

Bathymetric distribution of decapods associated with a *Posidonia oceanica* meadow in Malta (Central Mediterranean)

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ABSTRACT

To study the bathymetric distribution of decapods associated with a *Posidonia oceanica* meadow, samples were collected from four stations at depths of 6, 11, 16, and 21 m over a one year period, between August 1993 and September 1994, using a suction sampler and a hand held net. A total of 4607 individuals belonging to 41 species were collected. The hermit crab *Cestopagurus timidus* had the highest abundance in the suction samples, whilst the shrimp *Hippolyte inermis* had the highest abundance in the net samples. The suction sampler collected more than twice the number of species collected by the hand net; no brachyurans were collected by the hand held net. The application of Multidimensional Scaling to the decapod species-abundance data obtained from the suction samples gave three groups corresponding to three depth zones: 6 m, 11-16 m and 21 m. Shannon-Wiener's index of diversity was highest for the decapod assemblage inhabiting the middle part of the meadow, at a depth of 16 m. This part of the meadow also had the thickest 'matte'. Species richness and abundance of decapods varied significantly with bathymetry, and appeared to be correlated with changes in the morphology of the *Posidonia* meadow coincident with the depth gradient, particularly shoot density and structural complexity of the 'matte'. While some temporal changes in the structure of the decapod assemblages were evident, these were not significant.

1 INTRODUCTION

Decapods constitute one of the most conspicuous faunal groups inhabiting seagrass meadows and, together with other crustaceans, are important intermediaries in the transfer of energy in these ecosystems (Bell & Harmelin Vivien 1983, Chessa et al. 1983). As a result, they have received considerable attention in studies on seagrass associated fauna (e.g. Heck & Thoman 1984, Heck et al. 1989), in those on the relationship between meadow complexity and abundance of the associated fauna (e.g. Bell & Westoby 1986a, b, c), and those on predator-prey relationships in seagrass habitats (e.g. Heck & Thoman 1981, Nelson 1981, Leber 1985).

In the Mediterranean, extensive meadows are formed by the endemic *Posidonia*

oceanica, which occurs from ca 1 m down to ca 40 m (Mazzella et al. 1992). *P. oceanica* meadows are very important coastal biotopes supporting a high diversity of associated macrofauna, including decapods (Mazzella et al. 1989, Gambi et al. 1992, Mazzella et al. 1992, Scipione et al. 1996). However, there are relatively few published studies dealing specifically with the total decapod assemblage of these meadows (García Raso, 1990, Zupo 1990, García Raso et al. 1996). Most of the available information has been derived from general studies on the macroinvertebrates associated with this seagrass (e.g. Ledoyer 1962, Harmelin 1964, Scipione et al. 1983, Templado 1984, Mazzella et al. 1989, Cozzolino et al. 1992, Gambi et al. 1992, Pessani et al. 1995, Scipione et al. 1996); or from studies on particular sub-habitats of the *Posidonia* system (the leaf stratum, e.g. Falciai 1985-86; the algal epiphytes of the root-rhizome stratum e.g. García Raso 1988, López de la Rosa & García Raso 1992); or from others on particular decapod taxa (e.g. Vadon 1981, Manjón Cabeza & García Raso 1994, 1995). Moreover, much of this work has been carried out in the western Mediterranean but there is little information from the south-central and eastern regions of this sea.

The structure of *Posidonia* meadows changes with depth (Mazzella et al. 1992) and such changes have been shown to affect the associated macrofaunal assemblages, establishing a clear bathymetric zonation (Falciai 1985-86, Mazzella et al. 1989, Cozzolino et al., 1992, Gambi et al. 1992). However, these studies employed a sampling technique that is known to preferentially collect the vagile macrofauna of the leaf stratum (Borg 1991). Studies in which the vagile fauna of both the root-rhizome and the leaf strata was adequately sampled are lacking.

Dense meadows of *P. oceanica* occur over an extensive depth range in the Maltese Islands (Borg & Schembri 1995). We studied the distribution and abundance of decapods associated with one such meadow along a bathymetric gradient and during different times of the years, using two different techniques which together sample both the leaf and the root-rhizome strata. Our main objectives were to extend previous observations on the decapod assemblages of *Posidonia* meadows to the south central Mediterranean area and to the total decapod community of the meadow, and to correlate any patterns observed to meadow morphology.

