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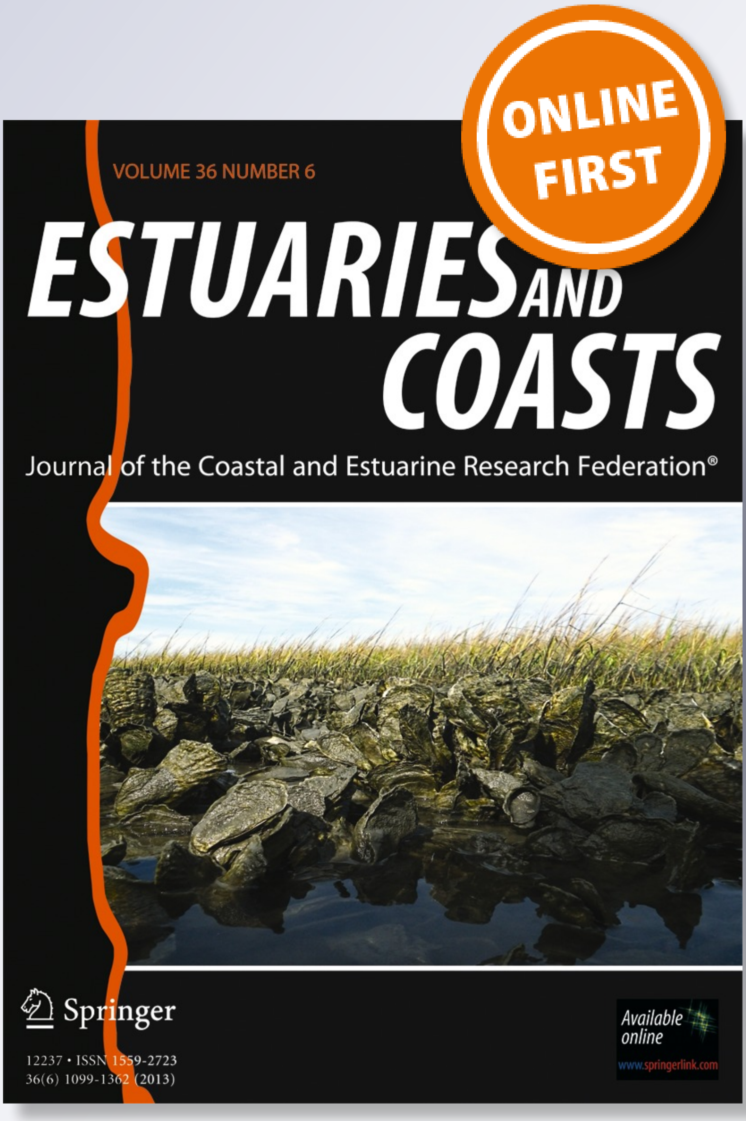

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Do *Spartina maritima* Plantations Enhance the Macroinvertebrate Community in European Salt Marshes?

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Abstract Ecological restoration of salt marshes using plantations may enhance the macroinvertebrate community, but little is known about the development of benthic macroinvertebrates after ecological engineering projects in European salt marshes. This study analyzed the environment and the macroinvertebrate community in European salt marshes 3 years after restoration using *Spartina maritima* plantations in comparison with non-restored and preserved marshes in Odiel Marshes (Southwest Iberian Peninsula). We hypothesized that planting *Spartina maritima* on intertidal mudflats would increase species richness and diversity (Shannon–Weaver index) of the benthic macroinvertebrate community by increasing environmental heterogeneity, providing feeding resources and improving sediments characteristics. Benthic macrofauna samples (composed mainly of annelids, crustaceans, and mollusks) were sampled in plots of 20 cm×25 cm to 5 cm depth between +1.8 and +3.0 m above Spanish Hydrographic Zero. Sediment organic matter content, bulk density, pH, and redox potential were the variables that best explained macroinvertebrate distribution. Restored marshes achieved similar diversity and even higher specific richness than preserved marshes, although with differences in species composition. Non-restored marshes showed the lowest diversity. Restored and preserved marshes did not differ in total abundance or biomass of macroinvertebrates, both being higher than in non-restored marshes. The macroinvertebrate communities in preserved and non-restored marshes showed the largest difference in taxa composition, with restored marshes occupying an intermediate position. Salt marsh restoration using *S. maritima* increased the complexity (ecological diversity and species richness) and abundance of the benthic macroinvertebrate community. Our study offers new information about the role of salt marsh plants in mediating faunal communities via ecological engineering projects.

Keywords Below-ground biomass · Disturbance · Ecological diversity · Odiel Marshes · Organic matter content · *Spartina densiflora*

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Introduction

Salt marshes are vitally important ecosystems that carry out many different economic, social and ecological functions (Silliman et al. 2009). Nevertheless, salt marshes are among the most impacted ecosystems in the world (Gedan et al. 2009) with their ecological restoration being very important to replace ecological functions and values lost when natural wetlands are degraded or destroyed (Zedler and Kercher 2005; Mitsch 2010). In this sense, monitoring the progression of marsh restoration projects is a key part of improving restoration practices (Konisky et al. 2006). Therefore, environmental monitoring of restored or created coastal wetlands has increased in recent years (e.g., Fell et al. 1991; Dionne et al. 1998; Gallego-Fernández and García-Novo 2007; Zedler et al. 2008).

Ecological restoration of salt marshes using plantations may enhance the macroinvertebrate community providing vegetated areas with a wide range of microhabitats that may increase the diversity of macroinvertebrates (Netto and Lana 1997; Warren et al. 2002). Thus, the study of benthic invertebrates is used to assess ecosystem development following salt marsh restoration, which has been studied mainly in *Spartina alterniflora* Loisel and *Spartina foliosa* Trin. North American salt marshes (Peck et al. 1994; Sacco et al. 1994; Levin and

Talley 1996; Levin and Talley 2000; Zedler and Lindig-Cisneros 2002; Levin and Talley 2002; Swamy et al. 2002; Craft and Sacco 2003). For example, Sacco et al. (1994) showed that natural *S. alterniflora* salt marshes had similar component organisms and proportions of trophic groups than restored marshes, but total density and densities within trophic groups were lower in the artificially established marshes planted with *S. alterniflora*, ranged in age from 1 to 17 years. Thus, the re-establishment of certain animal populations following the opening of marshes to tidal flow depends on the species (Warren et al. 2002). Levin and Talley (2000) hypothesized that environmental variables such as marsh age, elevation and salinity act over large space and time scales influencing the presence or absence of species whereas sediment properties and vegetation presence or type act on intermediate scales affecting macrofaunal abundance and composition. In this sense, it has been described that macroinvertebrate communities can be negatively affected by invasive halophytes (Levin et al. 2006; Zhou et al. 2009; Tang and Kristensen 2010), which can colonize salt marshes just after restoration (D'Antonio and Meyerson 2002). In addition, we should take into account that is inappropriate to assume, for natural and restored ecosystems, that equivalent structures means equivalent functions (Zedler and Lindig-Cisneros 2002).

In Europe, *Spartina townsendii* H. & J. Groves and *Spartina anglica* Hubb. have been transplanted extensively to help stabilize sediments, reduce wave erosion, and reclaim land for agriculture (Verhoeven 1938; Ranwell 1967; Bakker *et al*. 2002; Paramor and Hughes 2007). Castillo and Figueroa (2009) represent the first published description that we are aware of an ecological engineering project through plantation of small cordgrass, *Spartina maritima* (Curtis) Fernald. However, along the East Atlantic Coast, benthic assemblages of salt marshes have rarely been studied (Salgado et al. 2007). Thus, the development of benthic macroinvertebrate community after ecological engineering projects in European salt marshes using *S. maritima* is unknown.

Our study aimed to test the hypothesis that planting *S. maritima* on intertidal mudflats would increase species richness and diversity of the benthic macroinvertebrate community (composed mainly of annelids, crustaceans and mollusks). This was tested by recording sediment characteristics (belowground plant biomass, elevation, redox potential, pH, electrical conductivity, organic content, bulk density, and water content) and the macroinvertebrate community in restored marshes using *S. maritima* 3 years after planting (Castillo and Figueroa 2009) in comparison with non-restored and preserved marshes in Odiel Marshes (Southwest Iberian Peninsula). We sampled a wide set of sediment characteristics in order to clarify which of them influenced mainly the macroinvertebrate community. Non-restored marshes were similar to restored marshes prior to restoration, being invaded by the South American neophyte *Spartina densiflora* Brongn. and suffering high erosion rates, and preserved marshes reproduced the typical low salt marsh zonation being dominated by *S. maritima* and *Zostera noltii* Hornem. Comparisons between restored, non-restored and reference preserved marshes have proven to be an appropriate methodology to assess the success of restoration projects, allowing to determine the maturity and evolution of the restored ecosystem (Rodney and Paynter 2006; Armitage et al. 2007). Besides, our study provides scientific data on the macroinvertebrate community of the Odiel Marshes, where it has not been well studied (Sánchez-Moyano and García-Asencio 2010, Sánchez-Moyano et al. 2010), and broadly, it offers new information about the role of halophytes in mediating faunal communities via ecological engineering projects.

