds (Mateo and Romero 1996; Lepoint et al. 2006), and drift algae can also contribute to the detritus pools within *C. nodosa* meadows (Perez et al. 2001), as well as in supra-littoral leaf litter beds (Mateo et al. 2003). In our study area, it is likely that the nearby transitional system of the Cabras lagoon (Como et al. 2007) and the Tirso river (De Falco et al. 2006) contribute to a certain amount of labile organic matter. This labile organic matter is then entrapped within the interlacing of rhizomes and roots of *P. oceanica* and *C. nodosa*, or accumulated in the leaf litter beds.

Macrofaunal assemblages

Distribution and role of detritivores

The analysis of taxa identified by SIMPER indicated that polychaetes and crustaceans characterized all three different habitats in our study area. They included soft-bottom species, species associated with algal substrates, as well as ubiquitous and brackish species (sensu Guelorget and Perthuisot 1992). These associations of the species reflected the complexity of our study area, also influenced by the Cabras lagoon (Como et al. 2007). In all the three different habitats, i.e. *P. oceanica*, *C. nodosa* and *Leaf litter*, most of these taxa were detritivores. As an example, the polychaetes *Prionospio multibranchiata* found exclusively in *Leaf litter*, and *Ampharete acutifrons* found exclusively in the two seagrasses, are classically reported as soft-bottom deposit feeders (Fauchald and Jumars 1979). Similarly, crustaceans such as the isopod *Dynamene bidentatus*, found in

the *P. oceanica* and *C. nodosa* beds, and the amphipod *Corophium sextonae*, found in all the three investigated habitats, are known to feed on algal detritus (Holdich 1970; Ruffo 1982; Lardicci et al. 2001). *Corophium volutator*, a co-genus species of *C. sextonae*, has recently been shown to efficiently remove detritus derived from *Ulva* spp. in the sediment of a sandflat in the Oosterschelde estuary (The Netherlands) (Rossi 2007). As is consistent with our results, previous studies have shown that detritivores are the main faunal group associated to the rhizome of both *P. oceanica* (Giangrande 1986; Gambi et al. 1995) and *C. nodosa* meadows (Lanera and Gambi 1993). More recently, detritivores have also been described as being dominant in *Posidonia*-derived detritus such as dead "matte" in Mellieha Bay (Malta) (Borg et al. 2006), and in leaf litter beds in the Bay of Calvi (Corsica) (Gallmetzer et al. 2005) as well as in the Qortin and Armier bays (Malta) (Dimech et al. 2006). In fact, besides the well known structural complexity and facilitative role of seagrasses favoring animal colonization and increased diversity, increasing attention is being paid to the role of seagrass-derived detritus and the associated detritivores in the functioning of seagrass-dominated systems. In particular, food web studies in seagrass and leaf litter beds using $\delta^{13}C$ and $\delta^{15}N$ analysis have shown that the detrital pathway is the main way of transferring seagrass-derived organic matter to higher trophic levels, and that the associated macroinvertebrate detritivores can efficiently exploit *P. oceanica* detritus as both a carbon and a nitrogen source (Vizzini et al. 2002; Hyndes and Lavery 2005; Lepoint et al. 2006). Our results pointed in the same direction, suggesting that a functional link between the dominance of detritivores and the presence of relatively enriched detritus of both autochthonous (e.g., algae, bacteria, seagrass-derived) and allochthonous (lagoonal and riverine) origins exists for our study area, too.

Habitat comparison

Multivariate analyses revealed that macrofaunal assemblages in *P. oceanica* and *C. nodosa* were more similar to each other than to those found in *Leaf litter*. Based on a taxonomic classification (Table 2a), the analysis of SIMPER taxa revealed that the group "Others" contributed to the similarity between *P. oceanica* and *C. nodosa*. This group included pantopods (i.e. *Achelia echinata*) and tunicates (i.e. *Phallusia fumigata*), common on hard bottoms, and echinoderms (i.e. *Phyllophorus urna* and *Asterina gibbosa*), typically found in seagrass beds (Mazzella et al. 1992). Other species typically found in seagrass beds, such

as the polychaetes *Syllis garciai* and *Pista cretacea* and the decapod *Paguristes syrtensis* (Somaschini et al. 1994; Brito et al. 2005), further discriminated *P. oceanica* and *C. nodosa* from *Leaf litter*.