2 MATERIALS AND METHODS

2.1 Study area

The *P. oceanica* meadow studied was located off the White Tower headland (latitude 35°59.89'N, longitude 14°21.83'E) at the northern tip of the island of Malta (Fig. 1) in an area that has some of the most extensive and healthy seagrass meadows in the Maltese Islands (Borg & Schembri 1995). Here, the bottom slopes gently and supports a continuous *P. oceanica* meadow between depths of ca 5 and 25 m. In the 10-18 m depth range, the *P. oceanica* shoots grow on a thick mat whose upper 2-5 cm consist of a dense root-rhizome lattice in which the interstices are relatively free of sediment. The exposed roots and rhizomes support a rich, sessile epibiota dominated by calcareous algae and bryozoans. The absence of interstitial sediment from the surface layers of the mat is probably the result of winnowing by the strong cur-

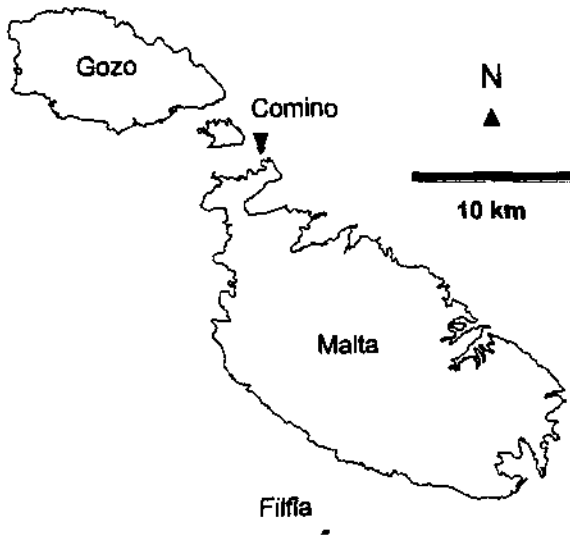


Figure 1. Map of the Maltese Archipelago showing the location of the study area (arrow). The islands are centered on latitude $35^{\circ}55.5'N$ and longitude $14^{\circ}23.5'E$.

rents that prevail in the area. The network of small spaces provided by the surface layers of the mat, and by the epibiota it supports, provides a complex microhabitat, especially for cryptic invertebrates such as decapods. At the shallower end of the meadow (6 m), the *P. oceanica* shoots mainly grow on medium to coarse sand, while in the deeper parts (21 m), the shoots grow on a thin mat or on coarse sand.

2.2 Sampling and data analyses

Four stations were established at depths of 6, 11, 16, and 21 m, along a shore-normal transect. For each of the four stations, *Posidonia* shoot density was estimated in August 1993 by counting the shoots within a 0.125 m^2 quadrat. Five replicate counts were taken at each station. Shoot density estimation was made once only, as negligible change was expected over a one-year period. Twenty five *P. oceanica* shoots were collected at random from each of the four stations in August and December 1993 and April 1994, to estimate mean leaf width, mean leaf length and the mean number of leaves per shoot. Shoot density, Leaf Standing Crop (LSC, dry weight gm^{-2}) and Leaf Area Index (LAI, $\text{m}^2\text{ m}^{-2}$) were used to quantify changes in meadow structure with depth.

Photographs of the mat surface were taken at each station using a Nikonos V camera equipped with a 35 mm lens with close-up attachment. A 'matte cavity index' was estimated from the photographs. This index represents a measure of the proportion of cavities (which appear in the photographs as very dark areas) in the mat surface layer and takes values between zero (no cavities) and one (100% cavities).

Sediment samples were collected from each station for determination of organic matter content and for granulometry using the method of Buchanan (1984).

The vagile fauna was sampled using a combination of the two most widely used samplers in studies of the macrofauna associated with *P. oceanica* meadows: the hand-held net and the suction sampler.

The suction sampler used was based on the design of Vadon (1981) and was fitted with a 1 mm mesh collection bag. A 1 m² sample was collected from each of the four stations in August and December 1993 and April 1994. The hand net samples were collected according to Russo et al. (1985). An area of ca 20 m² was sampled at each of the four stations in September and December 1993, and in March, June and September 1994.

All suction and hand net samples were sorted by hand to separate the decapods, which were transferred to 70% ethanol for preservation and subsequent identification and counting.