Materials and Methods

Study Site

Our study was carried out in the Odiel Marshes on the Atlantic coast of the Southwest Iberian Peninsula (37º15′–37º37′ N, 6º57′–6º58′ W). The semidiurnal tides have a mean range of 2.10 m and a mean spring tidal range of 2.97 m, representing 0.40–3.37 m above Spanish Hydrographic Zero (SHZ). Mean sea level is +1.85 m relative to SHZ. The Odiel Marshes are a significant wetland ecosystem recognized for their global significance with designations as a UNESCO Biosphere Reserve and the Ramsar Convention on Wetlands. The vegetation, physiography and climate have been described by Castellanos et al. (1994). Specifically, the benthic macroinvertebrate community was recorded in three low salt marsh areas:

(1) Restored salt marshes (RM) located next to the Chemical Pole and the city of Huelva, on the left bank of the "Canal del Padre Santo", the main channel of the estuary. Before the installation of an industrial site in the 1960s, these marshes were used by Huelva citizens as a recreational area, originally occupied by multiple *S. maritima* tussocks. Native vegetation was disappearing due to high erosion rates together with direct habitat destruction due to infrastructure construction, leading to the invasion of the South American neophyte *S. densiflora* that occupied 2.01 ha. The presence of native vegetation in the low marshes was restricted to one stand of *S. maritima* of 6,026 m^2 and isolated clumps of *Sarcocornia perennis* (Miller) A. J. Scott., *Sarcocornia perennis* x *fruticosa* (Figueroa et al. 2003), *Atriplex portulacoides* L., and the annual *Salicornia ramosissima* J. Woods. A degraded landscape dominated by unvegetated mudflats and growing patches of *S. densiflora* was the most obvious consequences of environmental degradation. These marshes

were restored from November 2006 to January 2007 with plantations of *S. maritima* (current relative cover 62±6 % in *Spartina* prairies) and *S. perennis* (isolated individuals) after the invasive *S. densiflora* was eliminated manually from 2.00 ha around the site (Castillo and Figueroa 2009).

(2) Adjacent non-restored salt marshes (NRM) invaded by *S. densiflora* (relative cover ca. 20 %), with high erosion rates (Castillo et al. 2000; Curado et al. 2012) and old and isolated *S. maritima* tussocks. These marshes were similar to RM prior to restoration. The colonization by *S. maritima* was restricted probably due to its dispersion limitation since this cordgrass have usually failed to reproduce sexually (Cooper 1993; Castellanos et al. 1998).

(3) Preserved salt marshes (PM) dominated by *S. maritima* (ca. 50 %) and *Z. noltii* (ca. 10 %) with *S. perennis* at the higher elevations. Every *S. maritima* population at channel edges in the Odiel Marshes have disappeared or have been degraded due to a combination of different anthropogenic impacts, erosion and the *S. maritima* dispersal limitation cited above. Thus, we decided to compare RM with both NRM and PM, since every preserved marsh area we found had no the same physiography than RM. RM and NRM were a combination of successional marshes (sites with a sediment dynamic dominated by accretion that favored succession development) and non-successional marshes (sites with a stabilized sediment dynamic and very slow or none succession development), being both on intertidal plains with very similar marsh physiography and located at opposite banks in the main channel of the estuary. PM were successional marshes located at a coastal lagoon presenting the typical native vegetation zonation at low marshes in Southwest Iberian Peninsula (Fig. 1). Sediment dynamic, the avian community and vegetation for the three studied areas have been described by Curado et al. (2012, 2013, 2014).

Macroinvertebrates Sampling and Laboratory Analysis

The sampling was conducted during September-October 2009 (September: mean temperature, 23.7 °C; number of daylight hours=8.2 h day^{-1}; October: mean temperature, 21.7 °C; number of daylight hours=8.0 h day^{-1}; INE 2009). Benthic macrofauna samples to 5 cm depth were collected by hand using a shovel and a handsaw to cut roots and rhizomes in plots of 20 cm×25 cm (0.05 m^2). Samples (plots) were collected every 20 m along transects orthogonal to the tidal line between +1.8 and +3.0 m above SHZ (9 transects and 26 plots in RM, 9 transects and 17 plots in NRM, and 6 transects and 15 plots in PM). Then, transects were considered replicates within the same marsh type (factor).

Once in the laboratory, sediment samples were sieved (1-mm mesh) very carefully, fixed with 70 % ethanol and stained with Rose Bengal. Macroinvertebrates were separated and cleaned carefully, and analyzed under a Leica binocular magnifying glass (model WildM3C). Samples were stored in 70 % alcohol until proceeding with the identification of the specimens and quantification of their biomass. To record biomass, samples were dried to constant dry weight (DW) at 80 °C during 48 h. Ash-free dry weight (AFDW) was recorded, by the loss-on-ignition method after 4 h at 500 °C (10 h for those species with shells, following Garnerd and Thomas (1987) and modified by Pagola-Carte et al. (2002)), to know the organic weight of the sample once the inorganic weight (ex. coriaceous tubes and shells) has been removed.

Environmental Variables

Below-ground plant biomass in macroinvertebrate samples was separated carefully, cleaned with tap water and dried for 48 h at 80 °C until they reached a constant weight. Elevation relative to SHZ, sediment redox potential, interstitial water pH and electrical conductivity, sediment organic and water contents and sediment bulk density were recorded between 0 and 5 cm deep in the area adjacent to every macroinvertebrate plot. Elevation was surveyed *in situ* to a resolution of 2 cm with a Leica NA 820 theodolite (Singapore); reference points were determined in relation to measurements of tidal extremes (Ranwell et al. 1964). Sediment redox potential was determined in the field with a portable meter and a macroelectrode system (Crison pH/mV p-506) that was inserted directly into the sediment to avoid sediment oxygenation. Every sample was the mean of three sub-samples. pH (pH/redox Crison with the electrode *M-506*) and electrical conductivity as an estimation of sediment salinity (conductivity meter, Crison-522) were recorded in the laboratory after adding distilled water to the sediment with 1:1, *v*/*v*, and 1:2, *v*/*v*, respectively. Sediment organic content was analyzed in triplicate sub-samples by the loss-on-ignition method after 4 h at 450 °C. Sediment bulk density was recorded by weighing the sediments collected in cylindrical cores of 5×5 cm after drying them at 80 °C during 48 h (DW). Sediment water content (%) was recorded as the difference between fresh and dry weights of ca. 100–150 g samples.

Macroinvertebrate Community

Fauna was sorted, identified to the lowest possible taxon and counted. Some unidentified taxa within polychaetes, called sp. 1 and sp. 2, were included in the inventory. The samples of each transect were grouped for analyses. The structure of the benthic community at each site was calculated in terms of total number of species (S_{total}), mean species number per sample (S_{mean}), mean number of individuals per sample (N_{mean}),

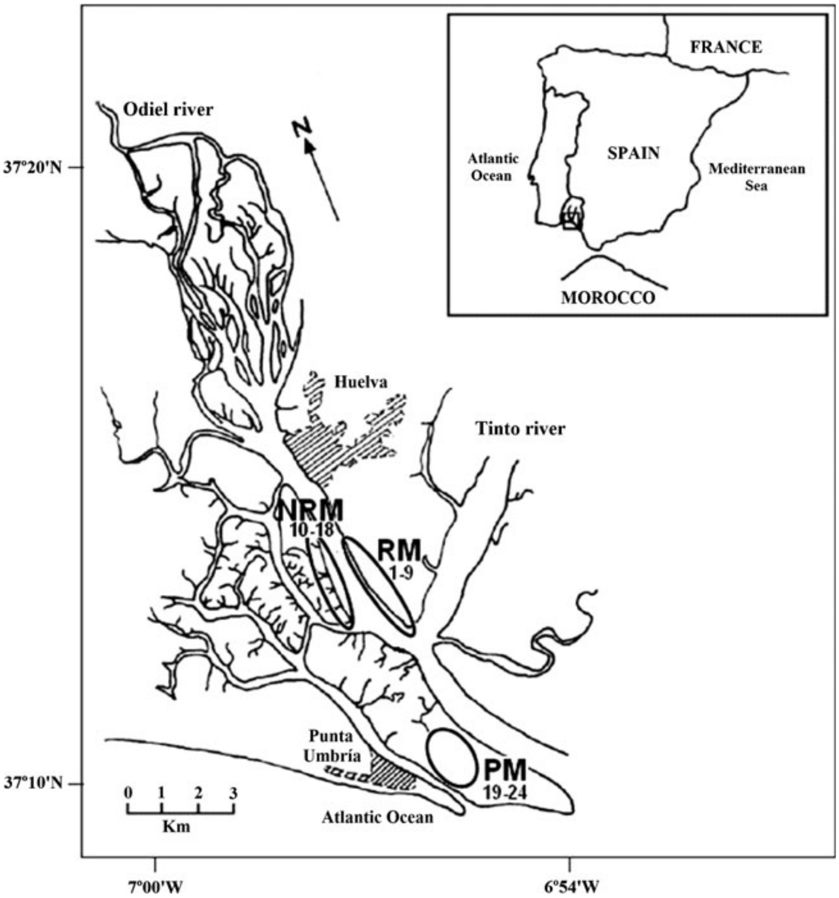

Fig. 1 Sketch map of the Odiel Marshes, showing the sampling points: *1–9* restored marshes, *10–18* non-restored marshes, and *19–24* preserved marshes

