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ORIGINAL ARTICLE

Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations

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Abstract

Molluscs associated with a *Zostera marina* bed from Cantarriján bay (Southern Spain, Alboran Sea) at 14–16 m depth were sampled monthly from October 1996 to September 1997. A total of 44,819 individuals belonging to 80 species were identified. In spite of the high species richness, only seven species of gastropods showed a dominance value (D) higher than 1%. *Jujubinus striatus* was the dominant species of the assemblage with 70.8% of the total abundance. The other dominant species were *Rissoa membranacea* (9.8%), *Nassarius pygmaeus* (5.8%), *Mitrella minor* (4%), *Smaragdia viridis* (1.9%), *Rissoa monodonta* (1.4%), *Bittium reticulatum* (1.3%). The dynamic pattern of the mollusc populations showed a temporal trend with monthly values of species richness and abundance ranging between 10 and 25 species and between 178 and 4412 individuals·222 m^{-2}. The species richness and abundance were higher in the spring and summer months than in the autumn and winter ones. The diversity (Shannon–Wiener, H') follows a similar trend, with increases from April to September and decreases from October to March. H' values (ranging from 0.45 to 3.10) are more influenced by the evenness (J) than by the species richness. A multivariate analysis (Cluster, Multi-dimensional Scaling) based on both presence/absence and quantitative data has also pointed out a temporal trend, with spring–summer samples significantly different from autumn–winter samples. The temporal changes in abundance seem related with the species' biology, such as recruitment events, as well as to the canopy features and shoot density variation in the *Zostera* meadow. From the biogeographical point of view, most of the molluscs (65%) found in the Cantarriján bed, have a Lusitanian–Mediterranean distribution (*sensu* Ekman 1953). The proximity to Africa is shown by the presence of four species with a mainly West African distribution. Only *R. membranacea* has a typical Atlantic distribution, driven by that of *Z. marina* in NW Europe.

Problem

The importance of seagrasses stems from their contribution to the production in the coastal area and their role in stabilization of the substrate (García & Duarte 2001; Templado 2004). They also provide habitats and resources to sustain rich invertebrate and fish communities (Webster *et al.* 1998; Attrill *et al.* 2000; Hemminga & Duarte 2000; Guidetti *et al.* 2002; Blanchet *et al.* 2005).

The eelgrass *Zostera marina* forms meadows with considerable spatial and temporal variation related to wave action, bottom topography, characteristics of substrate and climatic events such as storms or in the northern areas, thick ice-cover during the harsh winter (Middelboe *et al.* 2003). In the Mediterranean Sea, *Z. marina* is rare, being frequently confined to lagoons in the northern sector, where it can form extended meadows at shallow depths (Boudouresque *et al.* 1994; Guidetti *et al.* 2002).

According to Hemminga & Duarte (2000), molluscs can make a conspicuous contribution to the seagrass fauna, and therefore have been frequently studied in different seagrass beds. Previous studies regarding the Mediterranean have been carried out in *Posidonia oceanica* (Russo *et al.* 1984; Templado 1984; Gambi *et al.* 1992; García Raso *et al.* 1992; Scipione *et al.* 1996; Russo & Terlizzi 1998; Templado *et al.* 2004), and *Cymodocea nodosa* meadows (Scipione *et al.* 1996; Connolly & Butler 1996; Chemello *et al.* 1998; Terlizzi & Russo 1998; Sfriso *et al.* 2001; Ballesteros *et al.* 2004). *Zostera marina* has been seldom studied in the limited parts of the Mediterranean where the species occurs, *i.e.* the littoral of Málaga and Granada (Barrajón *et al.* 1996; Rodríguez & Cabrera 2002; García Raso *et al.* 2004), the lagoons of the French Mediterranean (Mars 1966), the Northern Adriatic (Sfriso *et al.* 2001) and the Turkish coast (Çinar *et al.* 1998). In some of these investigations, the molluscs are part of a broader study on associated fauna. Faunal structure has been sometimes studied in relation to changes in seagrass shoot density and canopy features (*i.e.* Connolly & Butler 1996, Scipione *et al.* 1996).

