Distribution patterns of molluscan fauna in seagrass beds in the Ensenada de O Grove (Galicia, north-western Spain)

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The distribution and composition of molluscan assemblages of seagrass beds in the Ensenada de O Grove (north-western Spain), are described in this paper. The studied bottoms were mostly muddy and colonized predominantly by Zostera marina L., Z. noltei Hornemann, or by both species. Molluscan fauna was dominated by gastropods and bivalves, in terms of both species richness and abundance. A total of 7641 individuals belonging to 68 taxa was identified. The most abundant species were the gastropods Peringia ulvae, Retusa truncatula and Calyptraea chinensis and the bivalves Abra alba, Loripes lucinalis and Kurtiella bidentata. Cluster and multidimensional scaling analyses based on Bray–Curtis similarity coefficient showed two distinct faunal assemblages. Group A comprised intertidal sites colonized either by Z. noltei or by Z. marina and Z. noltei on muddy sand and sandy mud bottoms and subtidal sites exclusively colonized by Z. marina in the outer part of the inlet on muddy sand with the highest values of species richness and diversity. Group B consisted of sites characterized by low values of species diversity and a species composition typical of a 'reduced Macoma community'. The sorting coefficient and the combination of gravel, sorting coefficient and carbonates content (BIOENV analyses) and the salinity of bottom water and depth (canonical correspondence analyses) were the most important abiotic variables in explaining the structure of the molluscan assemblage.

Keywords: molluscs, seagrass, Zostera, multivariate analysis, Atlantic Ocean, Spain

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INTRODUCTION

Seagrass meadows are present across the world in temperate and tropical latitudes (Hemminga & Duarte, 2000). The rhizomes, leaves and roots of seagrasses provide different microhabitats for a great diversity of associated organisms (Orth & Heck, 1980; Webster et al., 1998; Attrill et al., 2000) that can also provide shelter and protection from predators (Heck & Thoman, 1981). Seagrass meadows are areas of high productivity in estuarine and coastal environments (Hemminga & Duarte, 2000). Many organisms feed on the organic matter and detritus resulting from the decomposition and degradation of plant and supporting epiphytes as well as on particles retained among the leaves of seagrasses (Kitting et al., 1984; Fredriksen et al., 2004; Hily et al., 2004). Furthermore, seagrass beds are open systems that may act as nurseries and provide refuge and foraging habitats for fishes and crustaceans (Thayer et al., 1984; Gotceitas et al., 1997). The extensive rhizome network of seagrasses contributes to avoid coastal erosion by stabilizing sediments (Davison & Hughes, 1998).

Anthropogenic activities in coastal areas, such as dredging, construction of artificial structures and bottom trawling, are having a negative impact on seagrass meadows, which are being reduced in their extent or, in many cases, are completely disappearing from many areas (Sheridan, 2004; Waycott *et al.*, 2009). Loss and fragmentation of seagrass meadows can have important consequences for maintenance of biodiversity and productivity of coastal waters (Orth *et al.*, 1984, 2006; Rueda *et al.*, 2009b). Thus, there is a need to study and protect these important habitats.

Seagrass beds of *Zostera marina* L. and *Zostera noltei* Hornemann are a major feature of estuaries and shallow coastal areas in the northern hemisphere (Duffy & Harvilicz, 2001). On the Atlantic Coast of Spain, *Z. marina* and *Z. noltei* are mostly present along the Galician coast (northwestern Spain), forming extensive meadows in intertidal and shallow subtidal areas (Laborda *et al.*, 1997). Because of their importance seagrass meadows are protected through the 'Habitat' directive 92/43/CEE. However, studies on their associated macrofaunal assemblages along the Galician coast have been scarce (Currás & Mora, 1990; Currás *et al.*, 1993; Junoy, 1996; Esquete *et al.*, 2011).

Molluscs are important components of benthic marine fauna, both in abundance and species richness (Lewis & Stoner, 1983; Snelgrove, 1998; Webster *et al.*, 1998). Seagrass meadows house a large diversity of molluscs (Heminga & Duarte, 2000; Rueda & Salas, 2008) which can numerically dominate these habitats (Boström & Bonsdorff, 1997). For example, large densities of some epifaunal grazing gastropods, such as hydrobiids were recorded in *Zostera* beds (Currás & Mora, 1990) and the abundance of their populations may be explained by their relation to the presence of seagrass (Cardoso *et al.*, 2004).

The main objectives of this paper are to: (1) describe the composition and abundance of molluscan fauna in the extensive *Z. marina* and *Z. noltei* beds of the Ensenada de O Grove (Galicia, north-western Spain); (2) study the spatial distribution of the molluscs within *Z. marina* and *Z. noltei* beds; and (3) identify the main environmental variables that explain the observed patterns of distribution and diversity.

The benthic fauna of this inlet have not been extensively studied and therefore this paper represents the first quantitative survey on the molluscs associated with seagrass beds in the Ensenada de O Grove and it may provide baseline data for management and preservation of the aforementioned seagrass beds.

MATERIALS AND METHODS

Study area

The Ensenada de O Grove is located in the inner part of the Ría de Arousa (Galicia, north-western Spain) between $42^{\circ}41'N-42^{\circ}28'N$ and $9^{\circ}01'W-8^{\circ}44'W$ (Figure 1). This



Fig. 1. Map of the Ensenada de O Grove (Galicia, Spain) showing the location of sampling sites with seagrasses.

inlet with an area of 15 km² is sheltered from wave action and dominant winds due to the presence of the Peninsula de O Grove in the mouth. The Ensenada de O Grove is influenced by freshwater inputs from rivers in the mouth and inner part and its soft-bottoms are mostly intertidal or shallow subtidal $(\leq_{20} \text{ m})$ with large areas colonized by the seagrasses Z. marina and Z. noltei. This inlet has a great socio-economic importance, especially with regard to mussel culture on rafts, bivalve collection and fishing. This inlet of high ecological value and international importance is protected through the current legislation due to the presence of Zostera beds (Habitat Directive, Directive 92/43/CEE) and its ecological value for birds (ZEPAS, 1979 and RAMSAR Convention, 1990). In addition, this inlet has been included as a natural space of importance for the European Community and listed in the 'European Nature Net 2000'.

Sample collection

The present study was carried out in the soft bottoms colonized by *Z. marina* and *Z. noltei* located in the inner part of the Ensenada de O Grove. It was included in a broader cartography of the benthic fauna associated with the soft bottoms of the inlet. A total of 10 sites were quantitatively sampled during October and November 1996 with a Van Veen grab in order to compare our results with the remaining samples of the Ensenada de O Grove. Five replicate samples were collected from each site accounting for a total area of 0.28 m^2 . Samples were sieved through a 0.5 mm mesh and fixed in 10% buffered formalin. Samples of surface and bottom water were also taken at each site for salinity and temperature measurements. An additional sample of sediment was collected from each site in order to analyse particle-size composition and content in carbonate and organic matter.

Laboratory analysis

Molluscs were sorted out from the sediment under a stereomicroscope, identified (to species level when possible), counted and preserved in 70% ethanol. The scientific names and the systematic order of species were revised following the CLEMAN database (www.somali.asso.fr/clemam). Grain-size analyses were conducted considering the following granulometric fractions: gravel (>2 mm); very coarse sand (2-1 mm); coarse sand (1-0.5 mm); medium sand (0.5-0.25 mm); fine sand (0.25-0.125 mm); very fine sand (0.125-0.063 mm); and silt/clay (<0.063 mm). Median grain size (Q₅₀) and sorting coefficient (S₀) were also determined for each sample. Sedimentary types were characterized according to the findings of Junoy (1996). Carbonate content (%) was estimated by treating the sample with hydrochloric acid. Total organic matter (%) was estimated from the weight loss on combustion for 4 hours at 450°C.