species abundance (ind. m^{-2}), total abundance (ind. m^{-2}), species biomass ($g\,m^{-2}$), and total biomass ($g\,m^{-2}$). Ecological diversity was calculated following the Shannon-Weaver index (H'; Shannon and Weaver 1949). We also calculated maximum diversity (H_{max}), evenness (J), and the Simpson index of dominance (D; Simpson 1949) using the PRIMER 5.2.8 software package (PRIMER-E ltd).

Statistical Analysis

Deviations were calculated as the standard error of the mean (SEM). Pearson correlation coefficient for normal data and Spearman coefficient for non-normal data were used to analyze relationships between environmental variables and macroinvertebrate abundance and biomass. Environmental variables were compared between marsh areas by one-way ANOVA or Kruskal–Wallis test. B-Tukey or Mann–Whitney *U* test was used as post hoc analysis. These statistical tests were performed using SPSS 17.0 (SPSS Inc., Chicago, IL).

ABC (Abundance Biomass Comparison) curves are a graphical representation of both cumulative percentage of abundances and biomass and it was employed to detect community perturbation (Warwick 1986). The W statistic, which was performed from the ABC curves of the different marshes, was calculated according to Clarke (1990). This index is scaled so that complete biomass dominance and an even abundance distribution gives a value of +1 and the reverse case a value of −1. MDS (non-metric multidimensional scaling) is based on the Bray-Curtis similarity matrix, establishing affinities between sampled areas and taxa abundance. Taxa abundance data were standardized using the fourth root. We verified the validity of the analysis using the Kruskal stress coefficient. After testing the homogeneity of dispersion (PERMDISP), a one-way PERMANOVA was performed on the Bray-Curtis similarity matrix to test the null hypothesis of no significant spatial differences between sampled areas. Following Anderson et al. (2008), a posteriori pairwise comparisons with the PERMANOVA *t* statistic were performed. It was run in order to provide significant values for MDS and SIMPER analyses. Based on the similarity matrix obtained from the Bray–Curtis index, SIMPER (percentage of similarity analysis) was used to calculate the contribution of each taxon to the dissimilarity between groups of stations (Clarke 1993). We use PCA (Principal Components Analysis) to examine the influence of environmental variables in the studied stations, and BIOENV analysis to compare the rank similarity matrix of species abundance with the abiotic

Table 1 Elevation above Spanish Hydrographic Zero (m), sediment redox potential (mV), sediment electrical conductivity (mS cm^{-1}), sediment organic content (%), sediment pH, sediment water content (%), sediment bulk density (g cm^{-3}), and below-ground biomass (BGB, g m^{-2}) in the first 5 cm deep in three low marsh areas in the Odiel Marshes

Environmental variables	Restored marshes		Non-restored marshes		Preserved marshes	
	Mean±SEM	Max–min	Mean±SEM	Max–min	Mean±SEM	Max–min
Elevation	2.42 ± 0.08^{a}	3.15/1.77	2.58 ± 0.08^{a}	3.39/2.22	2.57 ± 0.05^{a}	3.05/2.29
Redox potential	24 ± 17^{a}	164/−117	23 ± 20^{a}	193/−81	-86 ± 15^{b}	37/−155
Conductivity	16.3 ± 1.5^{ab}	35.5/8.3	17.5 ± 0.5^{a}	21.1/12.7	15.4 ± 0.4^{b}	18.0/12.4
Organic matter content	5.0 ± 0.66^{a}	13.1/0.3	11.4 ± 0.6^{b}	16.7/8.1	4.6 ± 0.3^{a}	6.9/2.7
pH	7.1 ± 0.0^{a}	7.9/6.6	7.2 ± 0.1^{a}	8.0/6.8	7.4 ± 0.0^{b}	7.7/7.3
Water content	44 ± 3^{ab}	70/22	51 ± 1^{a}	58/43	36 ± 1^{b}	45/27
Bulk density	0.8 ± 0.1^{a}	1.4/0.2	0.7 ± 0.0^{a}	0.9/0.6	1.1 ± 0.0^{b}	1.3/0.8
Spartina maritima BGB	177 ± 46^{a}	451/37	8 ± 8^{b}	71/0	73 ± 21^{a}	174/28
Spartina densiflora BGB	0 ± 0^{a}	0/0	16 ± 6^{b}	41/0	0 ± 0^{a}	0/0
Sarcocornia perennis BGB	154 ± 51^{a}	375/0	85 ± 34^{a}	240/0	0 ± 0^{b}	0/0
Zostera noltii BGB	0 ± 0^{a}	0/0	0 ± 0^{a}	0/0	16 ± 6^{b}	33/0

Different letters indicate significant differences between marshes for the same environmental variable (N=15–26). Mean±standard error mean and maximum and minimum values are presented

variables (Clarke and Ainsworth 1993). These analyses were carried out using the software package PRIMER 5.2.8.

Table 2 Significant differences (ANOVA or Kruskal–Wallis test) between restored, non-restored, and preserved salt marshes for environmental variables and macroinvertebrate community characteristics in the Odiel Marshes (Southwest Iberian Peninsula)

Environmental variables	F	H	p	df
Redox potential		17.978	***	2
Conductivity		10.198	**	2
Organic matter content		29.608	***	2
pH	9.535		***	57
Water content		17.175	***	2
Bulk density		16.850	***	2
Spartina maritima below-ground biomass		15.213	***	2
Community structure				
S_{mean}	7.440		**	58
N_{mean}	6.628		*	2
Cyathura carinata abundance	9.052		**	23
Hediste diversicolor abundance		11.835	**	2
Total macroinvertebrate abundance	4.660		*	23
Macroinvertebrate community biomass		8.728	*	2
Ash-free dry biomass		6.219	*	2
H'		5.035	*	2
H_{max}		6.354	*	2

Abbreviations: S_{mean} mean species richness per sample, N_{mean} mean individuals number per sample, H' Shannon–Weaver ecological diversity index, H_{max} maximum ecological diversity

$^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

Results

Environmental Variables

Elevation above SHZ did not differ between marsh areas (ANOVA, $p>0.05$). PM (preserved marshes) showed lower sediment redox potential, lower conductivity and higher pH than RM (restored marshes) and NRM (non-restored marshes). Organic matter content was the highest in NRM (Tables 1 and 2). Sediment water content was lower in PM than in NRM (U test=

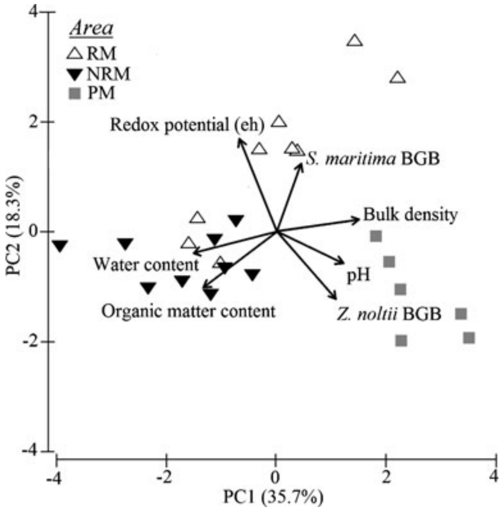

Fig. 2 PCA analysis plot for all transects from environmental variables within sediments. The percentage of variability explained by the two principal axes is given and vectors representing the most significant ($r>0.350$) sediment characteristics are shown. *RM* restored marshes, *NRM* non-restored marshes, *PM* preserved marshes

Table 3 Mean±SEM (n=6–9 transects) of abundance (ind. m^{-2}), dry biomass (DW), and ash-free dry biomass (AFDW; g m^{-2}) of all observed macroinvertebrate taxa in three marsh areas in the Odiel Marshes (Southwest Iberian Peninsula)