The Spanish southern littoral is the westernmost area of the Mediterranean Sea, in the Alboran Sea, with hydrological influence of the Atlantic ocean. Because of that, *Z. marina*, being a circumboreal species, is the most conspicuous seagrass, although with a patchy distribution and sometimes in mixed meadows with *C. nodosa* (Barrajón *et al.* 2004).

In the littoral of Southern Spain there are several upwelling areas, with a high density of suspended matter (Rodríguez 1982; Delgado 1990; see map in Gofas & García Raso 2004). In spite of a limited supply of light, *Z. marina* meadows extend between 5 and 20 m depth, in relatively open bays, along the shoreline (Moreno & Guirado 2003; Luque & Templado 2004). This distribution is deeper than that of the Atlantic eelgrass meadows or Mediterranean lagoonal ones, and seems to be related with the topography of the coast and wave action.

The littoral of Málaga and Granada (Southern Spain) experiences intense pressure from tourism, with an important increase of coastal constructions, and the subsequent impact on the littoral ecosystems, including seagrass meadows. In addition to that, continuous trawl-fishing activity has been detected on the seagrasses. In order to protect this important littoral ecosystem, the regional authorities (Junta de Andalucía) have declared the marine area of the 'Paraje Natural de los Acantilados de Maro – Cerro Gordo' zone, in which is located the Cantarriján bay, as protected. Nowadays, this protected area has been declared a Specially Protected Area of Mediterranean Interest (SPAMI, in Spanish ZEPIM) (Rodríguez *et al.* 2003).

The present study is part of a research program for the study of the macrofauna (molluscs, crustaceans and fishes) of seagrasses from Southern Spain. It represents the first annual survey on the molluscs from a deep *Z. marina* bed in the littoral of Southern Spain, the southernmost European eelgrass bed. It has been mainly focused on two objectives:

1 To know the species composition and biogeography of the molluscs inhabiting the *Z. marina* bed, taking into account the particular location of the study site in the Alboran Sea, near the Atlantic and in front of the African coast.

2 To analyse the structural changes in the mollusc populations in time. The working hypothesis was that the temporal variation in the canopy features and shoot density of the seagrass drive the main changes in the associated macrofauna.

Material and Methods

Study site

The studied *Zostera marina* bed is located in the Cantarriján bay, inside the protected marine area of 'Paraje Natural de los Acantilados de Maro-Cerro Gordo', littoral of Granada (Southern Spain) (36 °44.2′ N, 03 °46.6′ W) (Fig. 1). The studied bed extended from a depth of about 8–18 m on a gentle slope, and had a patchy distribution. The patches were surrounded by a sandy bottom. There is a temporal trend in the canopy development, with the highest shoot density and shoot length in the spring and summer months and a reduction of both variables in the autumn and winter ones (Bañares España *et al.* 2002). The shoot length of *Z. marina* within the protected area ranges from 22.53 ± 2.77 cm in December (n = 156 shoots) to 33.94 ± 3.72 cm in September (n = 172 shoots). The shoot density in the *Z. marina* beds within the area ranges between 204 (lowest winter value) and 428 (highest summer value) shoots·m^{-2}. These data have been obtained by a seasonal sampling program still in course (J.L. Rueda and C. Salas, unpublished data).

The bay of Cantarriján is relatively open to the sea and consequently is frequently affected by storms and wave action; because of that the *Z. marina* bed is one of the deeper known from both the Mediterranean and the Atlantic coasts of Europe.