Data analyses

Several univariate parameters were determined for each site: total abundance (N); species richness (S); the Shannon– Wiener diversity index (H', \log_2); and Pielou's evenness (J). Mollusc assemblages were determined through nonparametric multivariate techniques as described by Field *et al.* (1982) using the PRIMER 6 software package (Clarke & Warwick, 1994). Abundance data were previously fourthroot transformed to downweight the contribution of the most abundant species. A matrix of similarities among sampling sites was constructed using the Bray-Curtis similarity coefficient. From this matrix, a classification of the sampling sites was done by cluster analysis and tested by the Simprof test. A non-metric multidimensional scaling (MDS) was applied to show the ordination of sampling sites. The one-way ANOSIM test was used to determine differences in faunal composition among sites. The SIMPER procedure was also applied in order to identify species that contributed to dissimilarities among assemblages. Species presented in each assemblage were classified according to the Constancy and Fidelity indices. Species which occurred with more than 1% of the total specimens in a site or group of sites were considered as 'dominant' (Junoy, 1996). The Frequency \times Dominance product was calculated in order to know the numerical importance of species.

Relationships among mollusc distribution and the measured environmental variables were determined using the BIO-ENV procedure (PRIMER) and the canonical correspondence analysis (CCA) using the CANOCO v 4.02 (Canonical Community Ordination) package (Ter Braak, 1988). The forward selection was employed in the latter to detect which variables explained the most variance in the species data. The following variables were considered in these analyses: organic matter (%); carbonate (%); pH and temperature of surface and bottom water; pH and temperature of sediment; granulometric fractions (%); median grain size (mm); and sorting coefficient and depth (m). Variables expressed in percentages were previously $\log (x + 1)$ transformed. These variables and the aforementioned univariate measures were also analysed through the non-parametric Spearman's rank test in order to detect significant relationships among variables (SPSS 15 software package).

RESULTS

Sediments

Sites colonized by seagrasses had muddy sediments with moderate to high content of silt/clay (6–62%). Sand content was generally greater in subtidal sites and the sedimentary types ranged from muddy sand to mud (Table 1). Water salinity was mainly low (<33%) specifically in stations 34 and 37 close to the river (20‰). Carbonate content ranged from 5 to 10% and the percentage of organic matter ranged from low values in subtidal sites (1.3%) to higher ones (up to 15.5%) in intertidal inner areas (Table 1).

Abundance, species richness, diversity and evenness

A total of 7641 individuals belonging to 68 species were collected (Appendix). Bivalves and gastropods were the most abundant groups (51.9% and 47.9% of total abundance, respectively) and had the greater values of species richness (38 and 27, respectively). Polyplacophorans were represented by 3 species and 0.2% of total abundance. Among gastropods the families Trochidae (genera *Gibbula* and *Jujubinus*), Nassariidae (genera *Nassarius* and *Cyclope*) and Littorinidae (genus *Littorina*) comprised the higher number of species

| Grove. (| Granulometric fractions (%) (MS | s, medium sand; sedimentary ty | FS, fine sand ype (MS, mu | ; VFS, very fir ddy sand; SM | 1e sand); Q ₅₀ , I, sandy mud | median grain ; M, mud); % | size (mm); S OM, percenta | o, sorting coeffic 1ge of organic m | ient; Sel., sele 1atter; %Carb | ction (M, m ., carbonate | oderate; MWS s percentage. | s, moderate well | sorted; P, poor |); S. Type, |
|----------|---------------------------------|-----------------------------------|------------------------------|---------------------------------|---|------------------------------|------------------------------|--|-----------------------------------|-----------------------------|-------------------------------|------------------|-----------------|-------------|
| Site | Coordinates | Depth | SSW | SBW | MS | FS | VFS | Silt/clay | Q_{5o} | $\mathbf{S}_{\mathbf{o}}$ | Sel | S. Type | WO% | %Carb |
| 24 | 42°29′7 ″N8°50′15 ″W | S | 29.5 | 29.0 | 3.82 | 40.14 | 40.68 | 12.01 | 0.12 | 1.52 | М | MS | 3.93 | 7.58 |
| 26 | 42°28′45 ′′N8°50′45′′W | S | 28.0 | 30.0 | 10.19 | 46.14 | 25.89 | 6.41 | 0.17 | 1.50 | Μ | MS | 1.37 | 10.05 |
| 27 | 42°29′45 ′′N8°50′15 ′′W | S | 29.0 | 32.0 | 2.37 | 37.80 | 47.89 | 10.90 | 0.11 | 1.48 | Μ | MS | 2.98 | 8.46 |
| 31 | 42°28′15 ′′N8°50′45 ′′W | I | 32.0 | 32.5 | 4.76 | 58.03 | 23.20 | 10.59 | 0.16 | 1.45 | Μ | MS | 2.80 | 8.69 |
| 34 | 42°27′45 ″N8°50′15 ″W | I | 20.0 | 30.0 | 10.97 | 20.85 | 33.93 | 32.05 | 0.18 | 1.82 | Μ | SM | 5.08 | 7.22 |
| 35 | 42°27′45 ″N8°51′45 ″W | Ι | 32.0 | 30.5 | 14.48 | 64.63 | 11.40 | 6.75 | 0.19 | 1.30 | MWS | MS | 1.32 | 10.46 |
| 37 | 42°27′45 ′′N8°49′15 ′′W | I | 21.0 | 20.0 | 3.88 | 11.77 | 19.49 | 61.61 | 0.10 | 2.31 | Р | Μ | 15.55 | 5.41 |
| 38 | 42°27′15 ′′N8°52′15 ′′W | I | 32.0 | 33.0 | 5.13 | 18.51 | 29.66 | 37.02 | 0.11 | 1.70 | Μ | SM | 10.75 | 7.40 |
| 39 | 42°27′15 ″N8°51′15 ″W | Ι | 31.0 | 33.0 | 4.72 | 43.58 | 31.07 | 18.22 | 0.13 | 1.61 | Μ | MS | 3.32 | 9.59 |
| 40 | 42°27′15 ′′N8°51′45 ′′W | I | 28.0 | 32.0 | 9.71 | 18.36 | 13.17 | 27.44 | 0.18 | 1.99 | Ь | SM | 7.10 | 7.17 |
| | | | | | | | | | | | | | | |

Table 1. Geographical coordinates (Coord.), depth (S, subtidal; I, intertidal), salinity of surface water (%) (SSW), salinity of bottom water (SBW) and sedimentary characteristics of sampling sites at the Ensenada de O

(5, 5 and 3 spp., respectively) whereas the families Hydrobiidae, Retusidae, Trochidae and Calyptraeidae were the dominant in terms of abundance (2819, 296, 118 and 104 indiv./0.28 m², respectively). The gastropod Peringia ulvae (Pennant, 1777) was the numerically dominant species, particularly in site 37 (a muddy site colonized by Z. noltei close to a river) and site 40 (a sandy mud site with Zostera spp.). Other abundant and widespread gastropod species were Retusa truncatula (Bruguière, 1792) numerically dominant in sites 26, 27, 35 and 39, and Calyptraea chinensis (Linnaeus, 1758) dominant in sites 26, 27 and 31. Among bivalves, the family Veneridae comprised the highest number of species (7 spp.) including the genera Chamelea, Dosinia and Venerupis whereas the families Lucinidae (genera Loripes and Myrtea), Semelidae (genus Abra), Montacutidae (genus Kurtiella) and Cardiidae (genera Parvicardium and Cerastoderma) were the dominant in terms of abundance (2613, 731, 315 and 117 indiv/0.28 m², respectively). The bivalve Abra alba (Wood, 1802) was dominant in sites 35, 38, 39 and 40, and Loripes lucinalis (Lamarck, 1818) in sites 35, 37 and 40. On the other hand, the bivalve Kurtiella bidentata (Montagu, 1803) was abundant in sites colonized by Z. marina (24, 26, 27 and 31).

