



Ecological implications of removing seagrass beds (*Zostera noltii*) for bivalve aquaculture in southern Portugal

Susana CARVALHO^{1*}, Ana MOURA¹ and Martin SPRUNG²

(¹) Instituto Nacional de Investigação Agrária e das Pescas (INIAP/IPIMAR) - Centro Regional de Investigação Pesqueira do Sul (CRIPSul), Av. 5 de Outubro, s/n P-8700-305 Olhão, Portugal

*Corresponding Author: Tel: +351 289 700500, Fax: +351 289 700535, E-mail: scarvalho@crisul.ipimar.pt

(²) CCMAR-FCMA; Universidade do Algarve, Campus de Gambelas P-8000-139 Faro, Portugal

Abstract: In the Ria Formosa lagoon (southern Portugal), *Zostera noltii* meadows have been cleared to make way for bivalve aquaculture. The present study aims to investigate the potential ecological impacts of *Z. noltii* removal using amphipods as bioindicators. Sampling was undertaken between August 2000 and August 2001 in an intertidal region of Ria Formosa at two different areas. One of the areas supports an ongoing commercial venture for the extensive culture of marine bivalves (*Ruditapes decussatus*), where *Z. noltii* beds have previously been removed and sand added, while the other area represents a natural *Z. noltii* habitat. At each monthly sampling date five replicates (0.02 m² each) were taken from both areas with a corer and sieved through a 0.5 mm mesh. Multivariate analysis and analyses of variance of faunal data showed significant differences between the amphipod assemblages. In general, *Z. noltii* beds presented higher densities, number of species, diversity and evenness values than the unvegetated area. Within *Z. noltii* beds the community was characterized by *Microdeutopus chelifer*, *Melita palmata*, *Gammarus insensibilis* and *Ampelisca* sp. A., while the unvegetated area presented *Leptocheirus pilosus*, *Siphonoecetes sabatieri* and *Ampelisca brevicornis* as the most characteristic species. Within both areas, the univariate variables analysed peaked in summer. The amphipod patterns among areas were time-dependent and this should be taken into account in future studies. Amphipoda appeared to be a potential ecological indicator group regarding seagrass degradation.

Résumé : Implications écologiques de l'élimination d'herbiers (*Zostera noltii*) pour l'aquaculture de bivalves dans le sud Portugal. Dans Ria Formosa, une lagune au sud du Portugal, les herbiers à *Zostera noltii* ont été éliminés pour réaliser la production des bivalves. Cette étude vise à évaluer l'impact écologique potentiel de l'élimination de ces herbiers en utilisant les amphipodes comme groupe bio-indicateur. La faune a été échantillonnée d'août 2000 à août 2001 dans la zone intertidale de deux régions différentes : une région soumise à la production extensive de bivalves (*Ruditapes decussatus*), où l'herbier de *Z. noltii* a été éliminé en opposition avec une région ayant conservé sa population naturelle de *Z. noltii*. Cinq réplicats (0,02 m² chacun) ont été obtenus dans chaque région et tamisés avec un tamis de 0,5 mm. Les résultats montrent des différences significatives des peuplements d'amphipodes des deux régions. Généralement, l'herbier de *Z. noltii* présente des densités, nombre d'espèces, diversité et équitabilité supérieurs à la zone sans végétation. Le peuplement de l'herbier de *Z. noltii* est caractérisé par *Microdeutopus chelifer*, *Melita palmata*, *Gammarus insensibilis* et *Ampelisca* sp. A, et la région sans végétation par *Leptocheirus pilosus*, *Siphonoecetes sabatieri* et *Ampelisca brevicornis*. Dans les deux régions, les plus fortes valeurs des paramètres biologiques analysés ont été observées en l'été. La dynamique des amphipodes a divergé au

cours de l'année et ce résultat doit être considéré lors de futures études. Le groupe des amphipodes a le potentiel de groupe bio-indicateur pour mettre en évidence cette perturbation écologique.

Keywords: Seagrass meadows • Bivalve Aquaculture • Macrofauna • *Zostera noltii* • Ria Formosa lagoon • Southern Portugal

Introduction

Seagrass beds represent an ecologically important feature of shallow water areas throughout the world. Seagrasses play a major role in coastal processes by providing food, shelter and physical heterogeneity, increasing the productivity of coastal waters, trapping and recycling nutrients and stabilising sediments (Schneider & Mann, 1991a; Edgar et al., 1994; Turner & Kendall, 1999; Hughes et al., 2000; Guidetti & Bussotti, 2002). Therefore, benthic invertebrate assemblages among seagrass beds are usually more productive and present higher abundance than in adjacent non-vegetated areas (Stoner, 1980; Lewis, 1984; Currás et al., 1993; Connolly, 1994; Edgar et al., 1994).

The Ria Formosa lagoon is the most important wetland ecosystem on the southern coast of Portugal, classified by the Ramsar Convention as a wetland of international interest. Within this lagoon, seagrass beds cover large areas of the bottom, either at subtidal (mainly *Cymodocea nodosa* (Ucria) Ascherson, 1869, but also *Zostera marina* Linnaeus, 1758 and *Zostera noltii* Hornemann, 1832) or intertidal levels (*Z. noltii*) (Asmus et al., 2000), and are known to be particularly important as nursery areas. However, due to the excellent conditions for aquaculture (natural geomorphology, climate conditions and low levels of industrial and urban pollution), approximately 10 km² of the lagoon's intertidal flats are occupied by clam growth banks, predominantly of *Ruditapes decussatus* (Linnaeus, 1748) (Falcão & Vale, 1990). Within Ria Formosa, there are 1587 growth banks for the culture of this species, with an annual estimated production of up to 7000 ton (Cachola, 1996). To make way for bivalve aquaculture, *Z. noltii* meadows have been cleared and sand transported from local beaches to the growth banks (Falcão & Vale, 1990), changing the sediment characteristics. Bivalves are collected using a hand-harvesting knife, revolving the sediment. These environmental disturbances most likely affect resident benthic communities, particularly because they are known to be highly associated to the sediment characteristics, such as particle size, organic content and food availability (Snelgrove & Butman, 1994; Wu & Shin, 1997). From this perspective, many studies reported that after the destruction of these habitats, abundance and species richness of benthic invertebrates and fish decline (Connolly & Butler, 1996), and the recovery of these meadows might take several years (Almeida, 1988).