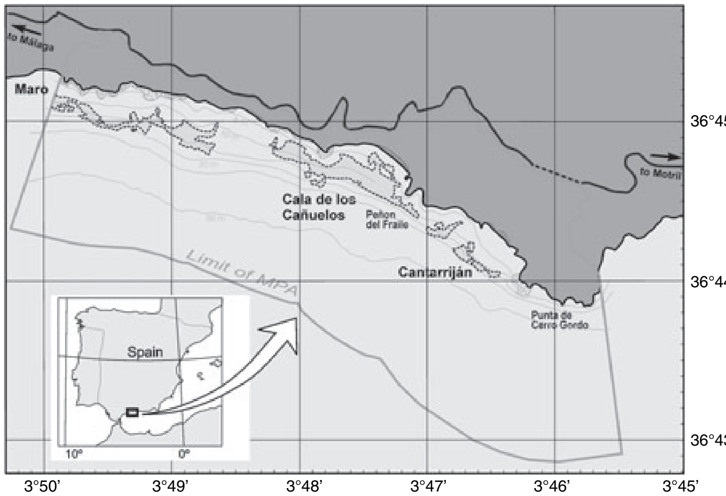

Fig. 1. Location of Cantarriján bay (sampling site) in the marine protected area of Maro-Cerro Gordo in the littoral of Granada and Málaga (Southern Spain). (Adapted from Bañares España *et al.* 2002). Shaded areas represent the approximative extension of *Zostera marina* beds.

Sampling procedures

Samples were collected monthly from October 1996 to September 1997, between 14 and 16 m depth where the bed was more continuous and dense, with a small Agassiz trawl of an opening of 72 cm length and 30 cm high; the mesh size was 3 × 3 mm from knot to knot. In spite of the relatively large mesh size, the usually large amount of bottom material collected clogged and stretched the net, reducing the effective mesh size and allowing the collection of a finer fraction. Therefore, the underestimation of the juvenile abundance was minimal and was comparable throughout the samples. This trawl was selected for collecting the epifauna because it was an effective but low impact gear and did not injure the seagrass. The sampling area for each haul was about 222 m^2; two to four (normally three) trawl replicates were made each month. The total number of replicates was 40. The sampled area was established taking into account a minimum sample area for crustaceans and fishes. The minimum area was estimated after collection of samples by increasing the trawling duration (*i.e.* 5, 10, 15 min), thus increasing the sampled area. Because of the higher dimensions and mobility of crustaceans and fishes, the sampling area is much greater than the minimum area required for the molluscs. For example, Russo & Vinci (1991) suggest that a minimum sampling area of 150 m^2 is appropriate for the epifaunal gastropods of the *Posidonia oceanica* beds. Biological samples were fixed in 70% ethanol and sieved on screens of different mesh sizes (10, 5, 3 and 1 mm). Molluscs were separated, determined and counted for each replicate. Whenever possible, juveniles of each species were annotated.

Information on the feeding of the dominant species has been obtained from the available literature (Peduzzi 1987; Lepoint *et al.* 2000; Kharlamenko 2001; Fredriksen *et al.* 2004; García Raso *et al.* 2004; Hily *et al.* 2004).

Data analysis

Frequency index (F) (percentage of samples in which the species is present) and Dominance index (D) (percentage of individuals of one particular species from the total) were calculated for each species.

The following parameters were also calculated on each monthly replicate: total abundance, number of species, Shannon–Wiener diversity (H') (Krebs 1989) and evenness index (J) (Pielou 1969).

Similarities/dissimilarities of the composition and structure of the mollusc assemblages were analysed by multivariate methods, using group-average sorting classification and non-metric Multi-dimensional Scaling (MDS) ordination with the Bray–Curtis Similarity Measure (Clarke 1993). Both sorting classification and MDS ordinations were calculated on the presence/absence of species in order to test the consistency of the taxocoenosis independently from the relative abundance, and quantitatively using the fourth root transformed abundance data in order to reduce abundance differences of the dominant species. The comparison of mollusc assemblages was carried out using an analysis of similarities (Bray–Curtis similarity, and ANOSIM test). A SIMPER test was performed to evaluate the contribution of the particular species to the similarity and dissimilarity between the spring–summer and autumn–winter samples. All these multivariate analyses were performed using the PRIMER from Plymouth Marine Laboratory, UK (Clarke & Warwick 1994).

