SCIENTIA MARINA

Influence of the structure of *Posidonia oceanica* meadows modified by bottom trawling on crustacean assemblages: comparison of amphipods and decapods*

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SUMMARY: The seagrass *Posidonia oceanica* plays an important role as habitat for invertebrates. A correlative study was done in El Campello (SE Spain) to understand the relationships between assemblage structure of crustaceans and modification of *P. oceanica* structure caused by bottom trawling. We compared the changes of community structure of the most important groups of crustaceans, amphipods and decapods with changes of cover, density, detritus and rhizome fragments. Sampling was carried out in four control and four impact locations, along a gradient of degradation (17 m depth, August 1992). Multivariate analysis was used for community data (nm-MDS) and *P. oceanica* structure (PCA). Both groups showed a similar number of species. The amphipod community showed a clear pattern of community changes with significant differences between impact and control locations (global R = 0.298, p<0.001) and with significant correlation with *P. oceanica* structure (global ρ = 0.21, p<0.05). Detritus (fine and coarse) and rhizome fragments had the highest influence on amphipod distribution. Spatial variability inside of locations was very high. Few species (*Dexamine spiniventris, Lysianassa longicornis* or *Ampelisca* spp.) were responsible for disimilarity among locations. Decapods did not show a correlation with the structure of *P. oceanica*. The amphipod community seems to be a strong indicator of the ecological implications of seagrass degradation.

Key words: Crustaceans, community structure, habitat complexity, *Posidonia oceanica*, Mediterranean Sea.

INTRODUCTION

Mobile invertebrates are distributed in seagrass meadows according to plant attributes. The changes in community structure can be determined by different variables existent in seagrass meadows such as biomass, density, epiphytes or detritus, and the influence that these variables place on each species (Heck and Wetstone, 1977; Stoner, 1980; Lewis, 1984; Stoner and Lewis, 1985; Howard *et al*., 1989; Edgar, 1990; Berggren, 1993; Harlin *et al*., 1996). Many manipulative and correlative studies have

been developed during the last decades to better understand the processes which influence the relationships between spatial distribution of invertebrates and habitat structure (Fonseca *et al*., 1990; Edgar, 1990; Schneider and Mann, 1991). However invertebrate-seagrass relationships in the *Posidonia oceanica* system are not well known.

Along the Mediterranean coast *Posidonia oceanica* develops meadows in shallow sandy bottoms (Buia and Mazzella, 1991), and is an important habitat for mobile invertebrates (Mazzella *et al*., 1989). Extensive degradation of *Posidonia oceanica* meadows due to bottom trawling has occurred in South-East Spain. The impact of trawling on *P. oceanica*

produces a reduction of canopy cover and an increase of detritus by erosion, which has an important influence on the invertebrate community (Sánchez Jerez and Ramos Esplá, 1996).

Among the invertebrates associated with seagrass meadows, crustaceans are the most important group, comprising a large number of species with substantial abundance and biomass, as well as being extraordinarily important as a trophic resource for fish populations (Bell and Harmelin, 1983; Edgar and Shaw, 1995a, b). To understand the effects of environmental impacts on the seagrass system it is very important to characterise the changes of crustacean assemblages due to the alteration of habitat features. Amphipods and decapods are the most abundant crustaceans in association with *P. oceanica* meadows (Mazzella *et al.*, 1989; García-Raso, 1990; Scipione and Chessa, 1993; Sánchez Jerez, 1997). Therefore, these groups should be affected by meadow modification, which concurrently affects the ecological processes of the overall community (Virnstein, 1987). However, depending on their different life history, these two groups can be influenced in different ways (Warwick and Clarke, 1991; Sánchez Jerez and Ramos Esplá, 1996).

For this study we were interested in testing two questions: (i) Which parameters of the meadow structure have the most influence on crustaceans, especially the decapod and amphipod communities? and (ii) Will these two groups, with different life histories, model similar patterns of response? A field experiment comparing decapod and amphipod community structures in several sites along a gradient of degraded (due to bottom trawling) *P. oceanica* meadow was designed to research the relationship between seagrass structure and crustacean assemblages.