Within seagrass meadows, Crustacea are one of the most important invertebrate group, both in terms of number of species and abundance, but also because of its importance as a trophic resource for fish (Edgar & Shaw, 1995; Hughes et al., 2000) and bird populations (Barnes, 1994). Because of their small size, high abundance, high growth rates, and consequently high secondary production rates crustaceans have a critical role in near-shore trophic transfer (Duffy & Hay, 2000). Among Crustacea, Amphipoda are probably the best studied worldwide and are considered as useful ecological indicators (Conlan, 1994; Conradi et al., 1997; Guerra-García & García-Gómez, 2001). In particular, with regards to seagrass meadows, they have already been pointed out as potential indicators of the ecological implications of seagrass degradation (Sánchez-Jerez et al., 2000) and are usually the best represented crustacean group (De Grave, 1999).

Several studies have been undertaken on the impact of seagrass meadow modification on benthic invertebrates (Connolly, 1994; Connolly, 1995; Connolly & Butler, 1996; Sánchez-Jerez et al., 2000), as well as on the comparison between vegetated and unvegetated areas (Currás et al., 1993; Edgar et al., 1994; Mattila et al., 1999; Turner & Kendall, 1999; Hindell et al., 2001; Barberá-Cebrián et al., 2002). Predation impact on benthic communities has also been the subject of other studies (Schneider & Mann, 1991b; Hindell et al., 2001). These works were, however, mainly focussed on *Posidonia oceanica* (Linnaeus) Delile, 1813, *C. nodosa* and *Z. marina* beds and less information is available regarding *Z. noltii* meadows (Currás & Mora, 1992; Sprung, 1994; Boaventura et al., 1999; Nakaoka et al., 2001).

The present study aims to investigate the impact of *Z. noltii* removal for bivalve aquaculture purposes, using amphipods as an indicator group of the benthic macrofauna, thus the hypothesis that the amphipod assemblages are similar in both natural and impacted areas was tested.

Material and Methods

The studied area, Ria Formosa lagoon, is a mesotidal lagoon extending for 55 km along the southern coast of Portugal (Algarve), covering an area of 100 km² (Sprung & Machado, 2000). Several barrier-islands protect a system of tidal flats and salt marshes of up to 3 km wide (Sprung,

2001) and lagoon waters are exchanged with the Atlantic Ocean by 6 deep inlets. Tidal amplitude varies from a maximum of 2.8 m during spring tide to 0.6 m at neap tide (Asmus et al., 2000). During mean low tide, approximately two thirds of the total area is intertidal whereas the remaining is occupied by salt marshes or salt-pans (Teixeira & Alvin, 1978 in Asmus et al., 2000).

The present survey was carried out in an intertidal area located near Olhão within the Ria Formosa Natural Park (Fig. 1). The study area is characterized by natural *Zostera noltii* meadows and ongoing commercial ventures for the extensive aquaculture of marine bivalves (*Ruditapes decussatus*) approximately 100 m apart. For the purpose of this study, the former will be termed either as vegetated or natural area, while the latter as unvegetated or impacted area.

Within the study area, sediments within *Zostera noltii* meadows were dominated by muddy sediments, with higher organic matter content than the observed for the unvegetated area (T. Drago, personal communication). The unvegetated area was characterized by muddy-sand sedi-

ments with low levels of organic matter. Porosity was also higher within the vegetated area. Generally, the nutrients analysed present higher values among the seagrass meadows than in the unvegetated area. The only exception was observed to the nitrate concentration, which was lower within vegetated sediments (Falcão & Gaspar, 2001).

Sampling was undertaken monthly between August 2000 and August 2001. All samples were taken at low tide using a corer and at each area 5 replicates (0.02 m² each) were collected randomly. The samples were sieved in the field through a 0.5 mm mesh and whenever possible identification was performed to species level.

Data on amphipod assemblages were analysed for abundance (A), the number of species (S), diversity (Shannon-Wiener index H' , \log_2) and evenness (Pielou's J') indices. These variables were calculated for each sampling area and period. Month and spatial differences in these variables were tested by analyses of variance (ANOVA) or Kruskal-Wallis (K-W) using month and area as fixed factors after verifying normality and homogeneity of variances. When ANOVA detected significant differences for any factor, the