Numerous studies have emphasized the facilitative role of seagrasses on the development of abundant and diverse macroinfaunal assemblages, as related to the belowground structural complexity of the interlacing rhizome layer and roots in the sediments, and favoring the successful recruitment and colonization of animals (Orth et al. 1984; Mazzella et al. 1992, 1993; Boström et al. 2006). Syllids, for instance, are interstitial animals whose presence in the rhizome layer of seagrasses has been related to the availability of interstices and crevices both in *C. nodosa* (Brito et al. 2005) and *P. oceanica* meadows (Somaschini et al. 1994). The successful recruitment of a number of hard-bottom species, as found in this study, may also be linked to the architectural complexity of the rhizome layer which stabilizes the sediment creating a more favorable environment than un-consolidated sediments as far as the successful recruitment of these species is concerned. Furthermore, the presence of holothurians in the rhizome-layer has been reported to favor sediment reworking thereby playing a positive feedback in the nutrient dynamics of entire seagrass meadows (Mazzella et al. 1992).

In addition to the differences found between seagrasses and *Leaf litter*, we also detected clear differences in the macrofaunal assemblages of *P. oceanica* and *C. nodosa*. Although a number of previous studies have focused on the belowground assemblages of either *P. oceanica* (Giangrande 1986; Gambi et al. 1995) or *C. nodosa* (Gambi et al. 1998; Terlizzi and Russo 1998; Sfriso et al. 2001; Brito et al. 2005), this is the first comparative study of these assemblages to our knowledge. In particular, here we show that belowground assemblages in *P. oceanica* have higher species richness [$E(S_{50})$] and are more diverse than those in *C. nodosa* (Fig. 2b; Table 2). Our results are consistent with the (few) comparative studies conducted on macrofaunal assemblages associated with the canopy of these two seagrasses, which also reported a higher diversity in *P. oceanica* than in *C. nodosa* (Scipione et al. 1996; Sánchez-Jerez et al. 1999; Cebrián et al. 2001). The observed results are also in agreement with Giangrande (1986) and Gambi et al. (1995) who studied polychaete assemblages in the rhizome layer of *P. oceanica* at Ischia Island (Italy) and Porto Conte bay (Sardinia, Italy), respectively. As for our study, the analysis of taxa based on their substrate affinity revealed highly diverse macrofaunal assemblages. As expected, differences in the morphology and size between *P. oceanica* and *C. nodosa*

may account for the differences in macrofaunal assemblages found in this study. In particular, the interlacing of rhizomes and roots of *P. oceanica* is known to form a belowground system which is more complex than that developed by the smaller *C. nodosa* which has thinner and shorter-living rhizomes (Mazzella et al. 1993; Marbà et al. 1996; Cancemi et al. 2002; Guidetti et al. 2002). A more developed rhizome layer of *P. oceanica* may thus increase the complexity and the availability of different microenvironments and allow the presence of more species.