	Restored marshes			Non-restored marshes			Preserved marshes		
	Abundance	DW	AFDW	Abundance	DW	AFDW	Abundance	DW	AFDW
Annelida									
Polychaeta									
Alkmaria romijni	0±0	–	–	0±0	–	–	48±37	0.006±0.003	0.002±0.002
Capitella capitata	106±46	0.004±0.001	0.004±0.001	0±0	–	–	30±12	0.015±0.008	0.010±0.005
Hediste diversicolor	126±38	0.964±0.247	0.865±0.230	40±4	0.227±0.027	0.207±0.074	4±3	0.008±0.007	0.006±0.006
Melinna palmata	0±0	–	–	0±0	–	–	2±2	0.001±0.001	0.001±0.001
Nephtys hombergii	2±1	0.001±0.001	0.000±0.000	0±0	–	–	13±9	0.020±0.011	0.010±0.007
Polychaete sp.1	1±1	0.009±0.009	0.003±0.003	0±0	–	–	0±0	–	–
Polychaete sp.2	0±0	–	–	0±0	–	–	2±2	0.002±0.001	0.001±0.001
Scolelepis cantabra cf.	9±5	0.001±0.001	0.001±0.001	0±0*	–	–	0±0	–	–
Oligochaeta	50±38	0.001±0.001	0.001±0.001	134±28	0.005±0.001	0.004±0.003	0±0	–	–
Arachnida									
Araneae	0±0	–	–	1±0	0.001±0.000	0.001±0.000	0±0	–	–
Acarina	3±2	0.000±0.000	0.000±0.000	0±0	–	–	0±0	–	–
Bryozoa									
Bugula neritina	0±0	–	–	0±0	–	–	1±1	0.022±0.019	0.006±0.006
Collembola									
Collembola	4±2	0.000±0.000	0.000±0.000	1±0	0.000±0.000	0.000±0.000	9±5	0.001±0.000	0.000±0.000
Anurida maritima	0±0*	–	–	1±0	0.000±0.000	0.000±0.000	0±0	–	–
Crustacea									
Isopoda									
Eurydice affinis	1±1	0.000±0.000	0.000±0.000	49±11	0.009±0.002	0.006±0.003	0±0	–	–
Lekanesphaera hookeri	14±3	0.034±0.004	0.016±0.002	7±2	0.021±0.007	0.008±0.007	9±3	0.022±0.013	0.006±0.005
Cyathura carinata	449±68	0.105±0.015	0.060±0.008	167±12	0.038±0.004	0.027±0.009	522±89	0.377±0.064	0.184±0.037
Paragnathia formica	16±16	0.003±0.003	0.003±0.003	81±19	0.023±0.006	0.020±0.015	32±28	0.009±0.007	0.006±0.006
Decapoda									
Juvenile decapoda	3±2	0.000±0.000	0.000±0.000	0±0	–	–	0±0	–	–
Carcinus maenas	7±3	0.354±0.246	0.143±0.099	1±0	0.009±0.003	0.004±0.004	6±4	0.218±0.046	0.070±0.056
Uca tangeri	2±1	0.044±0.035	0.019±0.016	3±1	0.006±0.003	0.005±0.005	2±2	0.069±0.057	0.025±0.025
Palaemonidae	1±1	0.000±0.000	0.000±0.000	0±0	–	–	0±0	–	–
Amphipoda									
Melita palmata	10±7	0.003±0.002	0.002±0.002	0±0	–	–	5±3	0.003±0.002	0.001±0.001
Orchestia stephenseni	0±0	–	–	1±0	0.001±0.000	0.000±0.000	0±0	–	–
Corophium multisetosum	0±0	–	–	0±0	–	–	37±16	0.017±0.007	0.010±0.005
Cirripedia									
Balanus sp.	5±3	0.009±0.006	0.002±0.001	7±1	0.046±0.014	0.001±0.001	6±3	0.061±0.039	0.005±0.003
Insecta									
Diptera									
Dolichopodidae	40±14	0.011±0.005	0.010±0.004	29±2	0.008±0.001	0.005±0.002	45±14	0.014±0.004	0.007±0.003
Diptera larva	1±1	0.000±0.000	0.000±0.000	7±1	0.000±0.000	0.000±0.000	0±0	–	–
Chironomus sp.	48±18	0.001±0.000	0.000±0.000	0±0*	–	–	0±0*	–	–
Hemiptera									
Hemiptero Sord. homoptero	4±4	0.000±0.000	0,00±0,00	0±0	–	–	0±0	–	–
Cicadellidae	2±2	0.000±0.000	0,00±0,00	0±0	–	–	0±0	–	–
Mollusca									
Opisthobranchia	3±3	0.000±0.000	0.000±0.000	0±0	–	–	0±0	–	–
Bivalvia									–
Abra tenuis	0±0	–	–	0±0	–	–	79±14	0.203±0.050	0.022±0.019
Cerastoderma edule	3±1	0.002±0.001	0.000±0.000	3±1	0.008±0.002	0.001±0.000	2±2	0.306±0.248	0.018±0.016

Table 3 (continued)

	Restored marshes			Non-restored marshes			Preserved marshes		
	Abundance	DW	AFDW	Abundance	DW	AFDW	Abundance	DW	AFDW
Gastropoda									
Hydrobia ulvae	0±0	–	–	0±0	–	–	5±5	0.015±0.013	0.001±0.001
Nemertea	0±0	–	–	0±0	–	–	3±2	0.004±0.002	0.002±0.001
Phoronidea	0±0	–	–	0±0	–	–	73±49	0.459±0.258	0.025±0.019
Total	910±121^{a}	1.546±0.456^{a}	1.133±0.278^{a}	532±95^{b}	0.402±0.034^{b}	0.291±0.079^{b}	935±90^{a}	1.855±0.621^{a}	0.419±0.103^{ab}

Values with the symbol (–) means absent. *Scolelepis cantabra* cf. (cf. = to confirm). The asterisk indicates that the species was present in the area with an abundance <0.01 ind. m^{-2}. Different letters indicate significant differences between marshes

2.000, $p<0.001$) and similar to RM, while sediment bulk density was the highest in PM (Tables 1 and 2).

Below-ground biomass of *S. maritima* was the lowest in NRM, showing similar values in RM and PM. *S. densiflora* was only sampled in NRM and *Z. noltii* in PM. *S. perennis* below-ground biomass was not recorded in PM and it was similar in RM and NRM (*U* test, $p>0.05$; Tables 1 and 2).

The variance explained by the two principal axes of PCA analysis was 54.0 % (eigenvalues 3.93 and 2.01, respectively). The principal axis discriminated transects mainly for sediment water content (−0.461), sediment bulk density (−0.458), sediment organic matter content (−0.408) and pH (+0.370), as stated by their eigenvectors. The second axis was mainly influenced by sediment redox potential (+0.514) and by specific below-ground biomass (*S. maritima* (+0.376), *Z. noltii* (−0.375), and *S. perennis* (+0.349); Fig. 2).

Macroinvertebrate Community

Thirty-seven species were recorded in all sampled marshes. PM had 8 species that were not present in the other areas, RM had 6 exclusive species and NRM had only 2 exclusive species. Generally, all exclusive species were recorded in low abundances, except for the phylum *Phoronidea*, the bivalve *Abra tenuis*, the polychaete *Alkmaria romijni* and the crustacean *Corophium multisetosum* that were abundant in PM (Table 3). MDS analysis clearly separated PM and NRM according to their species composition, while RM appeared in intermediate position (Fig. 3). In this sense, oneway PERMANOVA analysis showed significant differences between areas (*Pseudo*-$F=7.051$, $p<0.001$). The pairwise tests showed significant differences in all cases (RM-NRM: $t=2.53$, $p<0.001$; RM-PM: $t=2.61$, $p<0.001$; NRM-PM: $t=2.83$, $p<0.001$).

SIMPER analysis obtained the best discriminating taxa between marsh areas, showing the most differences between PM and NRM with *A. tenuis*, *Capitella capitata* (polychaete), *C. multisetosum*, and *Hediste diversicolor* (polychaete) as the species that contributed mainly to the dissimilarity. For RM and NRM were *C. capitata*, *Chironomus* sp., *Oligochaeta*, and *Lekanesphaera hookeri* (Isopoda). RM and PM showed a slightly lower dissimilarity with *A. tenuis*, *H. diversicolor*, *Chironomus* sp. and *C. multisetosum* as the most important species to separate both marsh areas (Table 4).

S_{total} was higher in RM than in NRM and PM. S_{mean} was higher for RM and PM than for NRM (Tukey, $p<0.05$). N_{mean} was maximum at PM and minimum at NRM; RM showed N_{mean} values more similar to PM (Tables 2 and 5).