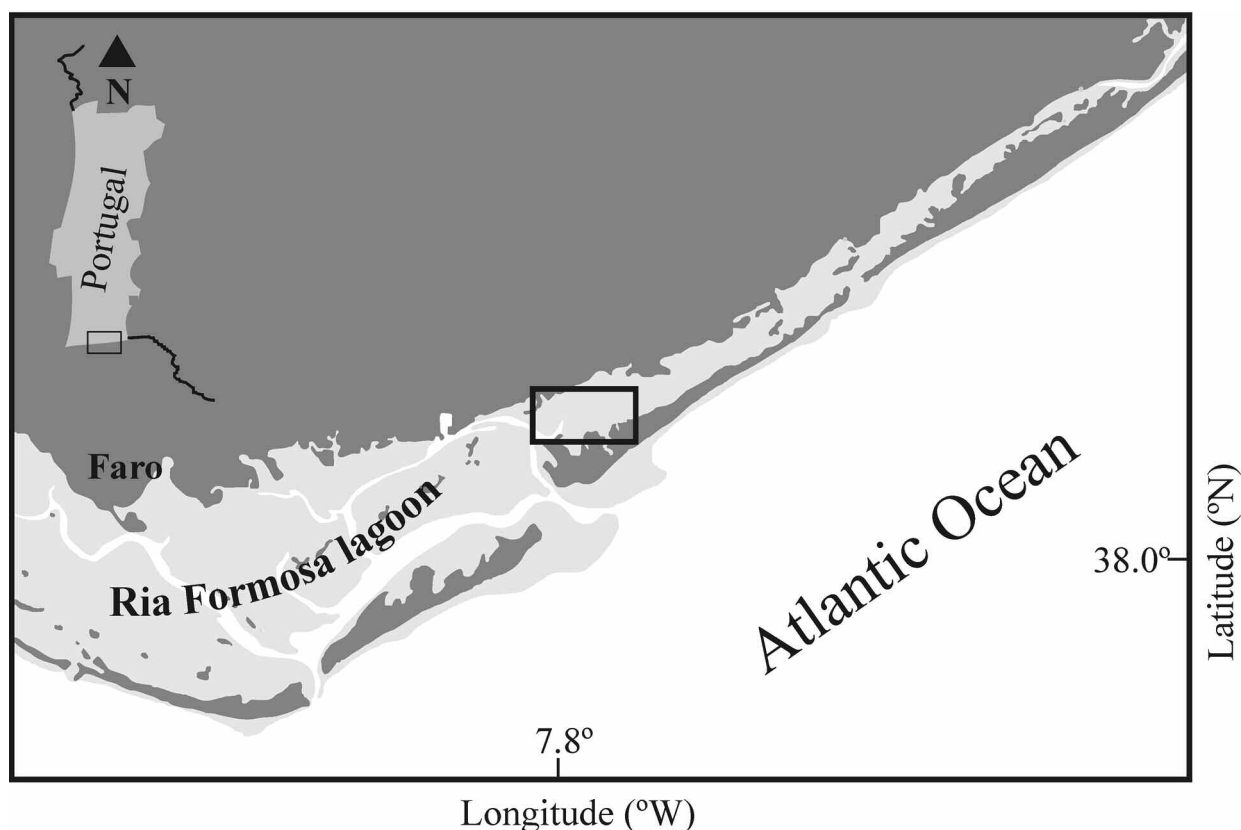


Figure 1. Ria Formosa lagoon, southern Portugal with reference to the location of the study area. Intertidal areas are shown in light grey.

Figure 1. Lagune de la Ria Formosa, au sud-est du Portugal indiquant la localisation de la zone d'étude. Les zones intertidales sont indiquées en gris clair.

Student-Newman-Keuls was applied. Statistical analyses were performed using SIGMASTAT statistical software.

Multivariate analyses were performed using the PRIMER v5.0 software package (Clarke & Gorley, 2001). Similarity between faunal data was analysed by ordination techniques (non-metric MDS) based on the Bray-Curtis similarity coefficient after square-root transformation and applying the unweighted pair group average algorithm. To test for statistically significant differences between the amphipod assemblages at the two study areas and sampling season, a two-way crossed ANOSIM test was performed using the same similarity matrix used for MDS ordination. After the detection of a significant difference, the same technique was employed to test pair-wise differences. In order to analyse the seasonal patterns during the sampling period, abundance data from each three months were pooled and analysed for autumn (September, October and November), winter (December, January and February), spring (March, April and May) and summer (June, July and August). Species having the greatest contribution to dissimilarity among areas and seasons were determined using the similarity percentages routine (SIMPER). The months of September and October from the unvegetated area were excluded from multivariate analysis, as no amphipods were present in the samples.

Results

A total of 1769 individuals belonging to 17 species were collected and identified. Within the *Zostera noltii* area, the mean number of species varied from 0.4 ± 0.5 species 0.02 m^{-2} (January) to 6.8 species 0.02 m^{-2} (June), while within the unvegetated area it ranged from 0 (September and October) to 3.2 ± 0.7 species 0.02 m^{-2} (August 2001; Fig. 2A). The mean abundance within the vegetated area varied from a minimum value of 0.6 ± 0.8 ind. 0.02 m^{-2} (January) to a maximum of 82.2 ± 23.0 ind. 0.02 m^{-2} (August 2001). In September and October no individuals were collected on the unvegetated area, while the maximum mean abundance (41.2 ± 47.9 ind. 0.02 m^{-2}) was observed in June (Fig. 2B). In both sampling areas, abundance varied strongly throughout the year with maximum values occurring during summer. Minimum values were obtained in spring, in the vegetated area, and in autumn for the impacted area (Fig. 2). The results of the two-way ANOVA showed a significant difference in Area ($F = 19.853$, $P < 0.001$) and in Month ($F = 10.258$, $P < 0.001$), as well as for the interaction between both factors ($F = 4.699$, $P < 0.001$). *Z. noltii* meadows showed a higher number of species than the impacted area, except in the February and April samples. Both areas were also statistically different with regards to this variable (K-W, $H =$

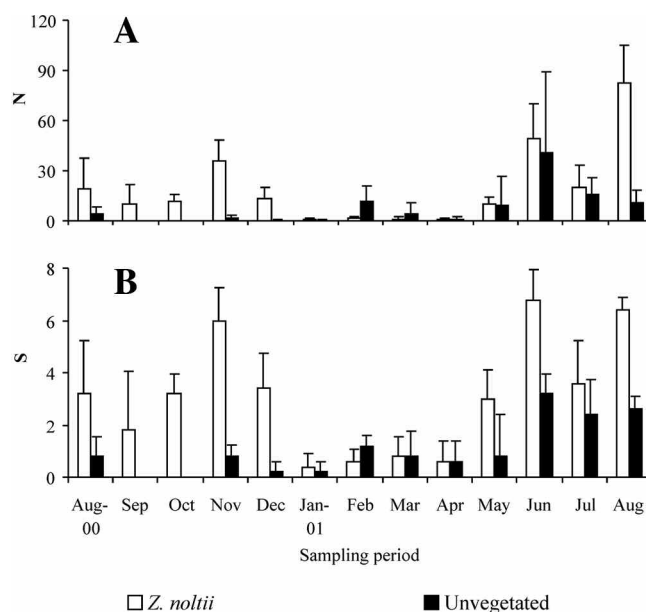


Figure 2. Temporal changes in (A) mean abundance (ind. $0.02\text{m}^{-2} \pm \text{SD}$) and (B) mean number of species at both areas.