Multivariate analyses of the species abundance data from the August and December 1993, and April 1994 suction samples were made using the PRIMER (Plymouth Routines in Multivariate Ecological Research) suite of programs (Clarke & Warwick 1994). The ordination method applied was Non-Metric Multidimensional Scaling (MDS) using the Bray-Curtis coefficient as a similarity measure (Field et al. 1982). Analysis of similarity (ANOSIM) was used to test the significance of differences in the composition of the decapod assemblages from the different depths and seasons. The contribution of the various species to the similarity/dissimilarity within and between stations was investigated using SIMPER (Clarke 1993). The relationship between the composition of the decapod assemblages and environmental parameters was investigated using the BIOENV procedure (Clarke & Ainsworth 1993). The parameters tested were: shoot density, LAI, LSC, 'matte cavity index', % organic matter, and median sediment grain size.

Changes in total abundance of decapods (N), Shannon-Wiener diversity (H') and Pielou's evenness (J) with depth were investigated using univariate methods. No statistical analyses were carried out on the data from the hand net samples as this sampler mainly collected decapods from the leaf stratum (see the results section below).

3 RESULTS

In general, *P. oceanica* shoot density and Leaf Area Index decreased with increasing depth. Leaf Standing Crop decreased with increasing depth in December but higher values were recorded at the 11 and 16 m stations than at the 6 m station during August and April. The mean 'matte cavity index' varied between a minimum of 0.03 at 6 m and a maximum of 0.35 at 16 m. The mean % organic matter content of the sediment (Morgan's ratio) varied between a minimum of 0.77 at 21 m and a maximum of 0.87 at 16 m. Sediment grain size varied between a minimum of 1.0 ϕ at 11 m and 1.51 ϕ at 16 m (Table 1).

A total of 4607 individual decapods belonging to 41 species were collected by the two sampling methods. Of these, 1768 individuals (38.4%) were collected by the suction sampler and 2839 individuals (61.6%) by the hand net. Of the 41 species recorded, 40 (97.6%) were collected by the suction sampler and 16 (39%) were collected by the hand net (Table 2). Therefore, although a larger number of individuals were collected by the hand net as compared to the suction sampler, less than half the total number of species were collected by the former method. Only a single species (*Anapagurus* cf. *chiroacanthus*) was recorded from the hand net samples only, while not a single brachyuran was collected using the hand net. The hermit crab *Cestopagu-*

Table 1. Mean values (\pm SD) of 'matte cavity index', % organic matter in the sediment, sediment grain size (graphic mean), shoot density, leaf area index (LAI), and leaf standing crop (LSC) for the four stations. Values are for August 1993, except in the case of LAI and LSC where values for August 1993 (top), December 1993 (middle) and April 1994 (lower) are given.

Station	Matte cavity index ($n = 3$)	% Organic matter ($n = 2$)	Sediment grain size (Md ϕ) ($n = 2$)	Shoot density ($n = 5$)	LAI ($m^2 m^{-2}$)	LSC (gdw m^{-2}) ($n = 1$)
6 m	0.03 \pm 0.02	0.81 \pm 0.01	1.19 \pm 0.05	787 \pm 19	20.2	710
					14.3	630
					13.1	660
11 m	0.32 \pm 0.07	0.82 \pm 0.11	1.0*	607 \pm 31	15.1	840
					14.5	550
					14.8	780
16 m	0.35 \pm 0.1	0.87 \pm 0.04	1.51 \pm 0.09	486 \pm 28	12.1	864
					9.6	350
					11.7	750
21 m	0.13 \pm 0.05	0.77 \pm 0.01	1.06 \pm 0.15	373 \pm 27	9.2	622
					8.8	440
					11.0	650

*Single measurement.

rus timidus had the highest abundance in the suction samples, whilst the shrimp *Hippolyte inermis* had the highest abundance in the net samples (Table 2).

Total decapod abundance in the suction samples decreased with increasing depth, with the greatest temporal variation being recorded from the 6 m station. Temporal variation in abundance at the other stations was very small (Fig. 2). Diversity and evenness increased with increasing depth, with maximum values at the 16 m station (Figs 3 and 4). The two-dimensional MDS ordination plot (Fig. 5) of the suction samples showed a distinct grouping of shallow (6 m) samples to the right. The remaining samples did not group as distinctly, although samples collected from intermediate depths (11 and 16 m) tended to group in the middle of the plot, while samples collected from the deep (21 m) station grouped towards the left (Fig. 5).

The ANOSIM analysis showed a significant difference between samples taken from different depths in each sampling session ($r = 0.562$, $p < 0.01$) but there was no significant difference between samples taken from the same depth at different times of the year.