Crustaceans and annelids were the major groups in all studied marshes. The most abundant species were present in all areas (except *Oligochaeta*, which did not appear in PM and *C. capitata* in NRM). The crustacean isopod *Cyathura carinata* was the most abundant taxon, its lowest abundance being in NRM and its highest in PM (Tukey, $p<0.05$). RM and PM showed higher total macroinvertebrate abundance than NRM (Tukey, $p<0.05$). *H. diversicolor* and *C. capitata* were abundant in RM, *Oligochaeta*, *Paragnathia formica* (isopoda) in NRM, and *A. tenuis* and *Phoronidea* in PM. *H. diversicolor* abundance in PM was lower than for the other two areas (*U* test, $p<0.05$; Tables 2 and 3, Fig. 4).

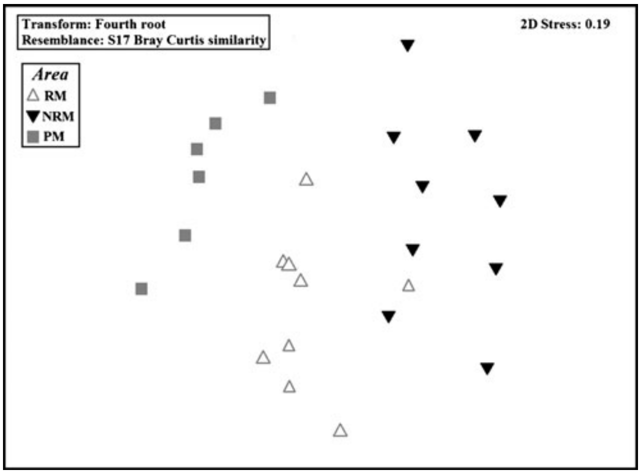

Fig. 3 MDS ordination using Bray–Curtis similarities on taxa abundance. *RM* restored marshes, *NRM* non-restored marshes, *PM* preserved marshes

Table 4 Zonal variation of the average abundance, average dissimilarity, ratio dissimilarity: standard deviation (SD), contribution to dissimilarity (%), and contribution to dissimilarity accumulated (%) of the most relevant taxa in restored marshes (RM), non-restored marshes (NRM), and preserved marshes (PM) in the Odiel Marshes

Taxa	Average abundance		Average dissimilarity	Dissmilarity:SD	Contribution to dissimilarity (%)	Dissimilarity accmulated (%)
Dissimilarity between areas						
	RM	NRM		(Average dissimilarity=58.08)		
Capitella capitata	2.44	0.00	5.84	1.60	10.05	10.05
Chironomus sp.	2.06	0.00	5.18	1.57	8.93	18.97
Oligochaeta	0.84	1.61	4.58	0.87	7.89	26.86
Lekanesphaera hookeri	1.90	0.49	4.18	2.07	7.19	34.05
Hediste diversicolor	3.08	2.15	3.12	1.20	5.37	39.42
Paragnathia formica	0.38	1.20	3.05	0.75	5.24	44.66
Eurydice affinis	0.18	1.11	3.00	0.78	5.16	49.82
	RM	PM		(Average dissimilarity=57.22)		
Abra tenuis	0.00	2.93	5.83	5.71	10.19	10.19
Hediste diversicolor	3.08	0.62	4.96	1.96	8.66	18.85
Chironomus sp.	2.06	0.00	4.03	1.63	7.05	25.90
Corophium multisetosum	0.00	1.77	3.51	1.35	6.13	32.03
Alkmaria romijni	0.00	1.63	3.24	1.18	5.67	37.70
Capitella capitata	2.44	1.96	2.95	1.20	5.16	42.86
Foronideo	0.00	1.27	2.30	0.69	4.02	46.88
	NRM	PM		(Average dissimilarity=65.82)		
Abra tenuis	0.00	2.93	7.21	5.24	10.95	10.95
Capitella capitata	0.00	1.96	4.68	1.87	7.12	18.06
Corophium multisetosum	0.00	1.77	4.34	1.34	6.59	24.65
Hediste diversicolor	2.15	0.62	4.23	1.53	6.43	31.08
Alkmaria romijni	0.00	1.63	4.01	1.18	6.09	37.17
Oligochaeta	1.61	0.00	3.90	0.76	5.93	43.10
Paragnathia formica	1.20	0.96	3.63	0.94	5.51	48.61

Taxa are listed in decreasing order according to its contribution to the average dissimilarity between areas

Macroinvertebrate community biomass was higher in PM and RM than in NRM. RM showed higher AFDW than NRM, while PM showed intermediate values (Tables 2 and 3). *H. diversicolor* showed the highest biomass and AFDW values in RM together with *Carcinus maenas* (decapoda; Table 3, Fig. 4).

RM and PM showed higher H' and H_{max} than NRM (Tukey, $p < 0.05$). J and D were similar for every marsh area (ANOVA, $p > 0.05$) with high J values and low D values (Table 2, Fig. 5).

Warwick (1986) suggested that the distribution of numbers of individuals among species should behave differently from the distribution of biomass among species when influenced by disturbance. Thus, the average ABC curve in RM, where the biomass curve was above that for abundance, indicated undisturbed conditions. For NRM the crossing of abundance and biomass curves suggested a moderate state of disturbance. In the case of PM, the ABC curve indicated disturbed conditions since the abundance curve was always above the biomass curve, showing the lowest W statistic value ($W = -0.07$; Fig. 6).

Environment-Macroinvertebrates

The results of BIOENV analysis evaluating the relationship between environmental variables and macrofauna presence indicated that the most significant correlations always occurred with sediment pH, redox potential, organic matter content and bulk density (maximum correlations of 0.441). Individually, organic matter content (0.398) and sediment

Table 5 Total species richness (S_{total}), mean species richness per sample (S_{mean}), and mean individuals number per sample (N_{mean}) in three salt marsh areas in the Odiel Marshes

Location	S_{total}	S_{mean}	N_{mean}
Restored marshes	26	5.6 ± 0.4^{a}	45.5 ± 6.2^{ab}
Non-restored marshes	18	3.6 ± 0.5^{b}	26.6 ± 4.9^{a}
Preserved marshes	23	6.1 ± 0.5^{a}	47.5 ± 6.5^{b}

Different letters indicate significant differences between areas (ANOVA or Kruskal–Wallis, $p < 0.05$)

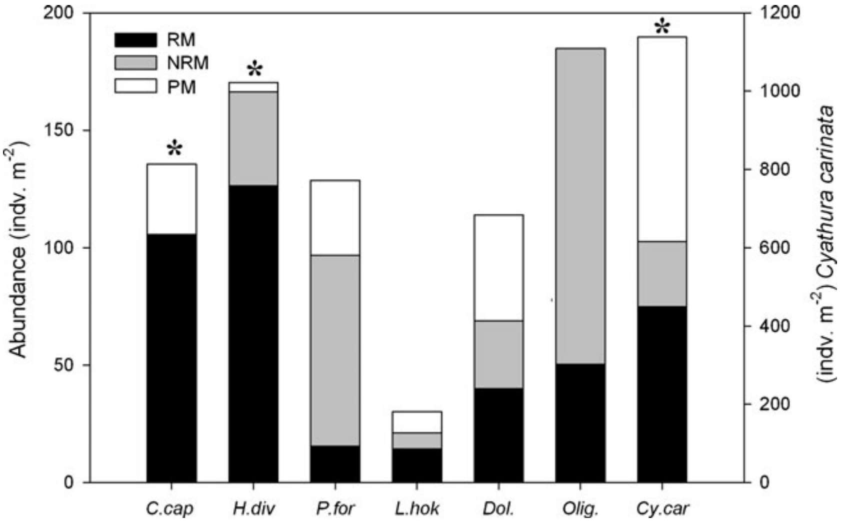

Fig. 4 Abundance (ind. m^{-2}) of the most abundant macroinvertebrate species in restored marshes (RM), non-restored marshes (NRM), and preserved marshes (PM). *C.cap Capitella capitata*, *H.div Hediste diversicolor*, *P.for Paragnathia formica*, *L.hok Lekanesphaera hookeri*, *Dol*. *Dolichopodidae*, *Olig*. *Oligochaeta*, *Cy.car Cyathura carinata*. The right axis (ind. m^{-2}) refers only to *C. carinata*. Asterisk indicates significant differences between marsh areas for the same species (ANOVA or Kruskal–Wallis, $p < 0.01$)

bulk density (0.334) were the variables that better explained the macroinvertebrates distribution. pH and redox potential presented lower correlations (0.261 and 0.181, respectively).

Total macroinvertebrate abundance decreased with increasing sediment organic matter content (Spearman, $R = -0.304$, $p < 0.05$, $n = 58$) and total AFDW increased with *S. maritima* below-ground biomass (Pearson, $R = 0.367$, $p < 0.01$, $n = 58$).