The lowest value of abundance was recorded in site 34 (178 individuals) and site 26 (358 ind.) whereas the greatest abundance were recorded in sites 37 (1896 ind.), 40 (1268 ind.) and 35 (1020 ind.) (Table 2). Species richness ranged from 30 (site 27) to 10-11 (sites 34 and 37). Diversity (H') showed generally moderate values (2.18-3.12). Lowest values were determined for sites 34, 37, 38 and 39 (<2). Evenness (J) showed moderate values which ranged from 0.44 to 0.64 except in sites 37 and 38 (0.15 and 0.20) where there was a low value of species richness and great numerical dominance by P. value (site 37) and L. lucinalis (site 38). Diversity showed a positive correlation through non-parametric Spearman's correlation coefficient with carbonate content (P < 0.01). Diversity and species richness were negatively correlated with silt/clay content and percentage of organic matter (P <0.01).

Multivariate analyses

The ANOSIM test revealed the existence of significant differences among sites (global R: 0.796, P < 0.001). Two main groups of sites were determined from the dendrogram resulting from cluster analysis at 45% similarity level (Figure 2).

Table 2. Total abundance (N, individuals per 0.28 m²), species richness
(S), Shannon-Wiener diversity index (H', log₂) and Pielou's evenness
(J) for each sampling site in the Ensenada de O Grove.

| Site | Ν | S | \mathbf{H}' | J |
|------|------|----|---------------|------|
| 24 | 544 | 20 | 2.37 | 0.55 |
| 26 | 358 | 22 | 2.81 | 0.63 |
| 27 | 544 | 30 | 3.12 | 0.64 |
| 31 | 454 | 22 | 2.60 | 0.58 |
| 34 | 178 | 10 | 1.45 | 0.44 |
| 35 | 1020 | 26 | 2.56 | 0.54 |
| 37 | 1896 | 11 | 0.50 | 0.15 |
| 38 | 642 | 18 | 0.83 | 0.20 |
| 39 | 737 | 20 | 1.87 | 0.43 |
| 40 | 1268 | 20 | 2.18 | 0.50 |



Fig. 2. Dendrogram produced by cluster analysis based on Bray-Curtis similarity index on fourth-root transformed data of mollusc abundances.

Group A consisted of 7 sites which were further grouped in three subgroups: A1 (sites 24, 26, 27 and 31); A2 (sites 35 and 39); and A3 (site 38). Subgroup A1 contained muddy sand bottoms with *Z. marina* and subgroup A2 comprised muddy sand and sandy mud bottoms colonized by *Z. noltei* or by both seagrass species. Group B comprised sites 34, 40 and 37; the first two had sandy mud colonized by both seagrass species (B1) and the third site was a muddy bottom exclusively colonized by *Z. noltei* (B2). MDS ordination (Figure 3) confirmed the groups determined from the dendrogram.

The SIMPER analysis (Table 3) showed that the species which had a major contribution to similarity among sites of subgroup A1 were *L. lucinalis, K. bidentata, P. ulvae, R. truncatula, Venerupis corrugata* (Gmelin, 1790) and *Parvicardium exiguum* (Gmelin, 1791). In the subgroup A2 the responsible species were *L. lucinalis, P. ulvae, R. truncatula, Cyclope neriteus* (Linnaeus, 1758) and *A. alba.* Subgroup B1 comprised sites 34 and 37 and the species which most contributed to similarity were *P. ulvae, A. alba* and *L. lucinalis.*

The major responsible taxa for dissimilarities between subgroups A1 and A2 were *K. bidentata* (mainly in group A1), *Eatonina fulgida* (Adams J., 1791) (absent in group A1), *Thracia papyracea* (Poli, 1791) (absent in subgroup A2) and *C. neriteus* (mainly in group A2) (Table 4). The species mostly contributing to dissimilarities between subgroup A1 and B1 were *K. bidentata*, *R. truncatula*, *C. chinensis* and *V. corrugata* (the latter absent in B1) and *R. truncatula*, *C. neriteus*, *E. fulgida* (absent in B1) and *L. lucinalis* (mainly in A2) between B1 and A2 subgroups.

The BIOENV procedure (Table 5) indicated that the environmental variable best explaining distribution of fauna was the sorting coefficient (ρ w: 0.700) and the combinations of gravel, sorting coefficient and carbonate content (ρ w: 0.680).

The CCA and Monte Carlo test showed that the ordination of sites was determined by sorting coefficient and depth. Axes I and II of CCA ordination accounted for 45.8% of variance. For this analysis only nine variables were used due to the low number of sites to avoid multicollinearity (Ter Braak, 1986; Mercier *et al.*, 1992). Sorting coefficient and coarse sand content showed a strong positive correlation with axis I. This axis also showed a negative correlation with carbonate content and salinity of bottom water, very fine sand content and depth. Axis II had a positive correlation with salinity of bottom water, carbonate content, medium sand content, median grain size and a negative correlation with depth, very fine sand content and sorting coefficient. The graphic representation of CCA showed that subgroup A1 (24, 26, 27 and 31) was related to very fine sand and depth (Figure 4).



Fig. 3. Non-metric multidimensional scaling ordination plot based on Bray-Curtis similarity index.

Table 3. Results of SIMPER analysis showing the main contributing taxa to the similarity among subgroups determined from dendrogram and non-metric multidimensional scaling. Average abundance (Av. Ab.), average similarity (Av. Simil.), ratio value (similarity/standard deviation, Sim./SD) and percentage of cumulative similarity (Cumul. Simil.) were also included.

| (Av. Simil : 60.87) | Av. Ab | Simil. Av | Sim/SD | Simil. | Cum. Simil (%) |
|----------------------|-----------|--------------|--------|--------|-------------------|
| | | | | (70) | 011111 (70) |
| Loripes lucinalis | 146.00 | 8.57 | 9.10 | 14.09 | 14.09 |
| Kurtiella bidentata | 77.75 | 6.32 | 11.36 | 10.39 | 24.48 |
| Hydrobia ulvae | 93.25 | 5.07 | 2.49 | 8.34 | 32.81 |
| Retusa truncatula | 24.50 | 5.02 | 9.60 | 8.25 | 41.07 |
| Venerupis corrugata | 18.00 | 4.92 | 8.30 | 8.08 | 49.15 |
| Parvicardium exiguum | 13.00 | 4.78 | 8.28 | 7.85 | 57.00 |

Group A2

Site 35 (intertidal, *Zostera noltei*) and site 39 (intertidal, *Z. marina* and *Z. noltei*)

| (Av. Simil.: 61.64) | Av. Ab. | Simil. Av. | Sim/SD | Simil. (%) | Cum. Simil. (%) |
|---------------------|------------|---------------|--------|---------------|--------------------|
| Loripes lucinalis | 432.50 | 11.08 | - | 17.98 | 17.98 |
| Peringia ulvae | 115.00 | 6.99 | - | 11.34 | 29.32 |
| Retusa truncatula | 92.00 | 5.89 | - | 9.55 | 38.87 |
| Cyclope neriteus | 19.50 | 5.17 | - | 8.38 | 47.25 |
| Abra alba | 117.00 | 4.33 | - | 7.02 | 54.27 |

Group B1

Sites 37 (intertidal, Z. noltei) and site 34 (intertidal, Z. marina and Z. noltei)

| (Av. Simil.: 54.90) | Av. Ab. | Simil. Av. | Sim/SD | Simil. (%) | Cum. Simil. (%) |
|---------------------|------------|---------------|--------|---------------|--------------------|
| Peringia ulvae | 879.50 | 15.37 | - | 28.00 | 28.00 |
| Abra alba | 67.50 | 13.63 | - | 24.82 | 52.82 |

These sites were mostly subtidal muddy sand bottoms colonized by *Z. marina*. Subgroups A2 (35 and 39) and A3 (38) and group B constituted by subgroup B1 (37 and 34) and subgroup B2 (40) were distributed along the positive region of Axis I. However, site 37, a mud flat exclusively colonized by *Z. noltei* and characterized by low values of salinity and carbonate content was represented apart from the other sites with a negative correlation with Axis II. Subgroups A2 and A3 appeared to be transitional groups between subgroup A1 and group B.