The SIMPER analysis showed that within groups of samples collected from the same station, samples collected from the 6 m station had the highest similarity (70.3%), while samples collected from the 21 m station had the lowest (55.1%). The analysis showed also that between groups of samples collected from different stations, the highest dissimilarity was between the 6 m and the 21 m stations (55.6%), while the lowest dissimilarity was between the 11 m and the 6 m stations (37.2%). While the hermit crab *C. timidus* had an overall significant contribution to 'within' station similarity (12.33% to 20.05%), this species had a much lower contribution to 'between' station dissimilarity (7.89% to 11.70%). Several species, including *Calcinus tubularis*, *Galathea bolivari*, *Pilumnus hirtellus* and *Eurynome aspera*, contributed significantly to 'between' station dissimilarity.

Table 2. List of decapod species collected by the suction sampler and the hand net. Stations = the number of individuals recorded from each station in the following order 6 m + 11 m + 16 m + 21 m; N = total number of individuals.

Species	Suction sampler		Hand net	
	Stations	N	Stations	N
1. <i>Athanas nitescens</i> var. <i>laevirhincus</i> (Risso, 1816)	43+68+40+43	194	0+1+2+1	4
2. <i>Alpheus dentipes</i> (Guérin, 1832)	11+14+15+11	51	1+1+1+1	4
3. <i>Alpheus macrocheles</i> (Hailstone, 1835)	0+3+3+5	11		
4. <i>Processa edulis</i> (Risso, 1816)	0+4+0+0	4	1+0+0+2	3
5. <i>Hippolyte inermis</i> (Leach, 1815)	9+2+13+9	33	377+ 307+523+553	1760
6. <i>Hippolyte garciarassoi</i> (d'Undekem d'Acoz, 1996)	1+2+0+0	3	2+2+11+21	36
7. <i>Thoralus cranchii</i> (Leach, 1817)	2+11+9+8	30	5+3+18+6	32
8. <i>Palaemon xiphias</i> (Risso, 1816)	1+0+0+0	1	11+1+10+7	29
9. <i>Palaemon longirostris</i> (A. Milne Edwards, 1837)	0+0+0+1	1	0+0+1+5	6
10. <i>Philocheilus fasciatus</i> (Risso, 1816)	1+0+0+1	2		
11. <i>Upogebia</i> cf. <i>nitida mediterranea</i> (Noel, 1992)	0+0+1+0	1		
12. <i>Callinassa</i> sp.	0+1+0+0	1		
13. <i>Calcinus tubularis</i> (Linnaeus, 1767)	113+10+7+2	132	12+8+3+13	36
14. <i>Cestopagurus timidus</i> (Roux, 1830)	707+135+25+38	905	137+290+178+280	885
15. <i>Anapagurus</i> cf. <i>breviaculeatus</i> (Fenizia, 1937)	0+0+1+0	1	1+0+0+0	1
16. <i>Anapagurus</i> cf. <i>chiroacanthus</i> (Lilljeborg, 1856)			0+0+1+0	1
17. <i>Pagurus chevreauxi</i> (Bouvier, 1896)	79+28+23+22	152	0+1+1+8	10
18. <i>Pagurus anachoretus</i> (Risso, 1827)	6+5+4+2	17	0+11+9+7	27
19. <i>Pagurus</i> cf. <i>cuanensis</i> (Bell, 1846)	0+0+1+0	1		
20. <i>Galathea bolivari</i> (Zariquiey Alvarez, 1950)	2+7+13+7	29	1+0+0+1	2
21. <i>Galathea squamifera</i> (Leach, 1814)	0+1+0+0	1		
22. <i>Pisidia longimana</i> (Risso, 1816)	27+17+7+1	52	1+1+0+1	3
23. <i>Dromia personata</i> (Linnaeus, 1759)	0+1+0+1	2		
24. <i>Ethusa mascarone</i> (Herbst, 1785)	1+0+0+1	2		
25. <i>Ebalia edwardsi</i> (O.G. Costa, 1838)	3+11+11+6	31		
26. <i>Liocarcinus corrugatus</i> (Pennant, 1777)	0+1+0+1	2		
27. <i>Pilumnus aestuarii</i> (Nardo, 1869)	1+0+1+0	2		
28. <i>Pilumnus</i> sp.	0+0+1+0	1		
29. <i>Pilumnus hirtellus</i> (Linnaeus, 1761)	27+10+1+0	38		
30. <i>Xantho incisus granulicarpus</i> (Forest, 1953)	4+1+0+0	5		
31. <i>Xantho pilipes</i> (A. Milne Edwards, 1867)	0+2+0+0	2		
32. <i>Paractea monodi</i> (Guinot, 1969)	0+0+0+1	1		
33. <i>Pisa muscosa</i> (Linnaeus, 1758)	0+1+1+4	6		
34. <i>Herbstia condyliata</i> (Fabricius, 1787)	8+10+7+5	30		
35. <i>Eurynome aspera</i> (Pennant, 1777)	0+1+5+3	9		
36. <i>Eurynome spinosa</i> Hailstone, 1835	0+0+1+0	1		
37. <i>Acanthonyx lunulatus</i> (Risso, 1816)	1+0+0+0	1		
38. <i>Inachus</i> cf. <i>phalangium</i> (Fabricius, 1775)	0+1+0+0	1		
39. <i>Achaeus cranchii</i> (Leach, 1817)	1+2+0+5	8		
40. <i>Achaeus gracilis</i> (O.G. Costa, 1839)	0+0+1+1	2		
41. <i>Macropodia czerniavskii</i> (Brandt, 1880)	1+0+1+0	2		
Total		1768		2839