Discussion

Our results show that the restoration of European salt marshes by planting the native *S. maritima* increases species richness, diversity, density and biomass of the macroinvertebrate community. Restored marshes 3 years after restoration showed an intermediated state according with their similarity (MDS analysis) between non-restored and preserved areas. In *S. alterniflora* created marshes in North America, however, macroinvertebrate density and species richness equivalent to reference marshes may be achieved within 8 years (Craft and Sacco 2003), full recovery, that is similar community composition satisfying the same ecological functions, relative to reference marshes, if it is ever achieved, may require more than two decades (Swamy et al. 2002). Thus, preserved marshes in our study presented the most different macrobenthos community, influenced mainly (according to BIOENV analysis) by higher sediment bulk density, higher pH and lower redox potential than restored and non-restored marshes. For example, *C. multisetosum* was recorded only in preserved marshes. Queiroga (1990) suggested that this species seems to avoid fine sediments, which is according with preserved marshes showing the highest sediment bulk density. In the case of *A. romijni*, also recorded only in preserved marshes, preferentially lives in intertidal areas without high hydrodynamics (Chaouti and Bayed 2006) as occurs in preserved marshes, being considered as a typical lagoon species (Barnes 1994). Therefore, the recorded differences in macrobenthos community composition, beyond the maturation state of the marshes, seemed also to be related with the physiography and the location of preserved marshes, a successional littoral lagoon colonized by *Z. noltii* close by the sea.

Beyond the above-mentioned differences in community composition, we recorded a fast recovery of the macroinvertebrate community in restored marshes, which was reflected, for example, in similar diversity and species richness values to preserved marshes and higher than in non-restored marshes due

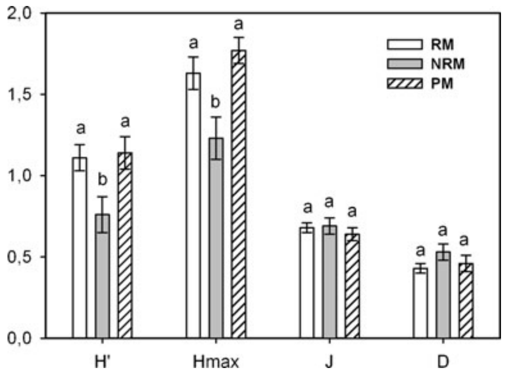

Fig. 5 Ecological diversity (H'), maximum ecological diversity (H_{max}), dominance (D), and evenness (J) of the more abundant benthic macroinvertebrates in restored marshes (RM), non-restored marshes (NRM), and preserved marshes (PM). Different letters indicate significant differences between marshes

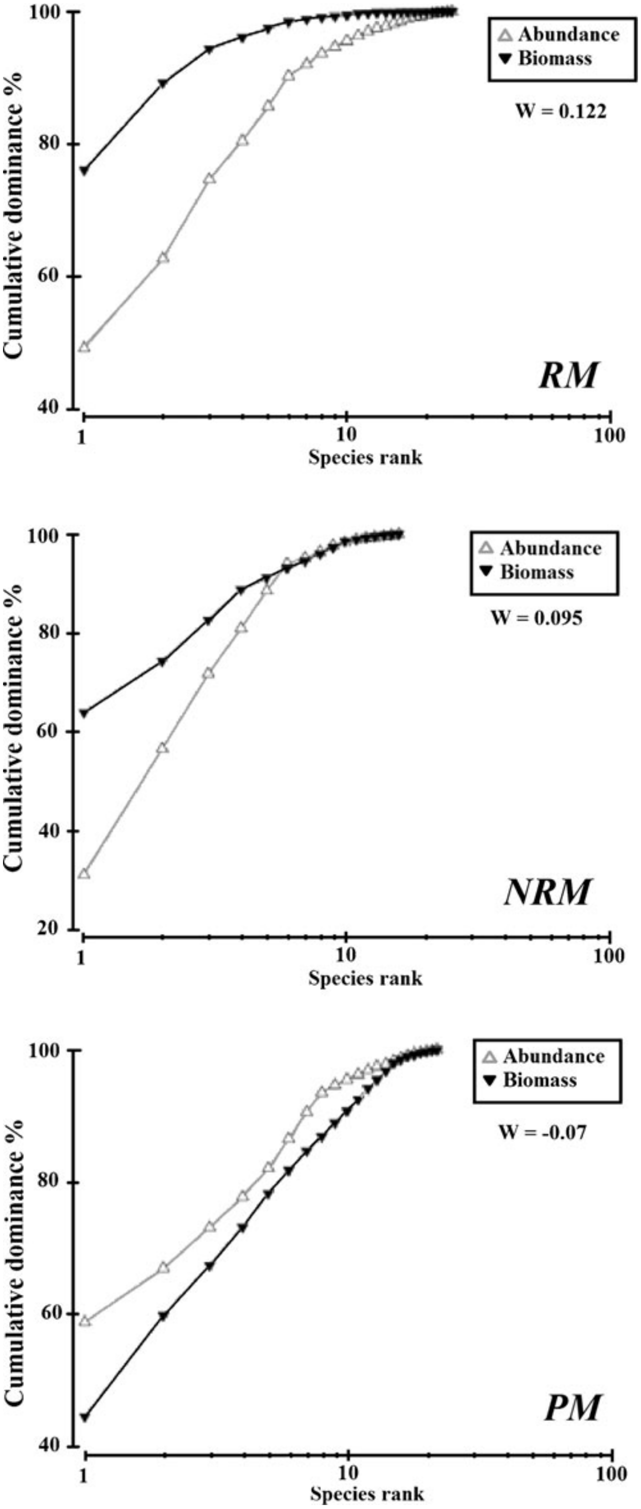

Fig. 6 Average abundance biomass comparison (ABC) curves at restored marshes (RM), non-restored marshes (NRM), and preserved marshes (PM)

to higher species richness. This seemed to be related with the development of planted cordgrass prairies playing key ecological functions for the macroinvertebrate community such as decreasing stress levels, and providing food, sediment oxygenation, substrata availability and protection against predators (Teal and Wieser 1966; Netto and Lana 1997). As in our study, diversity and dominance did not differ between created and natural North American marshes (Ferguson and Rakocinski 2008); however, species richness was higher in natural marshes. H' in restored and preserved marshes was similar to that reported for *S. maritima* marshes in the Tagus estuary during the same season (Salgado et al. 2007).

The beneficial effects of cordgrass plantation for the macroinvertebrate community were also reflected in macroinvertebrates abundance reaching similar values in restored and preserved marshes 3 years after restoration, as described for *S. alterniflora* and *S. foliosa* North American marshes (Peck et al. 1994; Havens et al. 1995; Swamy et al. 2002; Craft and Sacco, 2003; Levin and Talley, 2002; Warren et al. 2002). Total macrobenthos abundances were similar to those found for pioneer *S. maritima* marshes (Salgado et al. 2007) and slightly lower than those found in invaded Chinese *S. alterniflora* marshes (Chen et al. 2009). *Cyathura carinata*, a typical species in eutrophic marshes (Ferreira et al. 2004; Marques et al. 1994), showed much higher abundances in Odiel Marshes (167–522 ind. m^{-2}), highly polluted with nitrates (Elbaz-Poulichet et al. 1999), than in less contaminated Portuguese marshes (10–65 ind. m^{-2} following Salgado et al. (2007) and Cardoso et al. (2008)). The rest of the macroinvertebrate community reported by Salgado et al. (2007) for Atlantic Portuguese marshes was similar in species composition and abundances to our study, except for *Oligochaeta* that presented a higher density in the Tagus estuary, which may be related to its higher sediment organic matter content (Finogenova 1996). As in our study, Tavares et al. (2009) and Zhou et al. (2009) found a negative correlation between sediment organic matter content and macrobenthos diversity and abundance and Sacco et al. (1994) reported that high organic matter content may be a possible cause for high infaunal abundances at the North American Atlantic Coast. In our work, *Oligochaeta* presented higher density in non-restored marshes than in the other marshes likely due to higher sediment organic matter content or/and the elimination of competitors by predators. Thus, the polychaete *C. capitata*, well known as an indicator of organic enrichment (Warren 1977), was absent from non-restored marshes where vegetation cover was low and high shorebird densities have been recorded (Curado et al. 2013).

Comparing abundance and biomass curves is a method sensitive to various kinds of disturbance, both natural (physical and biological) and pollution-induced, to the macrobenthos community (Warwick et al. 1987); however, this method is not exempt of controversy (Beukema 1988; Craeymeersch 1991). In our study, ABC curves pointed to preserved marshes as the most disturbed area, and restored marshes the least. The three studied areas present similar and very high pollution levels (López-González et al. 2005), so the detected alteration levels seemed to be related to physical disturbances, high erosion rates in non-restored marshes and bait capture in preserved marshes, where the low density of *H. diversicolor* was probably due to the high extraction activity carried out in this area since this polychaete is used as fresh bait for fishing. Preserved marshes and non-restored marshes are included in the Natural Park, being the former used as a bait capture zone regulated by the protected area conservation management plan, while restored marshes are out of the protected area and included in those marshes under the Port of Huelva management, where bait capture is forbidden.