MATERIAL AND METHODS

The study was carried out in August 1992 on the *P. oceanica* meadow of El Campello (Alicante, SE Spain), which was modified by bottom trawling into a gradient of degradation. In south-east Spain, a majority of the soft bottom with a range of 5 to 23 m in depth is continuously covered by seagrass for tens of kilometres, with occasional patches of sand and *Cymodocea nodosa* meadows. It is estimated that 40% of *P. oceanica* in El Campello has been degraded by illegal bottom trawling (Sánchez Lizaso *et al.*, 1990) (Fig. 1). Nearly 200 trawlers fish around the
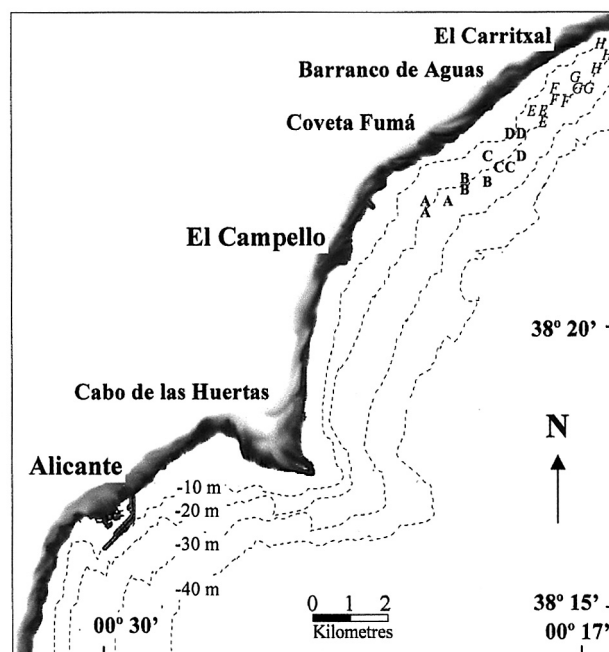

FIG. 1. – Geographical location of sampling sites. Sites A-D were in relatively non-impacted meadows, and sites E-H were on trawled meadows, at 17 m depth.

study area and it is a common practice to trawl in shallow bottoms, over seagrass meadow usually operating under cover of darkness, though it is illegal (at present the area is protected by an antitrawling artificial reef; Ramos Esplá *et al.*, 1999).

Based on preliminary studies (Sánchez Lizaso *et al.*, 1990; Ramos Esplá *et al.*, 1991) and personal prospecting, eight locations were selected along the El Campello coast at 17 m depth. At this depth the meadow was only partially degraded. The location selection was supported by the number of loose rhizomes on the bottom and the existence of gear erosion (long bands of dead meadow around 40 cm wide), covering a gradient of degradation from degraded meadow to pristine meadow. Control sites did not show any signs of direct erosion. Four locations (A-D) were in relatively pristine meadow (around 80% cover) and another four (E-H) in degraded meadow (around 65% cover). We randomly choose three sites inside of each location to avoid spatial pseudo-replication. Also to avoid temporal dependence of data, the sites were sampled randomly along the sampling time.

In each site, three random samples of 0.125 m^2 of the meadow were taken during the day, using a suction device (500 μm mesh size; Brook, 1979). This sampling method has been used by many authors with adequate results (e.g. decapods, Vadon, 1981; epifauna, Francour, 1990). The samples were taken

at the same time by scuba-diving. Shoot density inside the quadrants was measured after taking the samples. At the laboratory, amphipods and decapods were sorted and identified to species level. Detritus was sieved into two fractions: fine (1 to 8 mm), and coarse (> 8 mm). Fragments of dried rhizomes were also sorted. Detritus and rhizome fragments were dried in a dessicator for 24 h at 80°C (Romero *et al.*, 1992) and weighed.

Data on amphipod and decapod abundance was analysed by non-parametric multidimensional scaling (MDS) using PRIMER software (Plymouth Laboratory; Warwick and Clarke, 1993; Clarke and Warwick, 1994). The similarity matrix among samples was calculated by using the Bray-Curtis similarity index with a double square transformation of the data. It was used to construct bi-variate plots of MDS and to calculate a permutation test of significance (*analysis of similarities*, ANOSIM). Using SIMPER (*similarities percentage*), the percentage of influence of each species on the Bray-Curtis matrix values was calculated (Clarke, 1993).