Results

Composition of the mollusc assemblages

A total of 44,819 mollusc specimens, belonging to 80 species were collected during the whole study period (Table 1). The assemblage was heavily dominated by gastropods, with 55 species and 44,197 individuals (98.6% of the individuals collected). The bivalves, with 22 species and 596 individuals, represent only 1.3% of the total mollusc individuals. Only two species of cephalopods, *Octopus vulgaris* and *Sepia officinalis*, were collected; the latter, with 25 individuals, seems to be common in the *Zostera* bed (Table 1).

In spite of the high species richness found in the studied bed, only seven species of gastropods show dominance values (D) higher than 1% (Table 2). *Jujubinus striatus* is the dominant species of the assemblage with 71.8% of the total. The other dominant species were *Rissoa membranacea* (9.8%), *Nassarius pygmaeus* (5.8%), *Mitrella minor* (4.0%), *Smaragdia viridis* (1.9%), *Rissoa monodonta* (1.4%), *Bittium reticulatum* (1.3%).

In relation to the frequency index (F), only seven species show F values higher than 75%: *J. striatus*, *R. membranacea*, *S. viridis*, *N. pygmaeus*, *M. minor*, *R. monodonta* and *Calliostoma* cf. *planatum* (Table 2). The *Calliostoma* cf. *planatum* found in the seagrass bed is similar to the well known *Calliostoma laugieri* (Payraudeau, 1826) but seems to be a different species and is locally sympatric with unquestionable *C. laugieri*, living among brown algae and rocks nearer to the shore. Awaiting further systematic studies, we use the name *C.* cf. *planatum* Pallary, 1900, originally described from Oran, Algeria for this species, which adjusts to the morphological features here observed. The cephalopod *S. officinalis*, with a frequency of 35%, is a persistent predator in the *Zostera* bed.

The bivalves are scarcely represented in the studied mollusc assemblages, either by dominance (D) or by frequency (F). *Anomia ephippium* is the most frequent (60% of the samples) and the dominant bivalve (0.5% of total individuals), and usually occurs as an epibiont on gastropod shells. The other two bivalves with relatively high abundance were *Musculus subpictus* (0.31%) and *Mytilaster minimus* (0.16%). Both of them are epifaunal; the former living embedded in colonial ascidians.

Temporal changes in mollusc assemblages

Figures 2–5 show the values of the structural parameters of the mollusc assemblages. The mean abundance showed a continuous increment with low values in the autumn–winter months (between 178 ± 32 ind·222 m^{-2} in December and 1432 ± 663 ind·222 m^{-2} in February) and maximum value in September, with 4.412 ± 986 ind·222 m^{-2} (Fig. 2). A similar trend can be observed for species richness, with lower values in the autumn and winter months (between 10 ± 3 and 15 ± 1 species) than in the spring and summer ones (between 18 ± 2 and 25 ± 3 species) (Fig. 3).

The Shannon–Wiener Diversity Index (H') displays for most of months low values (Fig. 4), ranging from 0.45 in March to 3.10 in December. These low values are better related with evenness (J') (Fig. 5) than with richness (Fig. 3). The increase of evenness (Fig. 5) is related with the decrease of density of *J. striatus* in December. In general, the low evenness values are a result of the overwhelming abundance of *J. striatus* in nearly all the monthly samples (Table 1). Therefore, the temporal trend in evenness is similar to that observed for diversity and opposite to species richness.

Classification (Bray–Curtis Similarity) and MDS (Non-metric Multi-dimensional Scaling) based on the presence/absence data arrange the samples mainly according to sampling time (stress = 0.18) (Figs 6 and 7). The cluster analysis displays the various groups of samples linked at different similarity levels (between 50 and 60%) with a high degree of disjunction even among the replicates of the same month. However, within each small group of samples the autumn–winter and spring–summer samples are closely related.