Total AFDW increased with *S. maritima* below-ground biomass, which according to the PCA analysis marked important differences between areas. The crustaceans *C. maenas*, *C. carinata*, and *Uca tangerii* among others contributed considerably to the total biomass of *S. maritima* marshes in restored and preserved areas, together with *H. diversicolor* in restored marshes. These species, with a total relative abundance of 64 % in restored marshes and 58 % in preserved marshes, represented 96 % and 69 % of the total biomass, respectively. Previous studies have recorded higher abundances and biomasses of macroinvertebrates in *Spartina* and *Zostera* marshes than in mudflats (Almeida et al. 2008; Spruzen et al. 2008; Zhou et al. 2009; Tang and Kristensen 2010). Differences between biomass and AFDW in restored and preserved areas seemed to mainly be related to weight loss of inorganic matter adhered to the coriaceous tubes of the phylum *Phoronidea* and shells of the bivalves *Cerastoderma edule* and *A. tenuis*.

Conclusions

Our results show that the restoration of European salt marshes using *S. maritima* has a positive effect on the benthic macroinvertebrate community in relatively short periods of time increasing its complexity and abundance ca. 3 years after plantations. Restored marshes achieved similar diversity values and higher specific richness than preserved marshes and higher values for both parameters than non-restored marshes invaded by *S. densiflora*. In addition, restored and preserved marshes do not differ in total macroinvertebrate abundance neither in total biomass, being both higher than in non-restored marshes. Overall, our results point to the important role of cordgrasses used as bio-tools in salt marsh restoration projects, developing key ecological functions for the macroinvertebrate community. Nevertheless, restored marshes ca. 3 years after plantations showed still important differences in macroinvertebrate species composition compare to preserved marshes, reflecting that they may still play different ecological functions.

In view of our results, cordgrass plantations appear as a key action of ecological restoration projects at low-medium European salt marshes since they improve the macroinvertebrate community, which is central to the functioning of these ecosystems, for example, promoting organic matter decomposition (Pozo and Colino 1992) and representing an important trophic link between primary producers and consumer (fish, birds, etc.; Sarda et al. 1995). In addition, managers of European salt marshes should also pay attention, not only to salt marsh restoration, but to the conservation of existing *S. maritima* prairies, especially in a scenario of climate change and sea level rise. The lost of the small cordgrass would not only mean a loss of vegetation cover but the degradation of the macroinvertebrate community and subsequent effects.

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References

Almeida, C., R. Coelho, M. Silva, L. Bentes, P. Monteiro, J. Ribeiro, K. Erzini, and J.M.S. Goncalves. 2008. Use of different intertidal habitats by faunal communities in a temperate coastal lagoon. *Estuarine, Coastal and Shelf Science* 80: 357–364.

Anderson, M.J., R.N. Gorley, and K.R. Clarke. 2008. *PERMANOVA+ for PRIMER: Guide to Statistical Methods*. Plymouth: PRIMER-E.

Armitage, A.R., S.M. Jensen, J.E. Yoon, and R.F. Ambrose. 2007. Wintering shorebird assemblages and behavior in restored tidal wetlands in southern California. *Restoration Ecology* 15: 139–148.

Bakker, J.P., P. Esselink, K.S. Dijkema, W.E. van Duin, and D.J. de Jong. 2002. Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478: 29–51.

Barnes, R.S.K. 1994. A critical appraisal of the application of Guélorget and Perthuisot's concepts of the paralic ecosystem and confinement to macrotidal Europe. *Estuarine, Coastal and Shelf Science* 38: 41–48.

Beukema, J.J. 1988. An evaluation of the ABC-method (abundance/biomass comparison) as applied to macrozoobenthic communities living on tidal flats in the Dutch Wadden Sea. *Marine Biology* 99: 425–433.

Cardoso, I., J.P. Granadeiro, and H. Cabral. 2008. Benthic prey quantity and quality in the main mudflat feeding areas of the Tagus estuary: implications for birds and fish populations. *Ciencias Marinas* 34: 283–296.

Castellanos, E.M., M.E. Figueroa, and A.J. Davy. 1994. Nucleation and facilitation in salt marsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* 82: 239–248.

Castellanos, E.M., C. Heredia, M.E. Figueroa, and A.J. Davy. 1998. Tiller dynamics of *Spartina maritima* in successional and non-successional Mediterranean salt marsh. *Plant Ecology* 137: 213–225.

Castillo, J.M., C.J. Luque, E.M. Castellanos, and M.E. Figueroa. 2000. Causes and consequences of salt-marsh erosion in an Atlantic estuary in SW Spain. *Journal of Coastal Conservation* 6: 89–96.

Castillo, J.M., and M.E. Figueroa. 2009. Restoring salt marshes using small cordgrass, *Spartina maritima*. *Restoration Ecology* 17: 324–326.

Chaouti, A., and A. Bayed. 2006. First record of *Alkmaria romijni* Horst, 1919 (Polychaeta: Ampharetidae) from the Mediterranean coast (Smir Lagoon, Morocco). *Marine Life* 16: 15–19.

Chen, Z., L. Guo, B. Jin, J. Wu, and G. Zheng. 2009. Effect of the exotic plant *Spartina alterniflora* on macrobenthos communities in salt marshes of the Yangtze River Estuary, China. *Estuarine, Coastal and Shelf Science* 82: 265–272.

Clarke, K.R. 1990. Comparisons of dominance curves. *Journal of Experimental Marine Biology and Ecology* 138: 143–157.

Clarke, K.R. 1993. Non parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.

Clarke, K.R., and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92: 205–219.

Cooper, M.A. 1993. The status of *Spartina maritima* in Suffolk. *Suffolk Naturalists' Society Transactions* 29: 48–54.

Craeymeersch, J.A. 1991. Applicability of the abundance/biomass comparison method to detect pollution effects on intertidal macrobenthic communities. *Hydrobiological Bulletin* 24: 133–140.

Craft, C., and J. Sacco. 2003. Long-term succession of benthic infauna communities on constructed *Spartina alterniflora* marshes. *Marine Ecology Progress Series* 257: 45–58.

Curado, G., M.E. Figueroa, and J.M. Castillo. 2012. Sediment dynamics in *Spartina maritima* restored, non-restored and preserved salt marshes. *Ecological Engineering* 47: 30–35.

Curado, G., E. Figueroa, M.I. Sánchez, and J.M. Castillo. 2013. The avian communities in *Spartina maritima* restored and non-restored salt marshes. *Bird Study*. In press. doi: 10.1080/00063657.2013.790875

Curado, G., A.E. Rubio-Casal, E. Figueroa, and J.M. Castillo. 2014. Plant Zonation in restored, non-restored and preserved *Spartina maritima* salt marshes. *Journal of Coastal Research*, In Press

D'Antonio, C., and L.A. Meyerson. 2002. Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. *Restoration Ecology* 10: 703–713.

Dionne, M., F.T. Short, and D.M. Burdick. 1998. Fish utilization of restored, created, and reference salt-marsh habitat in the Gulf of Maine. In Fish habitat: essential fish habitat and rehabilitation, ed. Benaka, L. 384–404. American Fisheries Society Symposium 22, Bethesda, Maryland

Elbaz-Poulichet, F., N.H. Morley, A. Cruzado, Z. Velasquez, E.P. Achterberg, and C.B. Braungardt. 1999. Trace metal and nutrient distribution in an extremely low pH (2.5) river-estuarine system, the Ria of Huelva (South-West Spain). *Science of the Total Environment* 227: 73–83.

Fell, P.E., K.A. Murphy, M.A. Peck, and M.L. Recchia. 1991. Reestablishment of Melampus-bidentatus (Say) and other macroinvertebrates on a restored impounded tidal marsh - comparison of populations above and below the impoundment dike. *Journal of Experimental Marine Biology and Ecology* 152: 33–48.

Ferguson, H.J., and C.F. Rakocinski. 2008. Tracking marsh restoration using macrobenthic metrics: implementing a functional approach. *Wetland Ecology and Management* 16: 277–289.

Ferreira, S.M., M.A. Pardal, A.I. Lillebø, P.G. Cardoso, and J.C. Marques. 2004. Population dynamics of *Cyathura carinata* (Isopoda) in a eutrophic temperate estuary. *Estuarine, Coastal and Shelf Science* 61: 669–677.

Figueroa, M.E., J.M. Castillo, S. Redondo, T. Luque, E.M. Castellanos, F.J. Nieva, C.J. Luque, A.E. Rubio-Casal, and A.J. Davy. 2003. Facilitated invasion by hybridization of *Sarcocornia* species in a salt-marsh succession. *Journal of Ecology* 91: 616–626.

Finogenova, N.P. 1996. Oligochaete communities at the mouth of the Neva and their relationship to anthropogenic impact. *Hydrobiologia* 334: 185–191.