The third habitat investigated in this study, *Leaf litter*, differed most from the others. In particular, the analysis of SIMPER taxa revealed that mollusks, in addition to polychaetes and crustaceans, characterized *Leaf litter*. With the exception of the gastropod *Haminoea navicula* rest of them were bivalves (i.e., *Abra alba*, *Cerastoderma glaucum*, *Loripes lacteus* and *Ruditapes decussatus*). These results are in accordance with Mancinelli and Rossi (2002) who described several bivalve species, including *Ruditapes* sp., in seagrass leaf litter beds of the Po River delta (northwestern Adriatic Sea). The presence of bivalves in the leaf litter beds may be related to their relative tolerance of disturbance. In their review, Snelgrove and Butman (1994) presented several studies of successful recruitment of bivalves and their larvae in organic-enriched sediments and low oxygen conditions. Consistently, Gray et al. (2002) found that there is a decrease in sensitivity for sulfide in the sequence of fish, crustaceans and echinoderms, annelids and molluscs. The occurrence of high abundances of the crustacean *Nebalia bipes* in leaf litter beds of *P. oceanica* in the Bay of Calvi (Corsica) has also been related to occasional oxygen depletion as a result of organic matter decomposition (Gallmetzer et al. 2005). In our study area, organic enrichment of sediments was extremely high in *Leaf litter*, as indicated by the OM and TOC contents. Consistently, in our companion study conducted in the adjacent inlet of the Cabras lagoon, the highest acid-volatile sulfide concentrations were found seaward in the presence of seagrass-derived leaf litter with TOC and OM contents similar to those reported in this study (Como et al. 2007). This might also explain the bivalve association found in *Leaf litter* within our study area. It should also be noted that the absence of the interlacing of roots and rhizomes in *Leaf litter*, which otherwise binds the sediment in living seagrasses (Orth et al.1984), may have contributed to a reduced sediment

stability. This would account for a different species composition (Lee 1999; Morrisey et al. 2003; Gallmetzer et al. 2005), as well as influencing the recruitment of benthic individuals (Snelgrove and Butman 1994; Mancinelli and Rossi 2002).

Conclusions

This is the first study comparing species composition and richness of macrofaunal assemblages in *Posidonia oceanica*, *Cymodocea nodosa* and seagrass-derived leaf litter beds. This study confirms the facilitative role of living seagrasses on the successful colonization of numerous species from different substrates (e.g., hard bottom species), as related to the varying degree of the structural complexity of these seagrasses. Consistently, the highest species richness [$E(S_{50})$] and the most diversified macrofaunal assemblages were found in *P. oceanica*. This study also showed that leaf litter beds act as a particular environment where sediment instability, leaf breakdown, and organic matter enrichment and decomposition strongly influence animal distribution. In fact, *Leaf litter* showed the most differences between the three investigated habitats in terms of species composition, being characterized by mollusks (e.g., *Abra alba* and *Cerastoderma glaucum*) in addition to polychaetes and crustaceans. Finally, our results highlighted the ecological and trophic importance of seagrass-derived detritus and the associated macroinvertebrate detritivores within seagrass-dominated systems.

Appendix A

Table 3

Table 3 List of taxa and their distribution [(presence (+)/absence)] between habitats (i.e. *P. oceanica*, *C. nodosa* and *Leaf litter*)

Taxa	Substrate(s)	P. oceanica						C. nodosa					Leaf litter			
Gastropoda																
Nassariidae																
Cyclope neritea (Linnaeus, 1758)	SB															+
Marginellidae																
Gibberula miliaria (Linnaeus, 1758)	SB		+													
Haminoeidae																
Haminoea navicula (da Costa, 1778)[a]	AL/SB	+	+	+	+	+	+									
Bivalvia																
Semelidae																
Abra alba (Wood, 1802)[a]	SB												+	+	+	
Cardiidae																
Cerastoderma glaucum (Poiret, 1789)[a]	SSB												+	+	+	
Veneroida																
Circonphalus sp.	NI										+					
Loripes lacteus (Linnaeus, 1758)[a]	SB									+			+	+	+	
Ruditapes decussatus (Linnaeus, 1758)[a]	SB	+								+			+	+	+	
Mytiloida																
Modiolus barbatus (Linnaeus, 1758)	HB	+														
Solemyoidea																
Solemya togata (Poli, 1795)	SG/ SB			+												
Arcoidea																
Tetrarca tetragona Poli, 1795	HB		+													
Oligochaeta																
Tubificidae nc	NI		+	+									+	+		
Polychaetes																
Orbiniidae																
Phylo foetida (Claparède, 1870)[a]	SB	+		+		+			+				+	+	+	+
Spionidae																
Polydora ciliata (Johnston, 1838)	HB/SB [1]														+	
Prionospio cirrifera Wirén, 1883	SB [1,2]		+													
Prionospio malmgreni Claparède, 1870[a]	SB [1,2]	+	+	+					+	+	+				+	+
Prionospio multibranchiata Berkeley and Berkeley, 1927[a]	SB [1,2]												+	+		+
Spio decoratus Bobretzky, 1870	SB [1]															+
Streblospio shrubsolii (Buchanan, 1890)	SB [1]														+	
Paraonidae																
Aricidea cerrutii Laubier, 1967[a]	SB [3]	+				+		+	+							
Cirrophorus furcatus (Hartman, 1957)	SB [3]										+					
Paradoneis armata Glémarec, 1966	SB [4]															+
Paradoneis lyra (Southern, 1914)[a]	SB		+	+		+		+	+		+					
Cirratulidae																
Aphelochaeta marioni (Saint-Joseph, 1894)	SB [5,6]			+							+	+				
Caulleriella bioculata (Keferstein, 1862)	SB			+				+							+	
Caulleriella caputesocis (Saint-Joseph, 1894)	SB	+														
Cirriformia tentaculata (Montagu, 1808)	SB									+						
Monticellina dorsobranchialis (Kirkegaard, 1959)[a]	SB [5,6]			+		+		+	+		+	+				
Capitellidae																
Capitella cf *capitata*	SB	+	+						+	+			+			+
Heteromastus filiformis (Claparède, 1864)[a]	SB [5,6]									+			+	+		