In the MDS, the relatively high variability observed between replicate samples is remarkable, especially in the autumn and winter months (showed by the high scattering of samples in the graph). The spring and summer samples are less scattered. Although the various sampling periods are not distinctly separated, when tested, the spring and summer samples (warmer periods) were significantly different from the autumn and winter ones (colder periods) (one-way ANOSIM, Factor: warmer period *versus* colder period, $R = 0.501$, $P < 0.001$). The SIMPER analysis shows that no more than 10 species contribute 90% of the information regarding the similarity values among the autumn and winter samples (average similarity 52.7%). Eight of them (in decreasing order of contribution: *J. striatus*, *R. membranacea*, *A. ephippium*, *N. pygmaeus*, *S. viridis*, *M. minor*, *R. monodonta*, *Calliostoma* cf. *planatum*) are cited in Table 2 as dominant species. In the spring–summer samples, nearly twice as many (19) species are involved for contributing the same information (average similarity 60.3%). In this case, nine species (in decreasing order of contribution: *J. striatus*, *N. pygmaeus*, *N. reticulatus*, *S. viridis*, *M. minor*, *R. monodonta*, *B. reticulatum*, *R. membranacea*, *Calliostoma* cf. *planatum* are included among the 10 most dominant.

Classification and MDS ordination based on abundance data also resulted in an arrangement of samples according to sampling time (stress = 0.13) (Figs 8 and 9). The cluster analysis, at similarity level 50% shows three distinct

Table 1. Monthly abundance (individuals·222 m^{-2}) of the collected species in the *Zostera marina* bed from October 1996 to September 1997.

	1996									1997																																	
	O1	O2	O3	O4	N1	N2	N3	D1	D2	J1	J2	J3	J4	F1	F2	F3	F4	M1	M2	M3	Ap1	Ap2	Ap3	My1	My2	My3	Jn1	Jn2	Jn3	Jl1	Jl2	Jl3	Jl4	Au1	Au2	Au3	Au4	S1	S2	S3	*N*	*D*	*F*
Polyplacophora																																											
Polyplacophora								1																																		1	0.002	2.5
Gastropoda																																											
Calliostoma cf. *planatum*		2					1		1	5	1	4	2	3		2	3	1		1	6	15	10	6	4	5	11	10	6		3	3	9	13	10		8	47	12	32	236	0.527	75
Jujubinus striatus	12	347	60	323	16	54	408	36	22	146	217	688	425	481	28	2563	2314	644	754	112	310	643	830	1513	675	1331	1325	1615	1039	709	1050	1113	1227	1146	598	22	677	2310	1198	3185	32166	71.769	100
Gibbula magus																									1		3		3			1		1	1	8	1				19	0.042	20
Phorcus richardi																									1			1														2	0.004	5
Bolma rugosa				1								2										2		1		1	2	1	1			1	1					1		2	16	0.036	30
Smaragdia viridis		5	3	10	1		2	9	5		2	9	1	4		7	6	1	2		13	16	10	26	20	19	44	37	17	8	25	23	43	20	19	1	14	189	68	183	862	1.923	87.5
Bittium latreilli								3	1			1				1	2				2	2								1	2							6	2	9	32	0.071	30
Bittium reticulatum				1	3			27	9		2	7	3			23					1	4	1	6	3	4	2	7		9	43	118	221	13	10	2	5	16	8	23	571	1.274	67.5
Bittium submamillatum																																	1							1	0.002	2.5
Turritella communis																																			1					1	0.002	2.5
Turritella turbona																								1				1							1					3	0.007	7.5
Triphoridae																																								1	1	0.002	2.5
Epitonium turtonis																									1							2			1					4	0.009	7.5
Pusillina inconspicua								11	10												2																					23	0.051	7.5
Pusillina phillippi								4																																		4	0.009	2.5
Pusillina cf. *radiata*							1							1																					1						1			4	0.009	10
Rissoa membranacea	6	51	24	161	17	2	39	14	6	3	37	68	21	12	4	18	50	15	6	1	11	17	16	8	10	16	18	24	1	9	14	13	34	5	7			1371	786	1503	4418	9.857	95
Rissoa monodonta		16	4	41	1		7			1	1	5	4	3		10	5		4		2	4	4	13	5	14	14	12	6	13	19	20	29	25	17		15	129	63	131	637	1.421	80
Aporrhais pespelecani																			1	1				3	8	8	4	6	8			1	1							41	0.091	25
Calyptraea chinensis						4	2	1	4	5	1		4	1		1	1	1			1	2			6	2	4	2	2			4			12	38	1	2		1	102	0.228	60
Euspira macilenta																									2															2	0.004	2.5
Euspira pulchella			1				1							1	1			1							1			1	1		1				1		1	1			1	13	0.029	32.5
Payraudeautia intricata																			1													1								2	0.004	5
Tectonatica filosa																		1							1		2		1		1				2					8	0.018	15
Hexaplex trunculus				1																													1		1					3	0.007	7.5
Ocenebra erinaceus														1								1	1				2								1					6	0.013	12.5
Ocinebrina aciculata	1																1				1				2		1				1		1					2			10	0.022	20
Orania fusulus			1	1																																						2	0.004	5
Gibberula miliaria																									1									1	1					3	0.007	7.5
Nassarius cuvieri																																	1		1					2	0.004	5
Nassarius heynemanni																																			1					1	0.002	2.5
Nassarius incrassatus							1							8		2	4	1				2		2		1	2	4	1		1		3	3	4		1	27	2	35	104	0.232	47.5
Nassarius pygmaeus	1	1	2	7			6	4	2		3		2	13	1	7	26	16		7	13	30	8	16	35	30	174	138	129	32	23	90	55	826	285	26	160	298	103	22	2591	5.781	87.5
Nassarius reticulatus		1		2												2	11			1	2	4	3	2	9	13	25	35	39	1	2	5	2	40	19	2	17	18	1	18	274	0.611	62.5
Mitrella minor		4	2	23	2		15	1		1	4	4		10		1	5	2	2		2	6	2	13	15	14	63	52	18	24	13	28	30	19	22		2	508	255	637	1799	4.014	82.5
Fusinus pulchellus													1				1															2			1		1				6	0.013	12.5
Cancellaria cancellata															1						3	1	6	8	6	15	19	9	1		3	2	1	1	1	1	1		3	82	0.183	45
Bela costulata																							1					2		1	1	8	2	2	2	5				1	25	0.056	25
Bela nebula							1										1						3		4						1		6		1	1						18	0.040	20
Bela laevigata										1													6													1						8	0.018	7.5
Bela sp. 1										1					1					1	1	2	3	1		1				2		9		1	2	1				2	28	0.062	35