Description of faunal assemblages

Faunal assemblages of subgroups A1 and A2 and group B obtained through multivariate analyses are described below. Their faunistic and abiotic characteristics as well as the constant species for each group, the Fidelity index and Frequency \times Dominance (F \times D) product are summarized in Table 6.

Subgroup A1 was mainly characterized by subtidal muddy sandy bottoms with moderate selection, and low percentage of organic matter content. This group presented a high abundance (1900 ind.) and the greatest values of species richness (50 spp.) ranging from 20 to 30 species per site. The greatest value of species richness was recorded for site 27 (30). This subgroup was numerically dominated by the epifaunal gastropods *P. ulvae* and *C. chinensis*, the opisthobranch *R. truncatula* and the bivalves *L. lucinalis*, *K. bidentata*, *V. corrugata* and *P. exiguum*. Values of diversity ranged from 2.37 to 3.12 and evenness between 0.55 and 0.64.

Subgroup A2 only comprised two sites over muddy sand bottoms characterized by low values of percentage of organic matter content ranging from 1.32 to 3.32 and carbonate content ranging from 9.59 to 10.46. This subgroup A2

 Table 4. Results of SIMPER analysis showing the main contributing taxa to the dissimilarity among subgroups determined from dendrogram and nonmetric multidimensional scaling. Average abundance (Av. Ab.), average dissimilarity (Av. Disim.), ratio value (dissimilarity/standard deviation, Disim./ SD) and percentage of cumulative dissimilarity (Cum. Disim.) were also included.

Groups A1 and A2

A1: Sites 24, 26, 27 and 31 (subtidal, Zostera marina)

A2: Site 35 (intertidal, Zostera noltei) and 39 (intertidal, Z. marina and Z. noltei)

| Species | Av. | Av. | Disim. | Dis/SD | Disim. | Cum. Disim. |
|----------------------|----------|----------|--------|--------|--------|-------------|
| 1 | Ab. | Ab. | Av. | | (%) | (%) |
| | Group A1 | Group A2 | | | | |
| Kurtiella bidentata | 77.75 | 2.00 | 2.43 | 3.83 | 5.38 | 5.38 |
| Eatonina fulgida | 0.00 | 15.00 | 2.09 | 1.95 | 4.64 | 10.02 |
| Thracia papyracea | 4.50 | 0.00 | 1.95 | 6.89 | 4.33 | 14.35 |
| Cyclope neriteus | 0.50 | 19.50 | 1.86 | 2.11 | 4.12 | 18.47 |
| Myrtea spinifera | 16.00 | 0.50 | 1.85 | 1.90 | 4.09 | 22.56 |
| Peringia ulvae | 93.25 | 115.00 | 1.36 | 1.72 | 3.01 | 25.57 |
| Omalogyra atomus | 0.00 | 15.00 | 1.29 | 0.93 | 2.85 | 28.42 |
| Abra alba | 17.25 | 117.00 | 1.25 | 1.40 | 2.77 | 31.19 |
| Jujubinus striatus | 3.75 | 6.50 | 1.23 | 1.38 | 2.72 | 33.91 |
| Venerupis corrugata | 18.00 | 5.50 | 1.19 | 1.96 | 2.64 | 36.55 |
| Rissoa parv | 4.25 | 1.00 | 1.17 | 1.38 | 2.59 | 39.14 |
| Ebala nitidissima | 2.75 | 0.50 | 1.16 | 1.33 | 2.56 | 41.70 |
| Turbonilla acuta | 1.25 | 0.00 | 1.13 | 1.60 | 2.50 | 44.20 |
| Gibbula cineraria | 0.25 | 1.50 | 1.04 | 1.76 | 2.31 | 46.51 |
| Cerastoderma edule | 0.00 | 3.00 | 1.04 | 0.93 | 2.31 | 48.82 |
| Calyptraea chinensis | 22.25 | 7.50 | 1.03 | 1.75 | 2.27 | 51.09 |

Continued

Groups A1 and B1

A1: Sites 24, 26, 27 and 31 (subtidal, Z. marina)

B1: Site 37 (intertidal, Z. noltei) and site 34 (intertidal, Z. marina and Z. noltei)

| | Av. Dissim. = | 71.83 | | | | |
|-----------------------|------------------------|------------------------|---------------|--------|---------------|--------------------|
| Species | Av. Ab. Group A1 | Av. Ab. Group B1 | Disim. Av. | Dis/SD | Disim. (%) | Cum. Disim. (%) |
| Kurtiella bidentata | 77.75 | 0.00 | 5.04 | 7.57 | 7.01 | 7.01 |
| Retusa truncatula | 24.50 | 0.00 | 3.99 | 4.77 | 5.56 | 12.57 |
| Calyptraea chinensis | 22.25 | 0.00 | 3.76 | 6.30 | 5.23 | 17.80 |
| Venerupis corrugata | 18.00 | 0.00 | 3.70 | 6.36 | 5.15 | 22.95 |
| Nassarius reticulatus | 6.75 | 0.00 | 2.82 | 3.85 | 3.92 | 26.87 |
| Myrtea spinifera | 16.00 | 0.00 | 2.78 | 1.58 | 3.87 | 30.75 |
| Peringia ulvae | 93.25 | 879.50 | 2.65 | 1.54 | 3.69 | 34.44 |
| Loripes lucinalis | 146.00 | 74.00 | 2.64 | 1.81 | 3.67 | 38.11 |
| Thracia papyracea | 4.50 | 0.00 | 2.55 | 7.03 | 3.54 | 41.65 |
| Rissoa parva | 4.25 | 0.00 | 2.03 | 1.50 | 2.83 | 44.48 |
| Parvicardium exiguum | 13.00 | 2.50 | 1.95 | 1.05 | 2.72 | 47.20 |
| Littorina obtusata | 0.00 | 1.50 | 1.93 | 5.09 | 2.68 | 49.88 |
| Ebala nitidissima | 2.75 | 0.00 | 1.92 | 1.51 | 2.67 | 52.55 |