The Spearman's rank correlation coefficient was calculated to establish the correlation between the *P. oceanica* structure and community attributes, using RELATE (PRIMER; Clarke and Warwick, 1994). The similarity matrix of seagrass variables was calculated by Euclidean distances, using standardised data (Clarke and Warwick, 1994). To outline the optimal set of seagrass features that best explains the community structure we followed the BIO-ENV procedure defined by Clarke and Ainsworth (1993). Seagrass variables were analysed, as a whole, using a correlation-based principal components analysis (PCA). A lower triangular Euclidean distance matrix relating to the analyses was constructed (Clarke and Green, 1988). A graphical representation of the changes in *P. oceanica* structure was compared with fauna attributes (Clarke and Warwick, 1994). Additionally statistical differences of *Posidonia* features between impact and control sites were estimated by analysis of variance.

RESULTS

Community structure

Decapods were the best represented order, with a total of 34 species: 24 in the impacted sites and 29 in the control sites (Table 1). The community was dominated by *Thoralus cranchii* (Leanch, 1817),
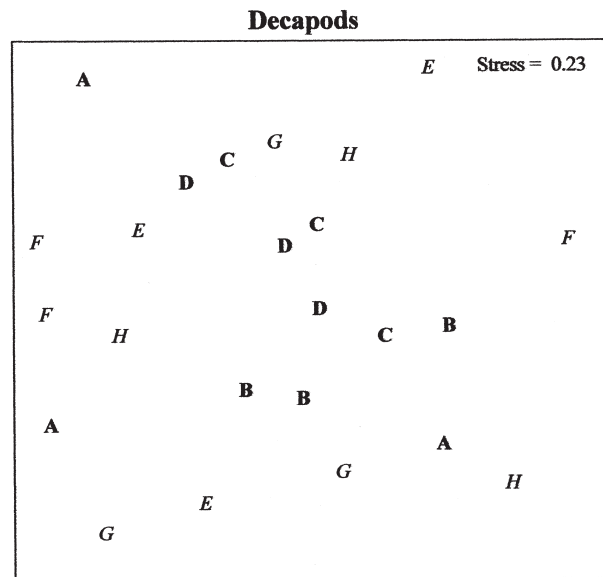

FIG. 2. – MDS bi-dimensional representation of decapod assemblages. A-D, control sites; E-H, impact sites.

Achaeus gracilis Costa, 1839 and *Athanas nitescens* (Leach, 1814). The amphipods had a species richness similar to that of the decapods (32 species): 22 species in the impacted site and 29 in the control sites. *Ampelisca* spp Kroyer, 1842, *Dexamine spinosa* (Montagu, 1813), *Maera knudseni* Reid, 1951 and *Lysianassa longicornis* Lucas, 1849 were the most abundant species (Table 1).

The MDS representation based on the decapod community displayed a scattered plot of sites without a pattern of aggregation related to degraded or control sites (Fig. 2), with a stress value of 0.23 which is relatively high. However, the bi-dimensional representation of amphipod MDS showed a certain segregation of sites from the control meadow (A-D) in comparison to sites of the impacted meadow (E-H), but also with a relatively high value of stress (Fig. 3). Also, the spatial heterogeneity among sites was very high, mainly among the control sites. It is important to remark that the interpretation of MDS should be done carefully because of the high values of stress.

The pattern observed in the amphipod community was consistently demonstrated by ANOSIM. This permutation test showed significant differences between control and impact sites with respect to amphipod community structure (global R = 0.298, p<0.001). Decapods did not show statistical differences (global R = 0.003, non significant). The amphipod species which had a higher influence on the dissimilarities among control and impact sites (SIM-

TABLE 1. – Average abundance of decapods and amphipods (ind. m^{-2}±SE) by sampling site: A-D, control sites; E-H, impact sites. Ratio shows the contribution of the most important species in the dissimilarities between control and impact sites after SIMPER.