Table 1. Continued.

	1996									1997																																	
	O1	O2	O3	O4	N1	N2	N3	D1	D2	J1	J2	J3	J4	F1	F2	F3	F4	M1	M2	M3	Ap1	Ap2	Ap3	My1	My2	My3	Jn1	Jn2	Jn3	Jl1	Jl2	Jl3	Jl4	Au1	Au2	Au3	Au4	S1	S2	S3	*N*	*D*	*F*
Mangelia attenuata										1				2			1			1		1	1					2	1			3	1		3	1	1		1		20	0.045	35
Mangelia paciniana																											1						1								2	0.004	5
Mangelia unifasciata																						1	1	1	1		2	1			1	1							2	3	14	0.031	25
Crassopleura maravignae																													1					1	1						3	0.007	7.5
Haedropleura septangularis																										1															1	0.002	2.5
Acteon tornatilis																										2														1	3	0.007	5
Haminoea sp.																									1	1												2			4	0.009	7.5
Aglaja tricolorata		1																																							1	0.002	2.5
Pleurobranchaea meckelii																																						1			1	0.002	2.5
Aplysia parvula																							1																		1	0.002	2.5
Aplysia punctata																																						7			7	0.016	2.5
Trapania cf. *lineata*		3																																							3	0.007	2.5
Polycera quadrilineata			1																																						1	0.002	2.5
Doto sp.		6																																							6	0.013	2.5
Bivalvia																																											
Modiolarca subpicta	1	9	6	16	3		8	34	52	3		1				1							3																		137	0.306	30
Musculus costulatus								3	5														1																		9	0.020	7.5
Mytilaster minimus						1		42	28																			1													72	0.161	10
Chlamys flexuosa																																			1						1	0.002	2.5
Pecten maximus																												1													1	0.002	2.5
Anomia ephippium		9	10	29	14	1	29	1	3	3	5	30	9	19	5	25	33	1	1			4	1	4										1			1			1	239	0.533	60
Digitaria digitaria																																			1		1				2	0.004	5
Acanthocardia aculeata																													1												1	0.002	2.5
Papillicardium papillosum														1																											1	0.002	2.5
Parvicardium scabrum											1																1									10					12	0.027	7.5
Parvicardium scriptum								9	8																																17	0.038	5
Spisula subtruncata																								1	1		2						1	1		3	2				11	0.025	17.5
Abra alba																								1																	1	0.002	2.5
Callista chione																										1								3		8	4				16	0.036	10
Chamelea gallina										1															1	1	1									1					5	0.011	12.5
Clausinella fasciata																																			1	3					4	0.009	5
Gouldia minima							1																	2			2	1		1			1			3					11	0.025	17.5
Pitar rudis																										1															1	0.002	2.5
Timoclea ovata																										1	2								1	2					6	0.013	10
Venerupis aurea																1																				1					2	0.004	5
Corbula gibba			1							1															1	1		1		1				8	5	17	10				46	0.103	25
Hiatella arctica				1																																					1	0.002	2.5
Cephalopoda																																											
Sepia officinalis		1					1																	2	3		1	2	2	2	2		1	1			1	2		2	23	0.051	35
Octopus vulgaris													1									1																			2	0.004	5