Figure 2. Variations temporelles dans (A) abondance moyenne (ind. $0.02\text{m}^{-2} \pm \text{SD}$) et (B) nombre moyen d'espèces dans les deux zones.

95.582 , $df = 25$, $P < 0.001$). This was also observed in Shannon-Wiener diversity (H' , K-W, $H = 97.040$, $df = 25$, $P < 0.001$) and evenness (J' , K-W, $H = 83.446$, $df = 25$, $P < 0.001$) values. Despite some exceptions, H' and J' values were higher for the *Zostera* bed than for the unvegetated area (Fig. 3). The lowest values of H' were observed in January, February and April, while the highest values were observed in summer and autumn. *Leptocheirus pilosus* Zaddach, 1844, *Melita palmata* (Montagu, 1804) and *Microdeutopus chelifer* (Bate, 1862) were the most abundant species during the sampling period.

The MDS ordination plot showed a clear separation between the two studied areas (Fig. 4). The results of the ANOSIM test showed that both amphipod assemblages were significantly different ($R = 0.864$, $P = 0.001$), and also significantly differed amongst seasons ($R = 0.292$, $P < 0.01$) (Table 1). Nevertheless, significant differences were only observed for summer/spring and summer/winter pairs. Regarding factor "Area", SIMPER analysis identified *Siphonocetes sabatieri* de Rouville, 1894, *M. palmata*, *Gammarus insensibilis* Stock, 1966, *Ampelisca* sp. A, *L. pilosus*, *M. chelifer* and *Ampelisca brevicornis* (A. Costa, 1853), as the species having the greatest contribution to the dissimilarity between the 2 assemblages. The unvegetated area was characterized by *S. sabatieri*, *L. pilosus* and *A. brevicornis*, the latter exclusive to this area and *S. sabatieri* almost exclusive, presenting here 98.7% of its total abun-

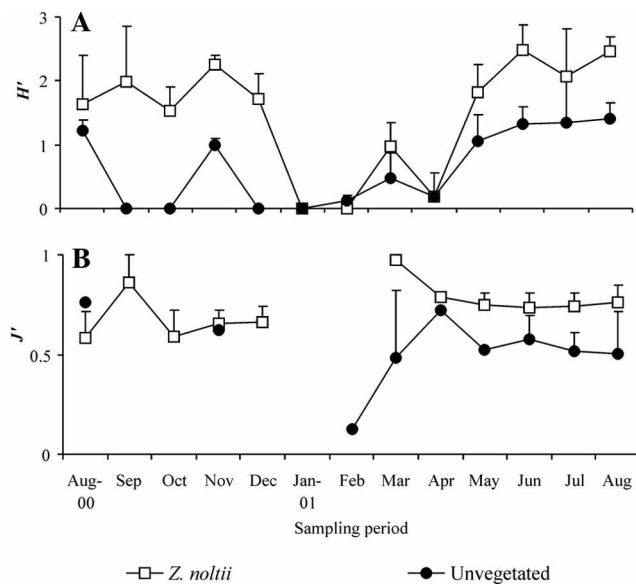


Figure 3. Temporal changes in (A) Shannon-Wiener diversity (H') and (B) Pielou's evenness (J') indices at both areas. Vertical lines indicates SD.

Figure 3. Variations temporelles dans (A) Diversité de Shannon-Wiener (H') et (B) Régularité de Pielou (J') indices des deux zones. Les lignes verticales indiquent SD.

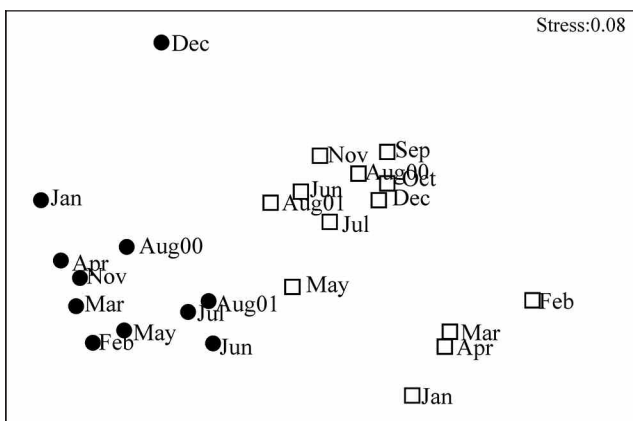


Figure 4. Non-metric multidimensional scaling analysis (MDS) using the square-root transformed abundance values. \square *Zostera noltii* samples; \bullet unvegetated area samples.

Figure 4. Analyse graduelle multidimensionnelle non-métrique (MDS) utilisant la racine carrée des valeurs d'abondance. \square échantillon de *Zostera noltii*; \bullet échantillons d'une zone sans végétation.

dance. Within *Z. noltii* beds, *M. palmata*, *Ampelisca* sp. A, *G. insensibilis* and *M. chelifera* were the most characteristic species. Despite this area's higher abundance, only *Ampelisca* sp. A was exclusive of this assemblage. The seasonal patterns of the most abundant species reflected the results of the species contribution along the study period -

factor "Season" (Table 1 & Fig. 5). *Leptocheirus pilosus* and *Perioculodes aequimanus* (Korssmann, 1880) were almost restricted to the summer months (Fig. 5). *Siphonocetes sabatieri* occurred throughout the year, but in lower numbers during autumn, while *Gammarella fucicola* (Leach, 1814) was representative of this season samples. *Gammarus insensibilis*, *M. palmata* and *M. chelifera* were more abundant from late spring to early winter (Fig. 5).