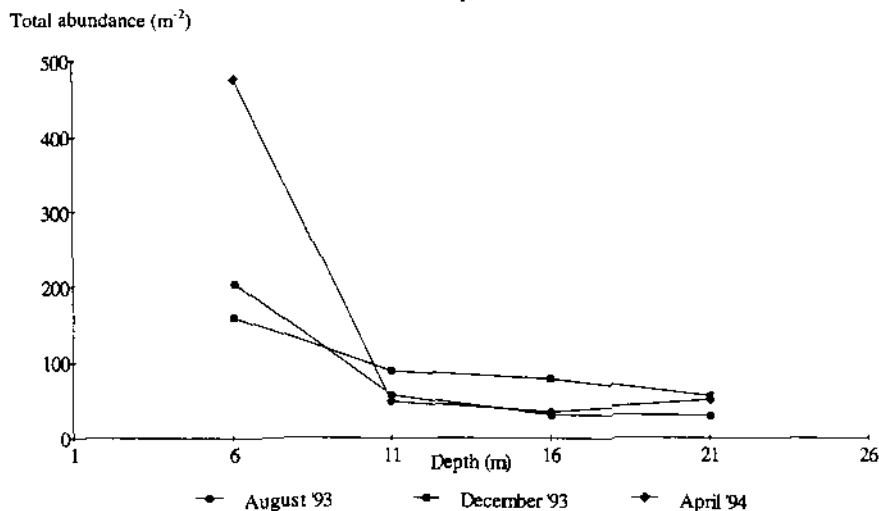


Figure 2. The total abundance of decapods in suction samples from the four stations.

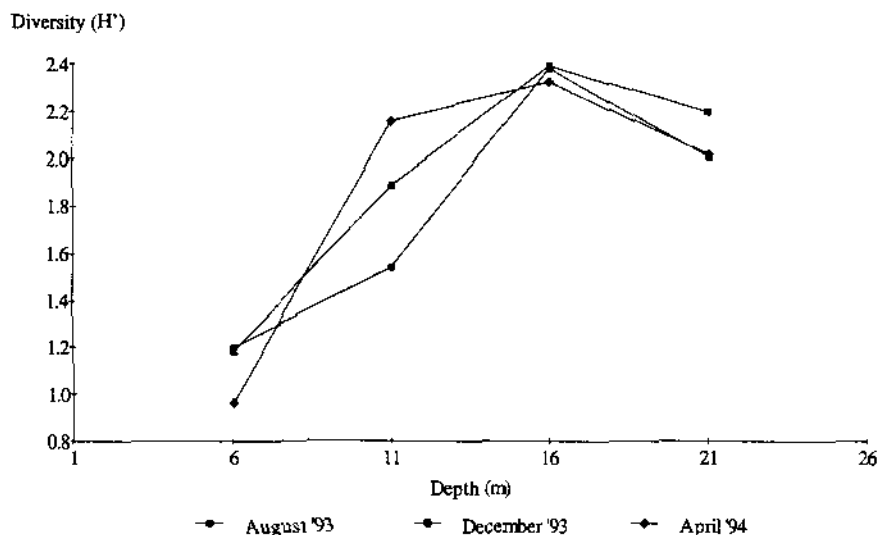


Figure 3. Values of Shannon-Wiener diversity (H') for suction samples from the four stations.