Groups B1 and A2

B1: Site 37 (intertidal, Z. noltei) and site 34 (intertidal, Z. marina and Z. noltei) A2: Site 35 (intertidal, Z. noltei) and site 39 (intertidal, Z. marina and Z. noltei)

| | Av. Dissim. = | 63.57 | | | | |
|-----------------------|------------------------|------------------------|---------------|--------|---------------|--------------------|
| Species | Av. Ab. Group B1 | Av. Ab. Group A2 | Disim. Av. | Dis/SD | Disim. (%) | Cum. Disim. (%) |
| Retusa truncatula | 0.00 | 92.00 | 4.80 | 6.70 | 7.55 | 7.55 |
| Cyclope neriteus | 0.00 | 19.50 | 3.59 | 7.13 | 5.65 | 13.20 |
| Eatonina fulgida | 0.00 | 15.00 | 2.97 | 1.75 | 4.68 | 17.88 |
| Loripes lucinalis | 74.00 | 432.50 | 2.89 | 1.10 | 4.55 | 22.43 |
| Jujubinus striatus | 0.00 | 6.50 | 2.72 | 7.88 | 4.28 | 26.71 |
| Calyptraea chinensis | 0.00 | 7.50 | 2.66 | 11.59 | 4.19 | 30.90 |
| Nassarius reticulatus | 0.00 | 4.50 | 2.48 | 8.46 | 3.90 | 34.81 |
| Venerupis corrugata | 0.00 | 5.50 | 2.30 | 4.92 | 3.62 | 38.42 |
| Peringia ulvae | 879.50 | 115.00 | 2.22 | 1.30 | 3.49 | 41.91 |
| Littorina obtusata | 1.50 | 0.00 | 2.08 | 4.90 | 3.27 | 45.17 |
| Kurtiella bidentata | 0.00 | 2.00 | 2.03 | 6.81 | 3.20 | 48.37 |
| Parvicardium exiguum | 2.50 | 12.50 | 1.95 | 1.31 | 3.07 | 51.45 |

| k | Spearman's armonic rank correlation Best combinations of variables | (ρ w) |
|---|---|---------------|
| 1 | So | 0.700 |
| 2 | GR-S _o | 0.595 |
| 2 | SBW-S _o | 0.578 |
| 3 | $GR - S_o - CARB$ | 0.680 |
| 3 | SBW-GR-So | 0.610 |
| 3 | CS-S _o -CARB | 0.585 |
| 4 | SBW-GR-So-CARB | 0.667 |
| 4 | GR-CS-So-CARB | 0.573 |
| 5 | SBW-GR-MS-S _o -CARB | 0.566 |
| 5 | SBW-GR-CS-S _o -CARB | 0.566 |

shared several species with subgroup A1. Total number of individuals and species was high (1757 ind. and 33 spp.) ranging from 720 to 1014 individuals and from 20 to 26 species per site, respectively. The bivalves *L. lucinalis* and *A. alba* and the gastropods *P. ulvae* and *C. neriteus* were the numerically dominant species. Values of diversity ranged from 1.87 to 2.56 and evenness between 0.43 and 0.54.

Group B comprised three sites corresponding to sandy muds colonized by both seagrass species and a muddy bottom exclusively colonized by *Z. noltei*. These sites were characterized by the lowest carbonate content and salinity values (especially site 37). This group had the greatest number of individuals (3342 ind.) whereas it comprised the smallest values of species richness (24 spp.) ranging from 10 to 20 species per site. Most of the specimens of *P. ulvae* were found in this bottom. The bivalves *L. lucinalis* and *A. alba* were also abundant in these sites. Diversity and evenness showed low values (H': 0.50-2.18; J: 0.15-0.50).

Table 4. Continued



Fig. 4. Canonical correspondence analysis ordination of sites and environmental variables relative to axes I and II for the Ensenada de O Grove. SBW, salinity of bottom water; GR, gravel; CS, coarse sand; MS, medium sand; VFS, very fine sand; Q_{50} , median grain size; S_0 , sorting coefficient; CARB, carbonate.

DISCUSSION

Molluscs are one of the principal components of benthic fauna together with polychaetes and crustaceans (Lewis & Stoner, 1983; López-Jamar & Mejuto, 1985). In the present study, molluscan assemblages in seagrass beds of the Ensenada de O Grove showed, in general, a large number of individuals (7641 individuals) and a high diversity in the number of species (68 spp.) and that these differed in their spatial distribution. In southern Spain, studies on several seagrass species also pointed out the high abundance and diversity of molluscs in these habitats. For instance, in several eelgrass beds in the Alborán Sea, Rueda et al. (2009a) reported a total of 1515 individuals belonging to 76 species and Rueda et al. (2009b) also collected a high number of species (162 spp.) mostly including gastropods (99 spp.) and bivalves (57 spp.). Nevertheless, comparisons between studies are difficult because of the use of different sampling methods (Agassiz trawl and quadrats) and temporal scales (months and day/night). Marina et al. (2012) reported from a temporal study in a Cymodocea nodosa bed a total of 64.824 individuals belonging to 54 mollusc species; the fauna was mainly composed of gastropods (99.56% of individuals, 43 spp.) and bivalves (0.41%, 10 spp.) represented by species with a wide geographical distribution in Europe, followed by strictly Mediterranean species (Marina et al., 2012).

Multivariate techniques determined the presence of two main molluscan assemblages in the studied seagrass meadows. Within group B, the faunal composition of site 37, a muddy bottom colonized by *Z. noltei*, had a certain parallelism with the 'reduced *Macoma* community', which was previously reported in the area by Cadeé (1968) and Mora (1982). On the Atlantic European coast, this community has been characterized by a strong dominance of *Peringia ulvae* (Pennant, 1777) (Currás & Mora, 1990; Olabarria *et al.*,

1998). This fact was also observed in the Ensenada de O Grove. Furthermore, this community can be located in areas with high silt/clay content sometimes colonized by Zostera noltei or by this species and Zostera marina. Site 37 also had the lowest diversity in species richness similarly to areas close to a river in the Ría del Eo (Currás et al., 1993) and the Ensenada de San Simón (Ría de Vigo) (Cacabelos et al., 2008). Sites 37 and 34 also had low values of evenness and this may be in relation to the great numerical dominance of P ulvae. The abundance of this species in these meadows may be explained by its eclectic feeding strategies (Jacobs et al., 1983) and its resilience to salinity changes in areas subjected to regular freshwater inputs. Sites 37 and 34 were also characterized by the presence of Venerupis aurea (Gmelin, 1790), Abra alba and Loripes lucinalis. This species composition was partially similar to that described from other Z. noltei beds in the North Sea (Reise, 1981) and in other Galician rias such as Ría de Foz (Junoy, 1996), Ría de Ferrol (Olabarria et al., 1998) and Ensenada de San Simón (Ría de Vigo) (Cacabelos et al., 2008).

Biocenotic characterization of subgroups A1 and A2 containing the major number of sites, could not be determined according to classic studies in terms of 'facies' and 'communities'. However, composition of the assemblage and abundance of species found in these subgroups are those typical of muddy sediments not subjected to strong fluctuations of salinity. Furthermore, there were no similar gradients in sedimentary composition and associated fauna as those reported from other Galician rias (e.g. Mora, 1982; Junoy, 1996; Moreira et al., 2005; Lourido et al., 2006). This may be due to the overall muddy composition of studied sediments and other similar shared features (i.e. percentage of organic matter and shelter from oceanic influence). Thus, besides the presence of several groupings derived from multivariate analysis, many taxa were present in all groups which was eventually reflected in SIMPER results.

Low values of species richness and diversity have traditionally been associated with muddy sediments (Olabarria *et al.*, 1998; Moreira *et al.*, 2005) whereas the opposite pattern was found in coarser sediments with small amounts of silt/clay content. Our results confirmed this pattern, thus diversity (H') presented a negative correlation with silt/clay content and percentage of organic matter. However, besides the muddy nature of the studied sites, species richness and diversity were high especially in muddy sand bottoms, which may be due to the very presence of seagrasses. For example, these seagrasses contribute to increase heterogeneity of habitat and provide refuge from predators for many species (Heck & Thoman, 1981; Orth *et al.*, 1984). Rhizomes and roots also increase stability of sediment, which in turn, is directly correlated with diversity (Persson, 1983).