|	Ratio	A-D	E-H
Decapoda			
Hippolyte inermis (Leach, 1815)	1.04	11.3 ± 3.3	4.7 ± 2.5
H. leptocerus (Heller, 1863)		0.6 ± 0.6	-
Thoralus cranchii (Leach, 1817)	1.15	35.3 ± 9.9	18.0 ± 7.3
Alpheus macrocheles (Hailstone, 1835)		0.6 ± 0.6	-
Athanas nitescens (Leach, 1814)	1.11	10.0 ± 3.0	15.3 ± 7.1
Processa modica Will. and Roch., 1979	1.12	13.3 ± 3.7	8.7 ± 4.2
Periclimenes scriptus (Risso, 1822)		1.3 ± 0.9	2.0 ± 1.4
Calcinus tubularis (Roux, 1830)		0.6 ± 0.6	0.6 ± 0.6
Cestopagurus timidus (Roux, 1830)		0.6 ± 0.6	0.6 ± 0.6
Diogenes pugilator (Roux, 1829)		2.0 ± 2.0	-
Paguristes eremita (Linnaeus, 1818)		-	0.6 ± 0.6
Pagurus cuanensis Bell, 1846	0.96	0.6 ± 0.6	3.3 ± 1.2
P. anachoretus Risso, 1827		1.3 ± 0.9	1.3 ± 0.9
P. chevreuxii (Bouvier, 1896)		-	0.6 ± 0.6
Anapagurus curvidactylus Chev. and Bour. 1892		-	2.0 ± 2.0
Galathea bolivari Zariquiey-Alvarez, 1968)		4.0 ± 2.3	2.6 ± 1.1
Pisidia longicornis (Linnaeus, 1767)		3.3 ± 1.5	-
P. longimana (Risso, 1816)		2.0 ± 1.4	-
Dromia personata (Linnaeus, 1759)		0.6 ± 0.6	-
Ethusa mascarone (Herbst, 1785)		2.0 ± 1.4	0.6 ± 0.6
Ilia nucleus (Linnaeus, 1758)		0.6 ± 0.6	-
Ebalia edwardsi Costa, 1838	1.07	8.0 ± 3.7	8.7 ± 2.3
Sirpus zariquieyi Gordon, 1953	0.89	4.0 ± 1.5	3.3 ± 1.54
Liocarcinus arcuatus (Leach, 1814)		0.6 ± 0.6	2.0 ± 1.43
Eurynome aspera (Pennant, 1777)		1.3 ± 0.9	1.3 ± 0.9
E. spinosa Hailstone, 1835	1.05	8.0 ± 2.6	2.6 ± 1.5
Achaeus gracilis Costa, 1839	0.96	16.0 ± 3.3	15.3 ± 4.6
Macropodia rostrata (Linnaeus, 1761)		0.6 ± 0.6	2.0 ± 1.0
M. czerniavskii Forest and Zariquiey, 1964		2.6 ± 2.6	0.6 ± 0.6
Inachus phalagium Fabricius, 1775		2.6 ± 1.1	3.3 ± 2.7
Pisa armata (Latreille, 1803)		1.3 ± 0.9	-
Maja crispata Risso, 1827		0.6 ± 0.6	-
Total density decapods		135 ± 27.1	102.0 ± 18.4
Species richness		29	24
Amphipoda			
Iphimedia minuta Sars, 1882	0.88	2.7 ± 2.0	4.0 ± 1.6
Ampelisca spp. Kroyer, 1842	1.21	2.7 ± 2.0	11.3 ± 3.9
Amphithoe ramondi Audouin, 1826	0.8	1.3 ± 1.3	4.7 ± 2.1
Cymadusa crassicornis (Costa, 1857)		2.0 ± 1.4	5.3 ± 3.3
Aora spinicornis Afonso, 1976	1.12	5.3 ± 4.2	12.0 ± 4.1
Leptocheirus guttatus (Grube, 1864)		0.7 ± 0.7	1.3 ± 0.9
Apherusa chiereguinii Giordani-Soika, 1950	0.83	22.6 ± 5.8	0.7 ± 0.7
A. vexatrix Krapp-Schickel, 1979	0.91	5.3 ± 1.8	1.3 ± 0.9
Corophium minimum Schiecke, 1979		0.7 ± 0.7	-
Siphonocetes spp. Kroyer, 1845	1.01	22.6 ± 5.8	5.3 ± 0.6
Atylus guttatus (Costa, 1851)		1.3 ± 1.3	-
A. vedlomensis (Bates and Westwood, 1862)	1.05	5.3 ± 2.0	9.3 ± 2.4
Dexamine spiniventris (Costa, 1853)	1.12	4.7 ± 1.5	13.3 ± 3.9
D. spinosa (Montagu, 1813)	1.04	2.0 ± 1.4	8.0 ± 2.4
Eusiroides dellavalei Chevreux, 1899	0.91	4.0 ± 1.2	-
Ceradocus semiserratus (Bate, 1862)		0.7 ± 0.7	-
Elasmopus rapax Costa, 1853		0.7 ± 0.7	-
Gammarella fucicola Leach, 1814		1.3 ± 0.9	0.7 ± 0.7
Maera grossimana (Montagu, 1808)		2.0 ± 1.4	1.3 ± 0.9
M. knudseni Reid, 1951	1.01	2.0 ± 1.4	12.7 ± 5.2
Leucothoe spinicarpa (Abildgaard, 1789)		2.0 ± 2.0	0.7 ± 0.7
Lepidepecreum longicorne (Bate andWestwood, 1861)		0.7 ± 0.7	-
Lysianassa longicornis Lucas, 1849	1.18	12.0 ± 3.3	1.3 ± 1.3
L. pilicornis Heller, 1866		-	1.3 ± 0.9
Orchomene humilis (Costa, 1853)		2.0 ± 1.4	0.7 ± 0.7
Monoculodes carinatus (Bate, 1857)		0.7 ± 0.7	-
Pereinotus testudo (Montagu, 1808)		0.7 ± 0.7	-
Hyale stebbingi Chevreux, 1888		2.0 ± 2.0	-
Caprella acanthifera Leach, 1814		0.7 ± 0.7	2.7 ± 1.1
Phtisica marina Slabber, 1769		2.0 ± 1.0	1.3 ± 0.9
Pseudoprotella phasma (Montagu, 1804)		-	0.7 ± 0.7
Total density amphipods		96.9 ± 19.8	114.0 ± 12.3
Species richness		29	22