Gallego-Fernández, J.B., and F. García-Novo. 2007. High-intensity versus low-intensity restoration alternatives of a tidal marsh in Guadalquivir estuary, SW Spain. *Ecological Engineering* 30: 112–121.

Gardner, P.A., and M.L.H. Thomas. 1987. Growth, mortality and production of organic matter by a rocky intertidal population of *Mytilus edulis* in the Quoddy Region of the Bay of Fundy. *Marine Ecology Progress Series* 39: 31–36.

Gedan, K.B., B.R. Silliman, and M.D. Bertness. 2009. Centuries of Human-Driven Change in Salt Marsh Ecosystems. *Annual Review of Marine Science* 1: 117–141.

Havens, K.J., L.M. Varnell, and J.G. Bradshaw. 1995. An assessment of ecological conditions in a constructed tidal marsh and two natural reference tidal marshes in coastal Virginia. *Ecological Engineering* 4: 117–141.

INE, 2009. Instituto Nacional de Estadística, España. http://www.ine.es. Accessed 02 May 2010

Konisky, R.A., D.M. Burdick, M. Dionne, and H.A. Neckles. 2006. A regional assessment of salt marsh restoration and monitoring in the Gulf of Maine. *Restoration Ecology* 14: 516–525.

Levin, L.A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. *Marine Ecology Progress Series* 141: 67–82.

Levin, L.A., and T. Talley. 2000. Influences of vegetation and abiotic environmental factors on salt marsh benthos. In Concepts and controversies in tidal marsh ecology, ed. Weinstein, M.P. and D.A. Kreeger.661-708. Kluwer Academic Publishers, Amsterdam, Netherlands

Levin, L.A., and T.S. Talley. 2002. Natural and manipulated sources of heterogeneity controlling early faunal development of a salt marsh. *Ecological Applications* 12: 1785–1802.

Levin, L.A., C. Neira, and E.D. Grosholz. 2006. Invasive cordgrass modifies wetland trophic function. *Ecology* 87: 419–432.

López-González, N., J. Borrego, B. Carro, and O. Lozano-Soria. 2005. Bioavailability of Fe and heavy metals in sediments from the Ria of Huelva (South-Western Spain). *Geogaceta* 37: 219–222.

Marques, J.C., I. Martins, C. Teles-Ferreira, and C. Cruz. 1994. Population dynamics, life history, and production of *Cyathura carinata* (Krøyer) (Isopoda: Anthuridae) in the Mondego estuary, Portugal. *Journal of Crustacean Biology* 14: 258–272.

Mitsch, W.J. 2010. Conservation, restoration and creation of wetlands: a global perspective. In *Ecological Restoration: A Global Challenge, ed. Comín, F.A*, 175–187. Cambridge: Cambridge University Press.

Netto, S.A., and P.C. Lana. 1997. Intertidal zonation of benthic macrofauna in a subtropical salt marsh and nearby unvegetated flat (SE, Brazil). *Hydrobiologia* 353: 171–180.

Pagola-Carte, S., J. Urkiaga-Alberdi, M. Bustamante, and J.I. Saiz-Salinas. 2002. Concordance degrees in macrozoobenthic monitoring programmes using different sampling methods and taxonomic resolution levels. *Marine Pollution Bulletin* 44: 63–70.

Paramor, O.A.L., and R.G. Hughes. 2007. Restriction of *Spartina* anglica (C.E. Hubbard) marsh development by the infaunal polychaete *Nereis diversicolor* (O.F. Müller). *Estuarine*. *Coastal and Shelf Science* 71: 202–209.

Peck, M.A., P.E. Fell, E.A. Allen, J.A. Gieg, C.R. Guthke, and M.D. Newkirk. 1994. Evaluation of tidal marsh restoration comparison of selected macroinvertebrate populations on a restored impounded valley marsh and an unimpounded valley marsh within the same salt marsh system in Connecticut, USA. *Environmental Management* 18: 283–293.

Pozo, J., and R. Colino. 1992. Decomposition processes of *Spartina maritima* in a salt marsh of the Basque Country. *Hydrobiologia* 231: 165–175.

Queiroga, H. 1990. *Corophium multisetosum* (Amphipoda: Corophiidae) in Canal de Mira, Portugal: Some factors that affect its distribution. *Marine Biology* 104: 397–402.

Ranwell, D.S., E.C.F. Bird, J.C.R. Hubbard, and R.E. Stebbings. 1964. *Spartina* salt marshes in Southern England, V. Tidal submergence and chlorinity in Poole Harbour. *Journal of Ecology* 52: 627–641.

Ranwell, D.S. 1967. World resources of *Spartina townsendii* (sensu lato) and economic use of *Spartina* marshland. *Journal of Applied Ecology* 4: 239–256.

Rodney, W.S., and K.T. Paynter. 2006. Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* 335: 39–51.

Sacco, J.N., E.D. Seneca, and T.R. Wentworth. 1994. Infaunal community development of artificially established salt marshes in North Carolina. *Estuaries* 17: 489–500.

Salgado, J.P., H.N. Cabral, and M.J. Costa. 2007. Spatial and temporal distribution patterns of the macrozoobenthos assemblage in the salt marshes of Tejo estuary (Portugal). *Hydrobiologia* 587: 225–239.

Sánchez-Moyano, J.E., and I. García-Asencio. 2010. Crustacean assemblages in a polluted estuary from South-Western Spain. *Marine Pollution Bulletin* 60: 1890–1897.

Sánchez-Moyano, J.E., I. García-Asencio, and J.C. García-Gómez. 2010. Spatial and temporal variation of the benthic macrofauna in a grossly polluted estuary from southwestern Spain. *Helgoland Marine Research* 64: 155–168.

Sarda, R., K. Foreman, and I. Valiela. 1995. Macrofauna of a southern New England salt marsh: seasonal dynamics and production. *Marine Biology* 121: 431–445.

Shannon, C.E., and W. Weaver. 1949. *A Mathematical Model of Communication*. Urbana, IL, EEUU: University of Illinois Press.

Silliman, B. R., E.D., Grosholz, and M.D. Bertness. 2009. Human impacts on salt marshes: a global perspective. University of California Press

Simpson, E.H. 1949. Measurement of Diversity. *Nature* 163: 688.

Spruzen, F.L., A.M.M. Richardson, and E.J. Woehler. 2008. Spatial variation of intertidal macroinvertebrates and environmental variables in Robbins Passage wetlands, NW Tasmania. *Hydrobiologia* 598: 325–342.

Swamy, V., P.E. Fell, M. Body, M.B. Keaney, M.C. Nyaku, E.C. Mcilvain, and A.L. Keen. 2002. Macroinvertebrate and fish populations in a restored impounded salt marsh 21 years after the reestablishment of tidal flooding. *Environmental Management* 29: 516–530.

Tang, M., and E. Kristensen. 2010. Associations between macrobenthos and invasive cordgrass, *Spartina anglica*, in the Danish Wadden Sea. *Helgoland Marine Research* 64: 321–329.

Tavares, P.C., D. Alves, and M. Shapouri. 2009. Structural Changes in Macroinvertebrate Communities Associated with Reduction in the Management of Coastal Saltpans. *Journal of Marine Biology*. doi: 10.1155/2009/629310.

Teal, J.M., and W. Wieser. 1966. The distribution and ecology of nematodes in a Georgia salt-marsh. *Limnology and Oceanography* 11: 217–222.

Verhoeven, A.G. 1938. *Fixation des terres alluviales*, 101–137. Zeeland: Congrès International Géographie. Amsterdam. Excursion A.

Warren, L. M. 1977. The ecology of *Capitella capitata* in British waters. *Journal of the Marine Biological Association of the United Kingdom* 57: 151–159.

Warren, R.S., P.E. Fell, R. Rozsa, A.H. Brawley, A.C. Orsted, E.T. Olson, V. Swamy, and W.A. Niering. 2002. Salt Marsh Restoration in Connecticut: 20 Years of Science and Management. *Restoration Ecology* 10: 497–513.

Warwick, R.M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* 92: 557–562.

Warwick, R.M., T.H. Pearson, and S. Ruswahyuni. 1987. Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. *Marine Biology* 95: 193–200.

Zhou, H.-X., J.-e. Liu, and P. Qin. 2009. Impacts of an alien species (*Spartina alterniflora*) on the macrobenthos community of Jiangsu coastal inter-tidal ecosystem. *Ecological Engineering* 35: 521–528.

Zedler, J.B., and R. Lindig-Cisneros. 2002. Functional equivalency of restored and natural salt marshes. In *Concepts and controversies in tidal marsh ecology, ed. Weinstein, M., and D. Kreeger*, 565–582. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Zedler, J.B., and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30: 39–74.

Zedler, J.B., and J.M. West. 2008. Declining diversity in natural and restored salt marshes: A 30-year study of Tijuana Estuary. *Restoration Ecology* 16: 249–262.