Discussion

In the present study, the vegetated area generally presented higher densities and number of species than the unvegetated area. This is in agreement with the results obtained by other authors (Edgar et al., 1994; Turner & Kendall, 1999; Hindell et al., 2001) and has been linked either to the structural habitat complexity and to the stability provided by the seagrass, to food availability and to the protection from predators (Schneider & Mann, 1991a; Connolly, 1994; Gambi et al., 1998; Olabarria et al., 1998). There is, however, no definitive explanation for this result. With regards to habitat complexity, invertebrates do not always select highly complex systems (Schneider & Mann, 1991a,b; Barberá-Cebrián et al., 2002). In a study performed on the relative importance of macrophyte shape and epiphyte cover in determining the distribution of epifaunal invertebrates within a seagrass bed, Schneider & Mann (1991a) found that both factors were determined by the distribution of epifaunal invertebrates, although the responses were highly specific. Thus, a positive correlation between habitat complexity and the increase in the number of species and abundance should not be regarded as a rule and should be interpreted considering the taxonomic group and the seagrass system (Barberá-Cebrián et al., 2002). The importance of predation in structuring assemblages of marine invertebrates has received considerable attention (Ambrose, 1984; Raffaelli & Milne, 1987; Mattila & Bonsdorff, 1989; Sardá et al., 1998; Hindell et al., 2001) but not a unique result. While for example, Raffaelli & Milne (1987), Mattila & Bonsdorff (1989) and Schneider & Mann (1991b) found that differential predation did not show evidence of a significant effect on the macrobenthic structure, Ambrose (1984) and Sardá et al. (1998) observed a positive correlation between predation and the composition of macrobenthic communities. The discrepancy may reflect the limitations of cage exclusion experiments on soft-bottoms (Ólafsson et al., 1994), indicating that the impact of predation cannot be generalized and that its nature and strength must consider different characteristics of the particular system being analysed (habitat, temporal scale, prey and predators characteristics) (Hindell et al., 2001). Concerning the relative importance of food and shelter for seagrass-associated invertebrates, Boström &

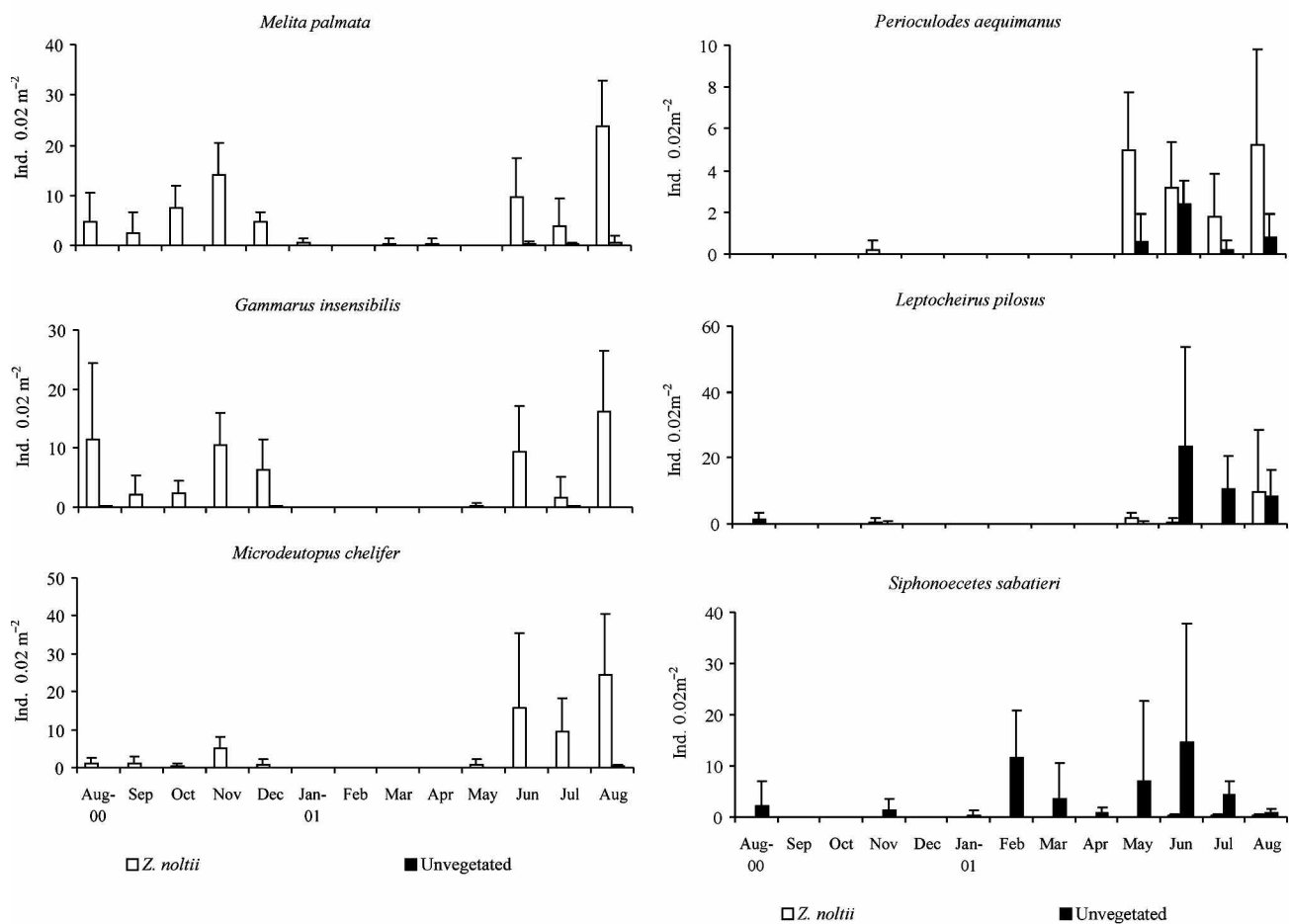


Figure 5. Temporal changes in the mean abundance (ind.0.02m⁻² ± SD) for the most abundant amphipod species within both areas.