Amphipods

Stress = 0.22
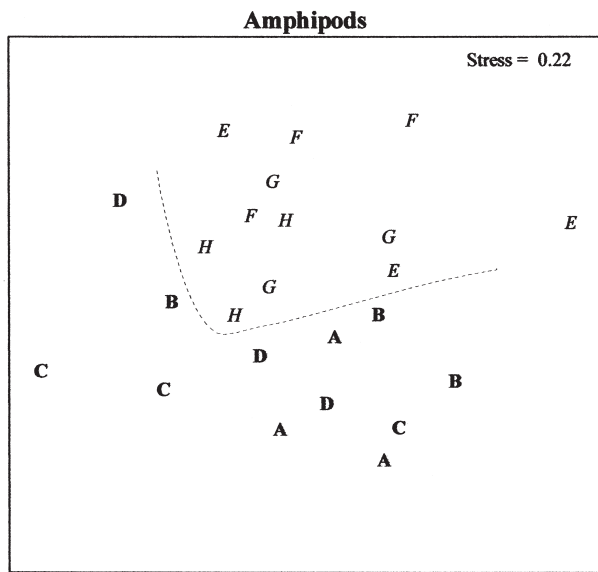
FIG. 3. – MDS bi-dimensional representation of amphipod assemblages. A-D, control sites; E-H, impact sites.

Posidonia oceanica

FIG. 4. – PCA bi-dimensional representation of *P. oceanica* structure. A-D, control sites; E-H, impact sites. PC1= 46.3 % and PC2= 23.6%.

PER, average dissimilarity of 71.12 %) were *Maera knudseni* (ratio 1.01), *Lysianassa longicornis* (ratio 1.18), *Ampelisca* spp. (ratio 1.21), *Siphonocetes spp.* (ratio 1.01), *Aora spinicornis* (ratio 1.12) and *Dexamine spiniventris* (ratio 1.12). The decapod assemblage produced only a 58.39 % dissimilarity between control and impact sites. The most important species were *Thoralus cranchii* (ratio 1.15), *Processa modica* (ratio 1.12), *Hippolyte* spp. (ratio 1.04), *Ebalia edwardsi* (ratio 1.07), *Athanas nitescens* (ratio 1.11) and *Eurynome spinosa* (ratio 1.05).