Table 3 continued

Taxa	Substrate(s)	P. oceanica				C. nodosa			Leaf litter			
Mediomastus capensis Day, 1961	SB		+									
Notomastus latericeus M. Sars, 1851[a]	SB [5, 6]	+								+		+
Maldanidae												
Euclymene santanderensis (Rioja, 1917)	SB [5, 6]	+										
Opheliidae												
Armandia cirrhosa Philippi, 1865	UB [7]						+		+			
Polyophthalmus pictus (Dujardin, 1839)[a]	AL/HB	+	+						+			
Phyllodocidae												
Eteone picta Quatrefages, 1865[a]	AL/SB	+	+	+	+	+	+	+	+	+		+
Genetyllis rubiginosa (Saint-Joseph, 1888)	SB	+	+	+					+	+	+	+
Mystides limbata Saint-Joseph, 1888	SB								+			
Spherodoridae												
Sphaerodorum gracilis (Rathke, 1843)	SB [8]			+								
Hesionidae												
Hesiospina cf similis	SB		+									
Podarkeopsis capensis (Day, 1963)[a]	SBB [9]	+							+		+	+
Syllidae												
Branchiosyllis exilis (Gravier, 1900)[a]	SG			+	+							
Paraehlersia ferrugina (Langerhans, 1881)	AL/HB [10]		+									
Exogone dispar (Webster, 1879)[a]	SB	+	+	+	+							
Exogone rostrata Naville, 1933	AL/HB [10]		+				+					
Haplosyllis spongicola (Grube, 1855)[a]	AL/HB [10]	+				+						
Parapionosyllis brevicirra Day, 1954[a]	SB	+	+	+	+	+	+	+				
Pionosyllis anophthalma Capaccioni and San Martin, 1989[a]	AL/HB [10]	+	+	+	+				+	+	+	
Pionosyllis longocirrata Saint Joseph, 1887	AL/HB [10]		+									
Trypanosyllis coeliaca Claparède, 1868	AL/HB		+									
Sphaerosyllis austriaca Banse, 1959	AL/HB										+	
Sphaerosyllis hystrix Claparède, 1863[a]	AL/SB					+	+		+		+	+
Sphaerosyllis pirifera Claparède, 1868	SB [11]					+						
Sphaerosyllis taylori Perkins, 1981	SB/HB [12]					+			+			
Syllides edentatus Westheide, 1974[a]	SG/SB		+	+	+	+	+	+				
Syllis garciai (Campoy, 1982)[a]	SG [13]		+	+	+	+	+					
Syllis prolifera Krohn,1852[a]	AL/HB [10]		+	+		+	+	+				
Syllis gerlachi (Hartmann-Schröder, 1960)[a]	AL/HB		+	+			+					
Syllis variegata Grube, 1860	AL/HB [10]	+										
Xenosyllis scabra (Ehlers, 1864)	SB [10]		+									
Nereididae												
Hediste diversicolor (O.F. Müller, 1776)	SBB								+			
Neanthes caudata (Delle Chiaje, 1828)	SG/SB [14]	+		+	+	+	+		+	+	+	+
Platynereis dumerilii (Audouin and Milne-Edwards, 1833)[a]	SG/AL/HB [10]	+	+									
Nephtyidae												
Nephtys hombergii Savigny, 1818[a]	SB				+	+	+	+	+	+		+
Polynoidae												
Harmothoe cf johnstoni	SB	+										
Harmothoe sp.[a]	NI	+	+									
Sigalionidae												
Pholoe minuta (Fabricius, 1780)[a]	AL/HB [10]	+	+	+	+							
Chrysopetalidae												