The results of the BIOENV analysis showed that the highest correlation between the species data and environmental parameters (0.501) was for a combination of two variables: shoot density and % organic matter in the sediment.

4 DISCUSSION

Although species richness was high, only twelve species had a relative abundance greater than 1%. Of these, the hermit crab *C. timidus* had the highest value (51.2%).

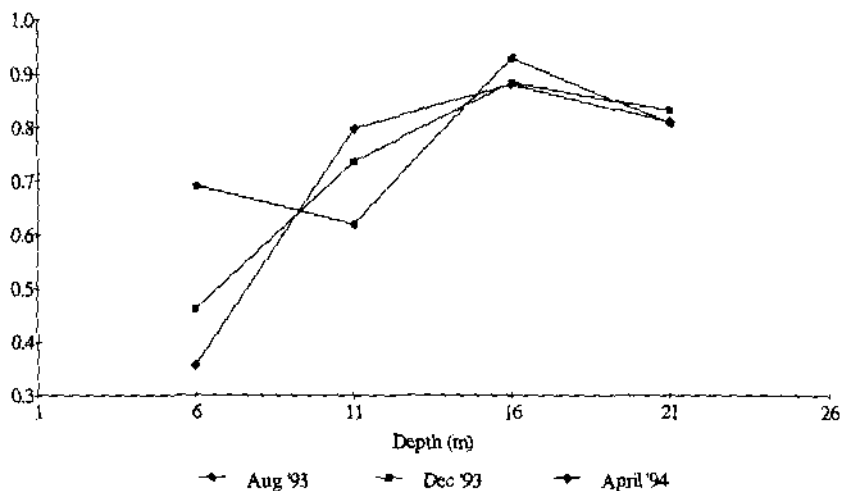
Evenness (J)

Figure 4. Values of Piclou's evenness (J) for suction samples from the four stations.

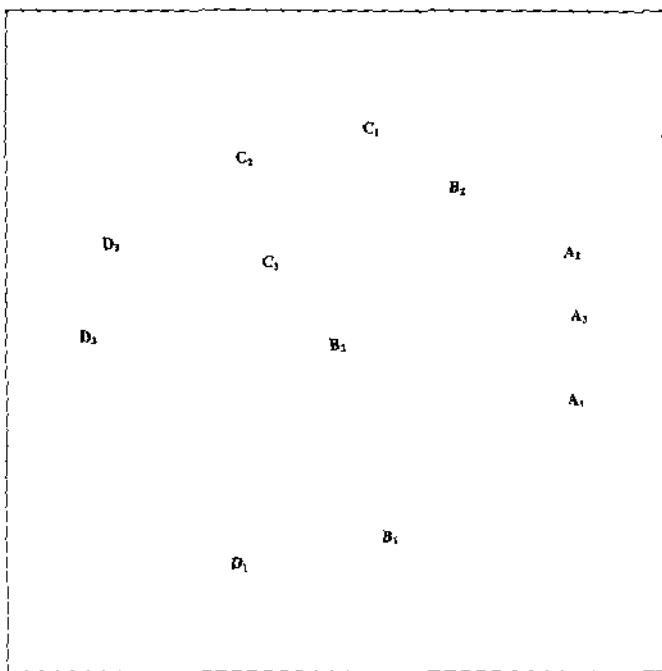


Figure 5. MDS plot for the decapod taxocene from the suction samples based on abundance after double square root transformation and using the Bray-Curtis similarity measure. Stress = 0.15. Letters represent depth stations as follows: A) 6 m, B) 11 m, C) 16 m and D) 21 m. The subscript indicates the collection period, 1) August 1993, 2) December 1993, 3) April 1994.

García Raso (1990) and Zupo (1990) obtained similar results from the Western and Central Mediterranean, respectively.