Figure 5. Variations temporelle de la moyenne d'abondance (ind.0.02m⁻² ± SD) pour la plus abondante des espèces d'amphipodes dans les deux zones.

Mattila (1999) found that food type might be regarded as the universal mechanism that partially determines the establishment of grazers among seagrasses, as in the absence of predators, food was more important than shelter. In the present study, it is difficult to indicate the reason for the results obtained. Nevertheless, more than a single factor, an interaction between multiple factors with species-specific responses may be a clue for the explanation of the results observed. This is supported by the fact that most species showed habitat and seasonal preferences with different abundance patterns, which is in agreement with results from Nakaoka et al. (2001) for a *Zostera noltii* bed. The seasonal patterns of these amphipod assemblages seem to reflect the life cycles of the most abundant species. Within the natural area, higher densities and number of species were observed during summer and autumn, while during the winter and spring there was a clear decline in both variables. The same pattern was observed by Currás &

Mora (1992), Cunha et al. (1999) and Nakaoka et al. (2001), but not by Sprung (1994) or Sardá et al. (1998) who found peaks of abundance from spring to early summer. The present results could be explained by: a) higher growth of *Z. noltii* leaves during summer, allowing an increase of the "cage effect" within these meadows, providing higher food availability, and space to be occupied by the organisms, especially for epifauna; or b) the presence of dense algal mats, which are produced during winter after the first rains in autumn, and then gradually disappear during the following spring (Sprung, 1994). Ólafsson (1988) showed that these mats could impede invertebrate larvae settlement or even smother established seagrass beds (den Hartog & Polderman, 1975), reducing the infauna (Nicholls et al., 1981). Within the unvegetated area, density was found to be particularly high during summer, as a result of *Leptocheirus pilosus* recruitment in June. Evidence from other authors supports this study in that amphipods seem to actively

Table 1. Two-way crossed ANOSIM test for differences between area and season, using square-root transformed species abundance data and the Bray-Curtis similarity measure. Significance level for each comparison is $p \leq 0.05$ (* indicates statistical significance). s = summer; a = autumn; w = winter; sp = spring. Contributing species are those presenting a consistently large contribution to differences between samples from each group tested. Species are listed by decreasing importance.

Tableau 1. Test ANOSIM à 2 facteurs pour la mesure des différences entre la zone et la saison, utilisant la racine carrée des données de l'abondance des espèces et la mesure de similarité Bray-Curtis. Le niveau significatif pour chaque comparaison est $p \leq 0.05$ (* indique la signification statistique). s = été ; a = automne ; w = hiver ; sp = printemps. Les espèces concernées sont celles qui présentent une contribution significative aux différences entre les échantillons de chaque groupe testé. Les espèces sont répertoriées par ordre décroissant.

Variable	Global R	Significance Level	Pairwise test	Statistic value	Significance level	Contributing species
Area	0.864	0.001*				<i>S. sabatieri</i> , <i>M. palmata</i> , <i>G. insensibilis</i> , <i>Ampelisca</i> sp. A, <i>L. pilosus</i> , <i>M. chelififer</i> , <i>P. aequimanus</i>
Season	0.292	0.008*	s,a	0.374	0.069	<i>L. pilosus</i> , <i>M. palmata</i> , <i>G. insensibilis</i> , <i>M. chelififer</i> , <i>S. sabatieri</i> , <i>G. fucicola</i> , <i>P. aequimanus</i>
			s,w	0.398	0.004*	<i>L. pilosus</i> , <i>S. sabatieri</i> , <i>M. palmata</i> , <i>G. insensibilis</i> , <i>M. chelififer</i> , <i>P. aequimanus</i>
			s,sp	0.657	0.005*	<i>L. pilosus</i> , <i>S. sabatieri</i> , <i>M. palmata</i> , <i>G. insensibilis</i> , <i>M. chelififer</i> , <i>P. aequimanus</i>
			a,w	-0.012	0.475	<i>M. palmata</i> , <i>G. insensibilis</i> , <i>S. sabatieri</i> , <i>G. fucicola</i> , <i>M. chelififer</i>
			a,sp	0.235	0.275	<i>M. palmata</i> , <i>G. insensibilis</i> , <i>S. sabatieri</i> , <i>G. fucicola</i>
			w,sp	-0.25	0.940	<i>S. sabatieri</i> , <i>M. palmata</i> , <i>Ampelisca</i> sp. A, <i>A. brevicornis</i>

choose their substrata (Stoner, 1980; Lewis, 1984; Schneider & Mann, 1991a). Although most species were present in both areas, the two amphipod assemblages were significantly different, especially due to the differences observed in species abundance. While *Microdeutopus chelififer*, *Melita palmata*, *Gammarus insensibilis* and *Ampelisca* sp. A were strongly associated with the seagrass area, *Siphonocetes sabatieri*, *Leptocheirus pilosus* and *Ampelisca brevicornis* were the characteristic species within the unvegetated area.

In general, during the study period diversity and evenness were higher within the natural area than within the impacted zone. This is of particular interest and concern as more diverse systems support a larger species pool, which in turn might lead to a more efficient use of resources (Chapin et al., 1997; Tilman, 1999). These systems also enhance the coexistence of functionally similar species, providing stability (resistance and resilience) against ecosystem disturbance and species extinction (Walker, 1995; Chapin et al., 1997; Naeem & Li, 1997), with ecosystem processes becoming less vulnerable to disturbance.