Table 3 continued

Taxa	Substrate(s)	P. oceanica				C. nodosa				Leaf litter			
Chrysopetalum debile (Grube, 1855)	AL/HB [10]		+										
Onuphidae													
Diopatra neapolitana Delle Chiaje , 1841[a]	SB			+	+						+		
Onuphis sp.	NI	+											
Eunicidae													
Nematonereis unicornis (Grube, 1840)	UB[10]	+											
Lumbrineridae													
Lumbrineris tetraura (Schmarda, 1861)[a]	SB	+		+									
Arabellidae													
Arabella iricolor (Montagu, 1804)[a]	SB [10]				+	+	+	+					
Dorvilleidae													
Pettiboneia urciensis Campoy and SanMartin, 1982	SB					+		+			+		
Protodorvillea kefersteini (Mc Intosh, 1879)[a]	UB		+							+	+	+	
Schistomeringos rudolphii (Delle Chiaje, 1828)	SB		+	+							+		
Flabelligeridae													
Piromis eruca (Claparède, 1870)[a]	SG/SB			+	+								
Ampharetidae													
Ampharete acutifrons (Grube, 1860)[a]	SB	+	+	+	+	+	+						
Terebellidae													
Eupolymnia sp.[a]	NI	+		+									
Pista cretacea (Grube, 1860)[a]	SG/SB	+	+	+	+	+	+	+	+				
Pista cristata (O.F. Müller, 1776)[a]	SB				+	+	+		+				
Pista sp.[a]	NI	+	+		+								
Terebellidae nc[a]	NI	+		+									
Sabellidae													
Amphiglena mediterranea (Leydig, 1851)	AL/HB [10]					+							
Chone collaris Langerhans, 1880	SG/AL/HB		+										
Chone dunerificta n. sp.[a]	SG/SB	+	+										
Amphipoda													
Ampeliscidae													
Ampelisca brevicornis (Costa, 1853)[a]	SB	+	+	+	+								
Ampelisca diadema (Costa, 1853)	SB			+							+		
Amphilochidae													
Amphilocus neapolitanus Della Valle, 1893	SB/SG/AL		+		+								
Corophidae													
Corophium sextonae Crawford 1937[a]	AL/SB	+	+	+	+	+				+	+	+	+
Dexaminidae													
Dexamine spiniventris (Costa, 1853)[a]	AL/SB	+	+										
Dexamine spinosa (Montagu, 1813)	AL/SG/SB	+									+		
Ischydoceridae													
Erichtonius brasiliensis (Dana, 1853)	AL/SG	+											
Gammaridae													
Gammarus aequicauda (Martynov, 1931)[a]	SBB	+	+							+	+		
Iphimediidae													
Iphimedia brachignatha Ruffo and Schiecke, 1979	AL/HB				+								
Leucothoidae													
Leucothoe venetiarum Giordani-Soika, 1950	SG/AL		+							+	+		
Meltidae													