Relationship with *P. oceanica* features

Density, cover and detritus characteristics of the *P. oceanica* meadows studied are shown in Table 2. Density was very similar among the sites, but showed significant differences ($p < 0.05$). The cover was reduced by around a 20% at the impact sites
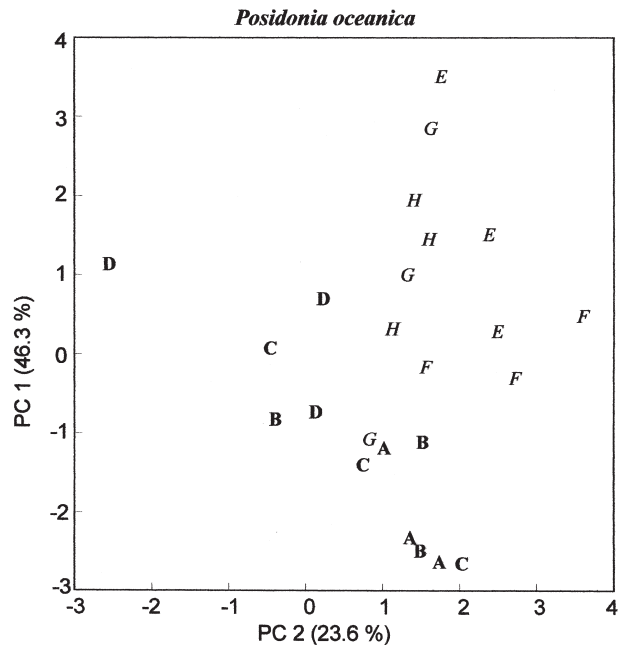
($p < 0.01$). Fine and coarse detritus were more abundant at the impact sites (5.08 and 4.42 gdw/m^2), showing significant differences. The fragments of rhizomes were a more variable feature among sites, with an average of 6.68 and 4.54 gdw/m^2 in control and impact sites, respectively, without showing significant differences (Table 2).

The ordination of PCA based on the overall *P. oceanica* features revealed the existence of clear differences among the different sampling sites, except for an impact site (G) which was distributed among the control sites (Fig. 4). The PC1 axis explains 46.3% of variation and the PC2 axis 23.6% of variation. By comparing Figures 3 and 4 it is possible to identify a similar pattern between the amphipod MDS and *P. oceanica* PCA.

TABLE 2. – Density of *Posidonia oceanica* (shoots per m^2), cover (%) and detritus (grams dry weight per m^2) values for the sampling locations.

Sampling locations	Density	Cover	Fine detritus	Coarse detritus	Fragmented rizhomes
A	25.6 ± 2.8	0.90 ± 0.03	2.39 ± 0.96	0.81 ± 0.02	1.55 ± 0.51
B	23.3 ± 1.4	0.87 ± 0.04	2.72 ± 0.57	1.50 ± 0.48	5.97 ± 3.77
C	22.3 ± 6.2	0.85 ± 0.06	2.27 ± 1.06	1.91 ± 0.88	7.66 ± 2.70
D	26.6 ± 3.8	0.85 ± 0.04	5.85 ± 0.78	3.34 ± 0.68	11.55 ± 3.47
Average (A-D)	24.5 ± 1.7	0.87 ± 0.02	3.31 ± 0.58	1.89 ± 0.38	6.68 ± 1.64
E	21.6 ± 0.6	0.61 ± 0.05	5.95 ± 1.12	5.84 ± 1.96	2.87 ± 1.26
F	19.7 ± 3.9	0.64 ± 0.06	3.78 ± 0.48	2.54 ± 0.49	2.22 ± 0.08
G	22.3 ± 1.3	0.70 ± 0.06	4.91 ± 1.87	4.85 ± 1.26	6.23 ± 0.55
H	21.3 ± 4.9	0.65 ± 0.05	5.65 ± 0.67	4.44 ± 1.22	6.82 ± 1.15
Average (E-H)	21.2 ± 1.4	0.65 ± 0.02	5.08 ± 0.56	4.42 ± 0.67	4.54 ± 0.71

Using RELATE, we confirmed this similar pattern between seagrass features and amphipod community, showing a significant value for the Spearman's rank correlation coefficient (global $\rho = 0.21$, $p<0.05$). Decapod community structure did not show significant correlation with seagrass features (global $\rho = -0.05$, not significant). BIO-ENV indicated that the features which better explain the amphipod distribution in *P. oceanica* meadows were detritus abundance (fine and coarse) and rhizomes fragments.

DISCUSSION

In the present study amphipod and decapod species were typically representative of *P. oceanica* community (García-Raso, 1990; Scipione, 1992). The crustacean communities showed different response to seagrass structure. Amphipod assemblages seem to be structured by the physical characteristics of *P. oceanica* meadows such as the remains of vegetal fragments. However biological relationship such as predation can also play an important role in structuring the communities (Martin-Smith, 1993). Decapods did not show any correlation with meadow structure. In both cases, the number of species was very similar between control and impact sites.