Although seagrass beds have been demonstrated to be a valuable ecological feature by acting as nursery areas to commercially important species, in the southern coast of Portugal, like in other parts of the world, these systems are becoming increasingly degraded either for aquaculture and

other fishing practices (Sánchez-Jerez et al., 2000) or by pollution (Hughes et al., 2000). In the present study, changes in habitat characteristics imposed by bivalve culture may be affecting benthic communities, as the significantly different amphipod assemblages at each study site demonstrate. This taxonomic group appears to be a potentially strong ecological indicator for assessing seagrass degradation, which corroborates the results of Sánchez-Jerez et al. (2000). More in-depth studies, on the role of the species on ecosystem processes and the identification of potential keystone species are essential to avoid the irreversible loss of such a valuable ecosystem. The amphipod patterns among areas were time-dependent and this should be taken into account in future studies.

Acknowledgements

In memoriam of Martin Sprung deceased in 18th of June 2003. The authors would like to thank to João Cúrdia for his help on statistical analysis.

References

- Almeida A.J.T. 1988. Estrutura, dinâmica e produção da macrofauna acompanhante dos povoamentos de *Zostera noltii*

- e *Zostera marina* do estuário do Rio Mira. PhD thesis, University of Algarve, Faro, Portugal.
- Ambrose W.G. Jr. 1984.** Role of predatory infauna in structuring marine soft-bottom communities. *Marine Ecology Progress Series*, **17**: 109-115.
- Asmus R.M., Sprung M. & Asmus H. 2000.** Nutrient fluxes in intertidal communities of a South European lagoon (Ria Formosa) – similarities and differences with a northern Wadden Sea bay (Sylt-Rømø Bay). *Hydrobiologia*, **436**: 217-235.
- Barberá-Cebrián C., Sánchez-Jerez P. & Ramos-Esplá A.A. 2002.** Fragmented seagrass habitats on the Mediterranean coast, and distribution and abundance of mysid assemblages. *Marine Biology*, **141**: 405-413.
- Barnes R.S.K. 1994.** Macrofaunal community structure and life histories in coastal lagoons. In: *Coastal lagoon processes* (B. Kjerfve ed.), pp. 311-362. Elsevier Science. Elsevier Oceanography Series, 60: Amsterdam.
- Boaventura D., Fonseca L.C & Teles-Ferreira C. 1999.** Trophic structure of macrobenthic communities on the Portuguese coast. A review of lagoonal, estuarine and rocky littoral habitats. *Acta Oecologica*, **20**: 407-415.
- Boström C. & Mattila J. 1999.** The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. *Oecologia*, **120**: 162-170.
- Cachola R. 1996.** Viveiros de amêijoas *Ruditapes decussatus* da região algarvia. Instituto de Investigação das Pescas e do Mar, Lisboa. 134 pp.
- Chapin F.S. III, Walker B.H, Hobbs R.J, Hooper D.U., Lawton J.H., Sala O.E. & Tilman D. 1997.** Biotic control over the functioning of ecosystems. *Science*, **277**: 500-504.
- Clarke K.R. & Gorley R.N. 2001.** PRIMER (Plymouth Routines In Multivariate Ecological Research) v5: User Manual/Tutorial. PRIMER-E Ltd, Plymouth. 91 pp.
- Conlan KE 1994.** Amphipod crustaceans and environmental disturbance: a review. *Journal of Natural History*, **28**: 519-554.
- Connolly R.M. 1994.** Removal of seagrass canopy: effects on small fish and their prey. *Journal of Experimental Marine Biology and Ecology*, **184**: 99-110.
- Connolly R.M. 1995.** Effects of removal of seagrass canopy on assemblages of small, motile invertebrates. *Marine Ecology Progress Series*, **118**: 129-137.
- Connolly R.M. & Butler A.J. 1996.** The effects of altering seagrass canopy height on small, motile invertebrates of shallow Mediterranean embayments. *P.S.Z.N. Marine Ecology*, **17**: 637-652.
- Conradi M., Lopez-Gonzalez P.J. & García-Gómez J.C. 1997.** The amphipod community as a bioindicator in Algeciras Bay (Southern Iberian Peninsula) based on a spatial-temporal distribution. *P.S.Z.N. Marine Ecology*, **18**: 97-111.
- Cunha M.R., Sorbe J.C. & Moreira M.H. 1999.** Spatial and seasonal changes of brackish peracaridan assemblages and their relation to some environmental variables in two tidal channels of the Ria de Aveiro (NW Portugal). *Marine Ecology Progress Series*, **190**: 69-87.
- Currás A. & Mora J. 1992.** Variación temporal de la fauna bentónica en un fondo de *Zostera noltii* situado en la ría del Eo (NO España). *Boletín del Instituto Español de Oceanografía*, **8**: 299-309.
- Currás A., Sánchez-Mata A. & Mora J. 1993.** Estudio comparativo de la macrofauna bentónica de un fondo de *Zostera marina* y un fondo arenoso libre de cubierta vegetal. *Cahiers de Biologie Marine*, **35**: 91-112.
- De Grave S. 1999.** The influence of sedimentary heterogeneity on within maerl bed differences in infaunal crustacean community. *Estuarine, Coastal and Shelf Science*, **49**: 153-163.
- den Hartog D. & Poldermann P.J.G. 1975.** Changes in the seagrass populations of the Dutch Waddenzee. *Aquatic Botany*, **1**: 141-147.
- Duffy J.E. & Hay M.E. 2000.** Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs*, **70**: 237-263.
- Edgar G.J., Shaw C., Watson G.F. & Hammond L.S. 1994.** Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology*, **176**: 201-226.
- Edgar G.J. & Shaw C. 1995.** The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology*, **194**: 107-131.
- Falcão M. & Vale C. 1990.** Study of the Ria Formosa ecosystem: benthic nutrient remineralization and tidal variability of nutrients in the water. *Hydrobiologia*, **207**: 137-146.
- Falcão M. & Gaspar M.B. 2001.** Evaluation of the physical and chemical changes in the sediment and water before, during and after turnover caused by fishing activity. Instituto de Investigação das Pescas e do Mar, Final Report, Lisboa.
- Gambi M.C., Conti G. & Bremec C.S. 1998.** Polychaete distribution, diversity and seasonality related to seagrass cover in shallow soft-bottoms of the Tyrrhenian Sea (Italy). *Scientia Marina*, **62**: 1-17.
- Guerra-García J.M. & García-Gómez J.C. 2001.** The spatial distribution of Caprellidea (Crustacea: Amphipoda): a stress bioindicator in Ceuta (North Africa, Gibraltar area). *P.S.Z.N. Marine Ecology*, **22**: 357-367.
- Guidetti P. & Bussotti S. 2002.** Effects of seagrass canopy removal on fish in shallow Mediterranean seagrass (*Cymodocea nodosa* and *Zostera noltii*) meadows: a local-scale approach. *Marine Biology*, **140**: 445-453.
- Hindell J.S., Jenkins G.P. & Keough M.J. 2001.** Spatial and temporal variability in the effects of fish predation on macrofauna in relation to habitat complexity and cage effects. *Marine Ecology Progress Series*, **224**: 231-250.
- Hughes R.G., Lloyd D., Ball L. & Emson D. 2000.** The effects of the polychaete *Nereis diversicolor* on the distribution and transplanting success of *Zostera noltii*. *Helgoland Marine Research*, **54**: 129-136.
- Lewis F.G., III 1984.** Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. *Marine Ecology Progress Series*, **19**: 101-113.
- Mattila J. & Bonsdorff E. 1989.** The impact of fish predation on shallow soft bottoms in brackish waters (SW Finland); an experimental study. *Netherlands Journal of Sea Research*, **23**: 69-81.