Subgroup A2 (sites 35 and 39) showed lower values of species richness and diversity than sites of group A1. The former can be considered as a transition between the richer assemblage of subgroup A1 and that of group B which shows lower values of species richness and diversity. Low values in the A2 and B groups can be explained by the greater silt/clay content and the intertidal nature of these sites with the associated stress derived from desiccation, temperature changes and food availability (Olabarria *et al.*, 1997). However, site 35 (subgroup A2), a muddy sand with *Z. noltei*, presented high diversity values (H': 2.56) and species richness (S: 26). These values contrast with the data described

| Table 6. Summary of biotic and physical characteristics of the three assemblages derived from multivariate analysis (values: mean \pm standard devi- |
|---|
| ation). First ten constant species are listed including their fidelity (EXC, exclusive; ELE, elective; ACE, accessory; OCA, occasional) and Frequency × |
| Dominance values (in parentheses). N, number of individuals per 0.28 m ² ; S, species richness per 0.28 m ² ; H', Shannon-Wiener diversity; J, Pielou's |
| evenness: %OM, percentage of organic matter: %CARB, carbonates percentage: O, median grain size |

| Assemblage | A1 (24, 26, 27, 31) | A2 (35, 39) | B (34, 37, 40) |
|----------------------|-----------------------|---|------------------------------------|
| Constant species | Loripes lucinalis | Loripes lucinalis | Peringia ulvae |
| | (OCA, 3131.4) | (OCA, 4988.5) | (OCA, 6659.6) |
| | Peringia ulvae | Abra alba | Loripes lucinalis |
| | (OCA, 2000.0) | (OCA, 1349.5) | (OCA, 1607.0) |
| | Kurtiella bidentata | Peringia ulvae | Abra alba |
| | (ACE, 1667.6) | (OCA, 1326.4) | (OCA, 1254.9) |
| | Retusa truncatula | Retusa truncatula | Haminoea navicula |
| | (ACE, 525.5) | (ACE, 1061,1) | (EXC, 81.3) |
| | Calyptraea chinensis | Cyclope neriteus | Littorina obtusata |
| | (ACE, 477.2) | (ELE, 224.9) | (EXC, 60.2) |
| | Venerupis corrugata | Eatonina fulgida | |
| | (ACE, 386.1) | (EXC, 173.0) | |
| | Abra alba | Parvicardium exiguum | |
| | (OCA, 370.0) | (ACE, 144.2) | |
| | Parvicardium exiguum | Calyptraea chinensis | |
| | (ACE, 278.8) | (ACE, 86.5) | |
| | Nassarius reticulatus | Jujubinus striatus | |
| | (ACE, 144.8) | (ELE, 75.0) | |
| | Thracia papyracea | Venerupis corrugata | |
| | (EXC, 96.5) | (ACE, 63.4) | |
| Seagrass species | Zostera marina | Zostera noltei, Z. marina and Z. noltei | Z. noltei, Z. marina and Z. noltei |
| N | 475 ± 88.79 | 878.5 ± 200.11 | 1114 ± 869.29 |
| S | 23.50 ± 4.43 | 23.00 ± 4.24 | 13.67 ± 5.51 |
| H′ | 2.73 ± 0.32 | 2.22 ± 0.49 | 1.38 ± 0.84 |
| J | 0.60 ± 0.04 | 0.49 ± 0.08 | 0.36 ± 0.19 |
| Depth | Subtidal-intertidal | Intertidal | Intertidal |
| SSW | 29.63 ± 1.70 | 31.50 ± 0.71 | 23.00 ± 4.36 |
| SBW | 30.88 ± 1.65 | 31.75 ± 1.77 | 27.33 ± 6.43 |
| %OM | 2.77 ± 1.06 | 2.32 ± 1.41 | 9.24 ± 5.55 |
| %CARB | 8.70 ± 1.02 | 10.03 ± 0.62 | 6.60 ± 1.03 |
| Q ₅₀ (mm) | 0.14 ± 0.03 | 0.16 ± 0.04 | 0.15 ± 0.05 |

by Junoy (1996) (H': 0.99) in the Ría de Foz (Spain) from similar habitats.

Biocenotic classification of muddy sand bottoms covered by Zostera is complex. Many species inhabiting sediments colonized by Z. marina are also present in unvegetated muddy sand assemblages (Pérès, 1958). Seagrass beds are open systems that may act as nurseries and provide refuge and foraging habitats for fishes and crustaceans (Larckum et al., 1989). In fact, edges of seagrass beds were considered as the first available refuge for organisms seeking refuge from predators among habitat patches (Sogard, 1989; Bologna, 2006). Seagrass meadows also export detritus to adjacent areas allowing the presence of detritivorous species. Previous works reported that edges of these structural habitats accumulate sediments (Orth, 1977) algae and detritus (Polis & Hurd, 1996; Brooks & Bell, 2001). Luque & Templado (2004) pointed out that a surprising feature of seagrass beds is the similarity of the trophic composition at the family, genera or species level among meadows of different parts of the world. In the case of molluscs, gastropods such as Trochidae, Nassaridae, Rissoidae and Littorinidae were common in the studied seagrass bed as well as in other seagrass beds elsewhere (Rasmussen, 1973; Olabarria et al., 1997; Luque & Templado, 2004). Among bivalves, only the Veneridae and Lucinidae families were well-represented in the studied meadows. Semelids (genus Abra) and lucinids (L. lucinalis) have been recorded as typical species in reduced sediments among mats of Zostera (Jacobs, 1980; Glémarec & Grall, 2000). Loripes lucinalis was also reported in association with Z. marina in Ría do Eo (Currás et al., 1993) and Gulbahace Bay (Aegean Sea: Cinar et al., 1998). On the Galicia coast, Cacabelos et al. (2008) reported a similar mollusc assemblage in Zostera beds in Ensenada de San Simón (Ría de Vigo, north-western Spain) with P. ulvae, Rissoa labiosa (Montagu, 1803), Turboella radiata (Philippi, 1836), Parvicardium exiguum, L. lucinalis, Abra nitida (Müller, 1789) and Chrysallida terebellum (Philipppi, 1844) as the most characteristic species. Similarly, Arroyo et al. (2006) described equivalent species for Z. marina beds located in southern Spain (Alboran Sea) with Jujubinus striatus (Linnaeus, 1758), Rissoa membranacea (J. Adams, 1800), Nassarius pygmaeus (Lamarck, 1822), Mitrella minor (Scacchi, 1836), Bittium reticulatum (da Costa, 1778) and Modiolarca subpicta (Cantraine, 1835), as the most frequent species. At aspecies level, the molluscan fauna in the Zostera beds in the Ensenada de O Grove is also comparable to that found in other eelgrass on the Atlantic coast of Europe where similar species were found such as the gastropods J. striatus, R. membranacea, Rissoa parva (da Costa, 1778), B. reticulatum, Nassarius reticulatus (Linnaeus, 1758), and the bivalves L. lucinalis, A. alba and Parvicardium exiguum (Jacobs & Huisman, 1982; Currás et al., 1993; Fredriksen

et al., 2005). Some of these species such as *J. striatus* and *R. membranacea* were also reported for *Cymodocea* meadows (Ballesteros *et al.*, 2004). In the present study the presence of Mediterranean species such as the gastropods *Cyclope neriteus* (very common in site 35) and *Nassarius pfeifferi* (only present in site 37) is remarkable. The presence of these foreign species in this area could be explained due to the important commercial exploitation and importation of oysters in the area (Rolán *et al.*, 1985).

In conclusion, our study shows that mollusc assemblages are well-represented and had a high diversity in the *Z. marina* and *Z. noltei* meadows in the Ensenada de O Grove. This information reinforces the importance of seagrass meadows for preservation of biodiversity. This is the first quantitative and systematic study based on the molluscan fauna associated with the seagrass beds of the inlet. So this paper can be useful as a baseline study for both further future studies and environmental management in order to protect these areas.