In all sampling sessions, the highest total abundance value recorded in the suction samples came from 6 m. Temporal variation in total abundance was significant at the 6 m station but not at the other depths sampled. The high total abundance recorded at this depth may be related to the high *P. oceanica* shoot density at this station and the proximity of a different habitat – rock with photophilic algae – that extends from mean sea level to the edge of the *Posidonia* meadow at 6 m. High seagrass shoot densities have been shown to be behaviourally selected for by decapods as a refuge from predation (Bell & Westoby 1986b). Dense meadows may provide additional living space and may supply more abundant food than sparser meadows by providing a larger surface area that can be occupied by epiphytes (Heck & Wetstone 1977, Leber 1985). The observed high abundance at the 6 m station was almost entirely due to three small hermit crabs, *Cestopagurus timidus*, *Calcinus ornatus* and *Pagurus chevreuxi*. It may be significant that these species are able to climb up the *Posidonia* leaves and forage in the foliar stratum. The proximity of a different habitat may be enhancing recruitment of some decapods; for example, the hermit crab *Calcinus ornatus* is known to occur also on rocky substrata supporting photophilic algae.

As *Posidonia* shoot density decreases with depth, so does the abundance of decapods. However, diversity was lowest at the 6 m station and highest at intermediate depth (16 m), although even at the deepest station (21 m), diversity was still higher than at the shallowest station. This also appears to be related to habitat complexity. Although shoot density is highest at the shallow station, here *Posidonia* was growing on sand. At the 11 m and 16 m stations, the thick mat present provides additional microhabitats for decapods. Although not as thick as at the intermediate depths, the mat is also present at the deepest station and diversity is still higher than for *Posidonia* growing on sand. It would appear therefore, that the decrease in habitat complexity of the foliar stratum resulting from a decrease in shoot density, is more than made up for by an increase in complexity in the root-rhizome stratum. While the importance of different sub-habitats within seagrass meadows in influencing the species richness and abundance of the associated macrofauna has been pointed out (e.g. Orth et al. 1980), this is an interesting result since studies on the relationship between bathymetry, meadow structural complexity and diversity of associated macrofauna are generally lacking.

Our results suggest that the root-rhizome stratum supports a higher diversity of decapods than the leaf stratum. This is in agreement with García Raso's (1990) findings for meadows from southeastern Spain and with the published observations of several authors on the importance of the root-rhizome mat in influencing diversity (e.g. Harmelin 1964, Templado 1984). However, some decapods cannot be easily classified as inhabitants of the leaf or root-rhizome strata since they occur in both microhabitats. For example, in the Maltese meadow studied, the hermit crab *Cestopagurus timidus* and the shrimp *Thorulus cranchii* occur equally abundantly in both the leaf stratum and the root-rhizome layer.

The decapods from the *P. oceanica* meadow studied could be divided into three sub-assemblages: a shallow water group (6 m), an intermediate group (11-16 m), and a deeper water group (21 m). The occurrence of these sub-assemblages appears to be correlated with changes in meadow structure as depth increases (Mazzella et al. 1989,

Gambi et al. 1992), and with the proximity of different habitats at the shallow and deep ends of the meadow. In turn, meadow structure is dependant on a number of physical factors, including availability of light and the hydrodynamic regime (Mazzella et al. 1989, Gambi et al. 1992). The species composition of the shallow (6 m) and deep (21 m) sub-assemblages is partly influenced by the occurrence of species which are not permanent residents of the *Posidonia* meadow but which migrate to it from nearby habitats. For example, *P. hirtellus*, which is a species typical of the assemblage of photophilic algae growing on rock (Vadon 1981), occurred predominantly at the shallower (6 m) end of the meadow which lies adjacent to exposures of bedrock with photophilic algae. This species may be using the shallow water *Posidonia* meadow as a nursery (Vadon 1981). The sub-assemblage from intermediate depths (11-16 m) had the highest diversity. This may be partly a result of the high structural complexity of the root-rhizome layer here, as already discussed, as well as of the greater availability of food – the intermediate stations had the largest 'matte cavity index' as well as the highest values of sediment organic content. Cryptic detritivorous species, such as *Athanas nitescens*, *Alpheus dentipes*, *Thorulus cranchii* and *Galathea bolivari*, were mainly restricted to the middle region of the meadow. The deepest station is different from the others more because of the absence of species that were present at intermediate depths than because of the presence of species restricted to this deeper station. This decrease may be correlated with both the sparse cover of *Posidonia* shoots and to the thinning matte, as well as to a reduction in sediment organic content.

It is very clear from our data that the hand held net was less efficient than the suction sampler in sampling the total decapod assemblage of the *P. oceanica* meadow studied; the hand net sampled mainly the leaf stratum. However, a comparative assessment of the suitability and efficiency of these two samplers is outside the scope of the present report.

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