Table 3 continued

Taxa	Substrate(s)	P. oceanica				C. nodosa				Leaf litter			
Maera grossimana (Montagu, 1808)[a]	AL/HB			+	+								
Aoridae													
Microdeutopus gryllotalpa Costa, 1853[a]	SBB					+				+	+		
Phliantidae													
Pereionotus testudo (Montagu, 1808)	SG/AL					+	+						
Poxocephalidae													
Phoxocephalus aquosus Karaman, 1985[a]	SB	+	+	+	+	+	+	+					
Caprellidae													
Pseudolirius kroyeri (Haller, 1879)[a]	SB		+				+			+	+	+	+
Pseudoprotella phasma (Montagu, 1804)	AL		+				+						
Ptisica marina Slabber, 1769[a]	SG/AL		+							+	+	+	+
Cumacea													
Nannastacidae													
Campylaspis glabra Sars, 1878	SB									+	+		
Diastylidae													
Diastylis rugosa Sars, 1865[a]	SB			+			+			+	+	+	+
Nannastacidae													
Hippolyte inermis Leach, 1815	SG/AL	+											
Bodotriidae													
Iphinoe serrata Norman, 1867[a]	AL/SB	+								+	+	+	+
Decapoda													
Diogenidae													
Paguristes syrtensis de Saint Laurent, 1971[a]	SG [15]	+	+	+	+	+	+	+	+				
Isopoda													
Arcturidae													
Arcturella dilatata (Sars, 1883)[a]	AL		+	+	+								
Sphaeromatidae													
Cymodoce truncata Leach, 1814	HB	+										+	
Dynamene bidentatus (Adams, 1800)[a]	AL [16]					+	+	+	+				
Gnathidae													
Gnathia phallonajopsis Monod, 1925[a]	AL				+	+	+	+	+				
Mysida													
Mysidae													
Anchialina agilis (Sars, 1877)	SB/HB					+							
Ostracoda													
Ostracoda nc[a]	NI					+	+		+	+	+		
Tanaidacea													
Apseudidae													
Apseudes latreillii (Milne-Edwards, 1828)	SB		+										
Paratanaidae													
Leptochelia savigny (Kroyer, 1842)	AL		+										
Tanais dulongii (Audouin, 1826)[a]	AL[17]	+								+	+		
Echinodermata													
Holothuroidea													
Phyllophorus urna Grube, 1840[a]	SG/SB		+	+	+	+	+	+	+				
Echinoidea													
Genocidaris maculata A. Agassiz, 1869	SB/HB					+							
Asteroidea													

Table 3 continued

Taxa	Substrate(s)	P. oceanica	C. nodosa	Leaf litter
Asterina gibbosa (Pennant, 1777)[a]	SG/HB	+ +	+	+
Ophiuroidea				
Amphiura chiajei Forbes, 1843[a]	SB	+ +	+ +	
Pantopoda				
Achelia echinata Hodge, 1864[a]	AL/HB	+	+	+
Callipallene emacinata (Dohrn, 1881)	AL/HB	+		
Tunicata				
Ascidiacea				
Phallusia fumigata Grube, 1864[a]	HB	+ + +	+ +	+ +

Each taxon was assigned to one or more substrates based on the substrate affinity according to the published literature: soft-bottom (*SB*), algae (*AL*), hard-bottom (*HB*), soft-bottom brackish (*SBB*), ubiquitous (*UB*), not identified (*NI*), and seagrass (*SG*). Substrate assignment was based on Fauvel (1923a, b), Day (1967a, b) and San Martin (1984) for polychaetes, Parenzan (1974, 1976) and Riedl (1986) for mollusks, and Ruffo (1982) and Riedl (1986) for crustaceans. Additional references are indicated by numbers.

[a] Indicates taxa that contribute most to the differences between the three investigated habitats, *P. oceanica*, *C. nodosa* and *Leaf litter* (SIMPER, cut-off 60%)

Additional references:[1]Lardicci 1989; [2]Light 1978; [3]Castelli 1985; [4]Glemarec 1966; [5]Martin et al. 2000; [6]Zuhlke 2001; [7]Fassari 1998; [8]Mollica 1995; [9]Sordino 1989; [10]Abbiati et al. 1987; [11] Parapar et al. 1994; [12]Nunez et al. 1992; [13]San Martin 1992; [14]Gambi et al. 1998; [15]Pipitone 1998; [16]Holdich 1970; [17]Kitsos and Koukouras 2003

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