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REFERENCES

- Arroyo M.C., Salas C., Rueda J.L. and Gofas S. (2006) Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations. *Marine Ecology: an Evolutionary Perspective* 27, 417–430.
- Attrill M.J., Strong J.A. and Rowden A.A. (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23, 114–121.
- Ballesteros E., García Raso J.E., Salas C., Gofas S., Moreno D. and Templado J. (2004). La comunidad de *Cymodocea nodosa*: Flora y Fauna. In Luque Á.A. and Templado J. (eds) *Praderas y bosques marinos de Andalucía*. Seville, Spain: Consejería de Medio Ambiente, Junta de Andalucía, pp. 146–153.
- **Bologna P.A.X.** (2006) Assessing within habitat variability in plant demography, faunal density, and secondary production in an eelgrass (*Zostera marina* L.) bed. *Journal of Experimental Marine Biology* and Ecology 329, 122–134
- **Boström C. and Bonsdorff E.** (1997) Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* L. beds in the Baltic Sea. *Journal of Sea Research* 37, 153–166.
- **Brooks R. and Bell S.** (2001) Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/sand ecotones. *Journal* of Experimental Marine Biology and Ecology 264, 67–84.
- Cacabelos E., Gestoso L. and Troncoso J.S. (2008) Macrobenthic fauna in the Ensenada de San Simón (Galicia, NW Spain). *Journal of the Marine Biological Association of the United Kingdom* 88, 237–245.
- Cadée G.C. (1968) Molluscan biocoenoses and thanatocoenoses in the Ría de Arosa, Galicia. *Zoologische Verhandelingen* 95, 1–121.
- Cardoso P.G., Pardal M.A., Lillebo A.I., Ferreira S.M., Raffaeli D. and Marques J.C. (2004) Dynamic changes in seagrass assemblages under

eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology* 302, 233-240.

- **Çinar M.E., Ergen Z., Ozturk B. and Kirkim F.** (1998) Seasonal analysis of zoobenthos associated with a *Zostera marina* L. bed in Gulbahce Bay (Aegean Sea, Turkey). *Marine Ecology* 19, 147–162.
- **Clarke K.R. and Warwick R.M.** (1994) *Change in marine communities: an approach to statistical analysis and interpretation.* Plymouth: Natural Environmental Research Council, UK, 144 pp.
- **Currás A. and Mora J.** (1990) Dinámica poblacional de *Bittium reticulatum* (Da Costa) e *Hydrobia ulvae* (Pennant) en fondos de *Zostera* spp. de la Ría del Eo (Galicia – Asturias). *Thalassas* 8, 93–99.
- **Currás A., Sánchez-Mata A. and 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.
- **Davison D.M. and Hughes D.J.** (1998) Zostera *biotope (Volume I): an overview of dynamics and sensitive characteristics for conservation management of marine SACs.* Oban: Scottish Association for Marine Science (UK Marine SACs Project), 95 pp.
- **Duffy J.E. and Harvilicz A.M.** (2001) Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Marine Ecology Progress Series* 223, 201–211.
- **Esquete P., Moreira J. and Troncoso J.S.** (2011) Peracarids assemblages of *Zoster*a meadows in an estuarine ecosystem (O Grove inlet, NW Iberian Peninsula): spatial distribution and seasonal variation. *Helgoland Marine Research* 65, 445–445.
- Field J.G., Clarke K.R. and Warwick R.M. (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8, 37–52
- Fredriksen S., Christie H. and Boström C. (2004) Deterioration of eelgrass (*Zostera marina* L.) by destructive grazing by the gastropod *Rissoa membranacea* (J. Adams). *Sarsia* 89, 218–222.
- Fredriksen S., Hartvig C. and Sæthre B.A. (2005) Species richness in macroalgae and macrofauna assemblages on *Fucus serratus L*. (Phaeophyceae) and *Zostera marina* L. (Angiospermae) in Skagerrak, Norway. *Marine Biology Research* 1, 2–19.
- **Glémarec M. and Grall J.** (2000) Les groupes écologiques et zoologiques d'invertébrés marins face aux dégradations de l'environnement côtier. *Bulletin de la Société Zoologique de France* 125, 37–48.
- Gotceitas V., Fraser S. and Brown J.A. (1997) Use of eelgrass beds (Zostera marina) by juvenile Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences 54, 306-1319.
- Heck K.L. Jr and Thoman T.A. (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* 3, 125–134.
- Hemminga M.A. and Duarte C.M. (2000) *Seagrass ecology*. Cambridge: Cambridge University Press, 298 pp.
- Hily C., Connan S., Raffin C. and Wyllie-Echeverria S. (2004) *In vitro* experimental assessment of the grazing pressure of two gastropods on *Zostera marina* L., epiphytic algae. *Aquatic Botany* 78, 183–195
- Jacobs R.P.W.M. (1980) Effects of the Amoco Cadiz oil spill on the seagrass community at Roscoff with special reference to the benthic infauna. *Marine Ecology Progress Series* 2, 207–212.
- Jacobs R.P.W.M., Hegger H.H. and Ras-Willems A. (1983) Seasonal variations in the structure of a *Zostera* community on tidal flats in the SW Netherlands, with special reference to the benthic fauna. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* (C) 86, 347–375.
- Jacobs R.P.W.M. and Huisman W.H.T. (1982) Macrobenthos of some Zostera beds in the vicinity of Roscoff (France) with special reference

to relations with community structure and environmental factors. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen—Biological, Chemical, Geological, Physical and Medical Sciences 85, 335–356.

- Junoy J. (1996) La Ría de Foz, comunidades bentónicas. Lugo, Spain: Servicio de Publicaciones de la Diputación Provincial de Lugo, 210 pp.
- Kitting C.L., Fry B. and Morgan M.D. (1984) Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. *Oecologia* 62, 145–149.
- Laborda A.J., Cimadevilla I., Capdevila L. and García J.R. (1997) Distribución de las praderas de Zostera noltii Hornem., 1832 en el litoral del norte de España. Publicaciones especiales del Boletín del Instituto Español de Oceanografía 23, 273–282.
- Larckum A.W.D., McComb A.J. and Shepherd S.A. (1989) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Amsterdam, The Netherlands: Elsevier.
- Lewis F.G. and Stoner A.W. (1983) Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bulletin of Marine Science* 33, 296–304.
- López-Jamar E. and Mejuto J. (1985) Bentos infaunal en la zona submareal de la Ría de La Coruña. I. Estructura y distribución espacial de las comunidades. Boletín del Instituto Español de Oceanografía 2, 99 – 109.
- Lourido A., Gestoso L. and Troncoso J.S. (2006) Assemblages of the molluscan fauna in subtidal soft bottoms of the Ría de Aldán (northwestern Spain). *Journal of the Marine Biological Association of the United Kingdom* 86, 129–140.
- Luque Á.A. and Templado J. (2004) Praderas y bosques marinos de Andalucía. Consejería de Medio Ambiente. Seville, Spain: Junta de Andalucía, 336 pp.
- Marina P., Urra J., Rueda J.L. and Salas C. (2012) Composition and structure of the molluscan assemblage associated with a *Cymodocea nodosa* bed in south-eastern Spain: seasonal and diel variation. *Helgoland Marine Research*. DOI: 10.1007/s10152-012-0294-3.
- Mercier P., Chessel D. and Dolédec S. (1992) Complete correspondence analysis of an ecological profile data table: a central ordination method. *Acta Oecologica* 13, 25–44.
- **Mora J.** (1982) Consideraciones generales sobre la macrofauna bentónica de la Ría de Arosa. *Oecología Aquatica* 6, 41–49.
- Moreira J., Quintas P. and Troncoso J.S. (2005) Distribution of molluscan fauna in subtidal soft-bottoms of the Ensenada de Baiona (NW Spain). American Malacological Bulletin 20, 75–86.
- **Olabarria C., Urgorri V. and Troncoso J.S.** (1997) Distribución y autoecología de la macrofauna infralitoral de la ensenada do Baño (Ría de Ferrol, NO de España). *Nova Acta Científica Compostelana* 7, 177–192.
- Olabarria C., Urgorri V. and Troncoso J.S. (1998) An analysis of the community structure of subtidal and intertidal benthic mollusks of the Inlet of Baño (Ría de Ferrol) (northwestern Spain). *American Malacological Bulletin* 14, 103–120.
- **Orth R.J.** (1977) The importance of sediment stability in seagrass communities. In Coull B.C. (ed.) *Ecology of marine benthos*. Columbia, SC: University of South Carolina Press, pp. 281–300.
- **Orth R.J. and Heck K.L. Jr** (1980) Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay Fishes. *Estuaries* 3, 278–288.
- Orth R.J., Heck K.L. and Van Montfrans J. (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7, 339-350.
- Orth R.J., Carruthers T.J.B., Dennison W.C., Duarte C.M., Fourqurean J.W., Heck K.L. Jr, Hughes A.R., Kendrick G.A., Kenworthy W.J.,