Degradation by bottom trawling changes the structure of *P. oceanica* seagrass, reducing density and cover, and increasing detritus compartment. The analysis of the overall structure of *P. oceanica* meadows showed the existence of a clear spatial gradient, which modified the habitat structure available to invertebrates. Variation in structural complexity may well be produced by other environmental factors, but human activities, such as trawling, play a very important role in the SE of the Iberian Peninsula because of the intensity of this impact (Sánchez Lizaso *et al.*, 1990).

Several studies have been conducted on amphipods associated with *P. oceanica* (Scipione and Fresi, 1984; Mazzella et al, 1989; Mazzella et al, 1992; Scipione, 1992; Scipione *et al.*, 1996). The amphipod species, which have emphasised the differences among meadows, have certain habitat fidelity. For example, *Lysianassa longicornis, Ampelisca* spp. and *Siphonocetes* spp. are related to soft bottoms and commonly associated with *P. oceanica* meadows, and *Dexamine spiniventris* is associated with leaf stratum (Ruffo, 1982, 1989, 1993; Scipione, 1992; Scipione *et al.*, 1996). The

importance of the depth gradient to the distribution of fauna has been stressed (Mazzella *et al.*, 1989). The present study has been carried out at the same depth (17 m depth) to avoid problems with the fauna change with depth.

The dependence of amphipod structure to the habitat created by seagrass blades near the sediment suggests the importance of complex habitat at this level and the predation pressures during daylight. Amphipod distribution can be correlated to the irregular and patchy distribution of detritus at the same depth, hence also affecting food availability for fish. The importance of seagrass litter to meadow structure has been previously reported. Basically, detritus is valuable both as a food source and for providing protection from predation due to the increase of habitat complexity. Major foods available to small mobile invertebrates within seagrass detritus include various phytoplankton, other invertebrates such as meiofauna, microscopic benthic food such as fungi, bacteria, microalgae, and macroscopic algae, and the detritus themselves (Darnell, 1967).

Direct behavioural observations show that many of these invertebrates appear to be concentrated along the leaf stratum at night when feeding frequencies are highest. For example, peracarids are known to nocturnally climb to and reside in the seagrass canopy while during the day they reside near the bottom (Howard, 1987; Sánchez Jerez *et al.*, 1999 a). If feeding was more selective with regards to dead material and detritus on the sediment, feeding frequencies would tend to show an opposite pattern. Feeding would have been concentrated while animals were on the sediment (Kitting, 1984).

Inversely, decapods did not show a correlation or statistical differences in relation to habitat disturbance. This result coincides with other studies which concluded that decapods do not establish a local population due to their great mobility and larval dispersion, and hence are not useful as community descriptors (Amanieu *et al.*, 1981). Many species of decapods in their postlarval stage are strong swimmers (5-10's of cm s^{-1}), they tend to be fairly long and are capable of swimming appreciable distances. Concurrently the currents over continental shelves have a potential role in the dispersal of decapod adults and larvae (Shanks, 1995). The combination of all of these processes, active and passive transportation, explains the lack of patterns of decapods in function to seagrass environment. Other works confirm this conclusion on large scales. For example,

density of seagrass shoots in beds was of little importance in determining the abundance of associated decapod assemblages over a large spatial scale in *Zostera capricorni* meadows, and showed confusing results in *Posidonia australis* (Worthington *et al.*, 1992). A model to account for variation in distribution and abundance of decapods settling to seagrass from plankton, points out that the abundance of animals among separate beds reflects the supply of larvae to this site (Bell and Westoby, 1986).

Previous attempts to correlate faunal densities within habitat parameters in seagrass meadows have described relationships between some parameters, such as leaf density, biomass, and habitat heterogeneity, with abundances of single species and the overall community structure (Jacobs and Huisman, 1982; Russo, 1989; Edgar, 1992; Edgar and Robertson, 1992; Connolly, 1995; Harlin *et al.*, 1996; Barberá *et al.*, 1997; Sánchez Jerez, *et al.* 1999 b). Most environmental impact studies focus on communities, because the structure at this level of investigation represents an integration of environmental conditions over a period of time (Warwick, 1993). Research on the amphipod community for detecting the influence of *P. oceanica* modification seem to be a strong indicator of the ecological implications of seagrass degradation, but also the study of single populations such as *Dexamine spiniventris, Lysianassa longicornis* or *Ampelisca* spp can be useful.

ACKNOWLEDGEMENTS

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