- Mattila J., Chaplin G., Eilers M.R., Heck K.L. Jr., O'Neal J.P. & Valentine J.F. 1999.** Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research*, **41**: 321-332.
- Naeem S. & Li S. 1997.** Biodiversity enhances ecosystem reliability. *Nature*, **390**: 507-509.
- Nakaoka M., Toyohara T. & Matsumasa M. 2001.** Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otusuchi Bay, Japan. *P.S.Z.N.: Marine Ecology*, **22**: 379-395.
- Nicholls D.J., Tubbs C.R. & Haynes F.N. 1981.** The effect of green algal mats on intertidal macrobenthic communities and their predators. In: *Lower Organisms and their Role in the Food Web*. (G. Rheinheimer, H. Flugel, J. Lenz & B. Zeitzschel eds). *Kieler Meeresforschungen*, **5**: 511-520.
- Olabarria C., Urgorri V. & Troncoso J.S. 1998.** An analysis of the community structure of subtidal and intertidal benthic molluscs of the Inlet of Baño (Ría de Ferrol) (North-Western Spain). *American Malacological Bulletin*, **14**: 103-120.
- Ólafsson E.B. 1988.** Inhibition of larval settlement to a soft bottom benthic community by drifting algal mat: an experimental test. *Marine Biology*, **97**: 571-574.
- Ólafsson E.B., Peterson C.H. & Ambrose W.G.Jr. 1994.** Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: An Annual Review*, **32**: 65-109.
- Raffaelli D. & Milne H. 1987.** An experimental investigation of the effects of shorebird and flatfish predation on estuarine invertebrates. *Estuarine, Coastal and Shelf Science*, **24**: 1-13.
- Sánchez-Jerez P., Barberá-Cebrian C. & Ramos-Esplá A.A. 2000.** Influence of the structure of *Posidonia oceanica* meadows modified by bottom trawling on crustacean assemblages: comparison of amphipods and decapods. *Scientia Marina*, **64**: 319-326.
- Sardá R., Foreman K., Werme C.E. & Valiela I. 1998.** The impact of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks. *Estuarine, Coastal and Shelf Science*, **46**: 657-669.
- Schneider F.I. & Mann K.H. 1991a.** Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies. *Journal of Experimental Marine Biology and Ecology*, **145**: 101-117.
- Schneider F.I. & Mann K.H. 1991b.** Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *Journal of Experimental Marine Biology and Ecology*, **145**: 119-139.
- Snelgrove, P.V.R. & C.A. Butman, 1994.** Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: An Annual Review*, **32**: 111-117.
- Sprung M. 1994.** Macrobenthic secondary production in the intertidal zone of the Ria Formosa – a lagoon in Southern Portugal. *Estuarine, Coastal and Shelf Science*, **38**: 539-558.
- Sprung M. & Machado M. 2000.** Distinct life histories of peracarid crustaceans in a Ria Formosa salt marsh (S. Portugal). *Wetlands Ecology and Management*, **8**: 105-115.
- Sprung M. 2001.** Larval abundance and recruitment of *Carcinus maenas* L. close to its southern geographic limit: a case of match and mismatch. *Hydrobiologia*, **449**: 153-158.
- Stoner A.W. 1980.** Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Marine Ecology Progress Series*, **3**: 105-111.
- Tilman D. 1999.** The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**: 1455-1474.
- Turner S.J. & Kendall M.A. 1999.** A comparison of vegetated and unvegetated soft-sediment macrobenthic communities in the River Yealm, south-western Britain. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 741-743.
- Walker B. 1995.** Conserving biological diversity through ecosystem resilience. *Conservation Biology*, **9**: 747-752.
- Wu R.S.S. & Shin P.K.S. 1997.** Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology*, **128**: 475-487.