Olyarnik S., Short F.T., Waycott M. and Williams S.L. (2006) A global crisis for seagrass ecosystems. *BioScience* 56, 987–996.

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- Pérès J.M. (1958) Essai de classement des communautés benthiques marines du globe. *Recueille des Travaux de la Station Marine* d'Endoume 22, 23-54.
- Persson L.E. (1983) Temporal and spatial variation in coastal macrobenthic community structure, Hanó-Bay (Southern Baltic). *Journal* of Experimental Marine Biology and Ecology 68, 277–293.
- **Polis G. and Hurd S.** (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147, 396–423.
- Rasmussen E. (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11, 1–507.
- Reise K. (1981) High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 34, 413-425.
- Rolán E., Trigo J., Otero-Schmitt J. and Rolán-Álvarez E. (1985) Especies implantadas lejos de su distribución natural. *Thalassas* 3, 29-36.
- **Rueda J.L. and Salas C.** (2008) Molluscs associated with a subtidal *Zostera marina* L. bed in southern Spain: linking seasonal changes of fauna and environmental variables. *Estuarine, Coastal and Shelf Science* 79, 157–167.
- Rueda J.L., Gofas S., Urra J. and Salas C. (2009a) A highly diverse molluscan assemblage associated with eelgrass beds (*Zostera marina* L.) in the Alboran Sea: micro-habitat preference, feeding guilds and biogeographical distribution. *Scientia Marina* 73, 669–700.
- Rueda J.L., Marina P., Urra J. and Salas C. (2009b) Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea). *Journal of the Marine Biological Association of the United Kingdom* 89, 1319–1330.
- Sheridan P.F. (2004) Comparison of restored and natural seagrass beds near Corpus Christi, Texas. *Estuaries* 27, 781–792.
- **Snelgrove P.V.R.** (1998) The biodiversity of macrofaunal organisms in marine sediments. *Biodiversity and Conservation* 7, 1123–1132.
- **Sogard S.** (1989) Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. *Journal of Experimental Biology and Ecology* 133, 15–37.
- **Ter Braak C.** (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- **Ter Braak C.** (1988) A Fortran program for canonical community ordination by partial, detrended, canonical correspondence analysis, principal components analysis and redundancy analysis. Ithaca, New York: Agricultural Mathematics Group, Ministry of Agriculture and Fisheries, 95 pp.
- Thayer G.W., Bjorndal K.A., Ogden J.C., Williams S.L. and Zieman J.C. (1984) Role of larger herbivores in seagrass communities. *Estuaries* 7, 351–376.
- Waycott M., Duarte C.M., Carruthers T.J.B., Orth R.J., Dennison W.C., Olyarnik S., Calladine A., Fourqurean J.W., Heck K.L. Jr, Hughes A.R., Kendrick G.A., Kenworthy W.J., Short F.T. and Williams S.L. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106, 12377–12381.

and

Webster P.J., Rowden A.A. and Attrill M.J. (1998) Effect of shoot density on the infaunal macro-invertebrate community within a Zostera marina seagrass bed. Estuarine, Coastal and Shelf Science 47, 351–257.

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Appendix

Taxonomic list of molluscan species reported in the present study

Phylum Mollusca

Class Polyplacophora Leptochiton cancellatus (Sowerby, 1840) Lepidochitona cinerea (Linnaeus, 1767) Lepidochitona iberica Kaas & Van Belle, 1981 **Class Gastropoda** Diodora graeca (Linnaeus, 1758) Puncturella noachina (Linnaeus, 1771) Gibbula adansonii (Payraudeau, 1826) *Gibbula albida* (Gmelin, 1791) Gibbula cineraria (Linnaeus, 1758) Gibbula magus (Linnaeus, 1758) Jujubinus striatus (Linnaeus, 1758) Bittium reticulatum (da Costa, 1778) Cerithiopsis tubercularis (Montagu, 1803) Littorina littorea (Linnaeus, 1758) *Littorina fabalis* (Turton, 1825) Littorina obtusata (Linnaeus, 1758) Skeneopsis planorbis (O. Fabricius, 1780) Eatonina fulgida (J. Adams, 1797) Rissoa membranacea (J. Adams, 1800) Rissoa parva (da Costa, 1778) Peringia ulvae (Pennant, 1777) *Hyala vitrea* (Montagu, 1803) Calyptraea chinensis (Linnaeus, 1758) Nassarius ovoideus (Locard, 1886) Nassarius pfeifferi (Philippi, 1884) Nassarius pygmaeus (Lamarck, 1822) Nassarius reticulatus (Linnaeus, 1758)

Cyclope neriteus (Linnaeus, 1758) Omalogyra atomus (Philippi, 1841) Chrysallida indistincta (Montagu, 1808) Turbonilla acuta (Donovan, 1804) Ebala nitidissima (Montagu, 1803) Opistobranchia, genera et sp. indet. 1 Opistobranchia, genera et sp. indet. 2 Opistobranchia, genera et sp. indet. 3 Diaphana minuta T. Brown, 1827 *Retusa truncatula* (Bruguière, 1792) Retusa sp. 1 Haminoea navicula (da Costa, 1778) Elvsia viridis (Montagu, 1804) Doris verrucosa Linnaeus, 1758 **Class Bivalvia** Modiolarca subpicta (Cantraine, 1835) Modiolula phaseolina (Philippi, 1844) Loripes lucinalis (Lamarck, 1818) Myrtea spinifera (Montagu, 1803) *Thyasira flexuosa* (Montagu, 1803) Montacutidae genera et sp. indet. 1 Kurtiella bidentata (Montagu, 1803) Carditidae, genera et spp. indet. Digitaria digitaria (Linnaeus, 1758) *Parvicardium exiguum* (Gmelin, 1791) Cerastoderma edule (Linnaeus, 1758) Spisula subtruncata (da Costa, 1778) Lutraria lutraria (Linnaeus, 1758) Solen marginatus Pulteney 1799 Angulus tenuis (da Costa, 1778) *Tellina fabula* (Gmelin, 1791) Gari (Gobraeus) sp. Abra alba (W.Wood, 1802) Chamelea striatula (da Costa, 1778) Dosinia exoleta (Linnaeus, 1758) Dosinia sp. 1 *Venerupis aurea* (Gmelin, 1791) *Venerupis rhomboides* (Linnaeus, 1767) *Venerupis corrugata* (Gmelin, 1791) Venerupis decussata (Linnaeus, 1758) Sphenia binghami Turton, 1822 *Thracia papyracea* (Poli, 1791)