N, cumulative abundance; D, dominance (%); F, frequency (%).

Table 2. List of the dominant and frequent species in the *Zostera marina* bed from Cantarriján Bay.

Species	D	F
Jujubinus striatus	71.8	100
Rissoa membranacea	9.8	95
Nassarius pygmaeus	5.8	87.5
Mitrella minor	4.0	82.5
Smaragdia viridis	1.9	87.5
Rissoa monodonta	1.4	80
Bittium reticulatum	1.3	67.5
Nassarius reticulatus	0.6	62.5
Calliostoma planatum	0.5	75
Anomia ephippium	0.5	60

D, dominance percentage; F, frequency percentage.

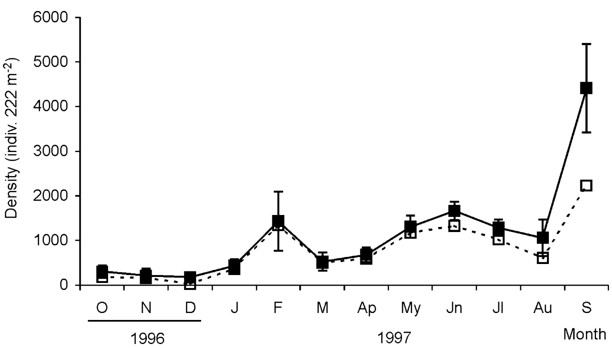

Fig. 2. Monthly values (average of the replicates ± SE) of abundance of molluscs (density: individuals per 222 m^2) from October 1996 to September 1997. Solid line and black symbols represents total density of molluscs. Dotted line and empty symbols represents the mean monthly density values of *Jujubinus striatus*.

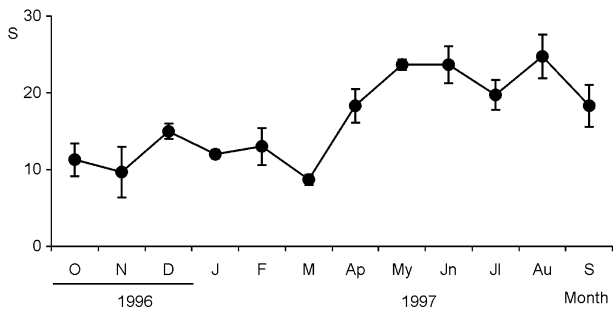

Fig. 3. Monthly values (average of the replicates ± SE) of species richness (S) from October 1996 to September 1997. Line and black symbols represents mean number of species per 222 m^2.

groups. Most of the autumn and winter samples cluster together, whereas a single larger cluster groups most of the spring and summer samples, except August and July (Fig. 8). In the MDS ordination, the sample scattering, indicating sample variability is lower in this analysis with

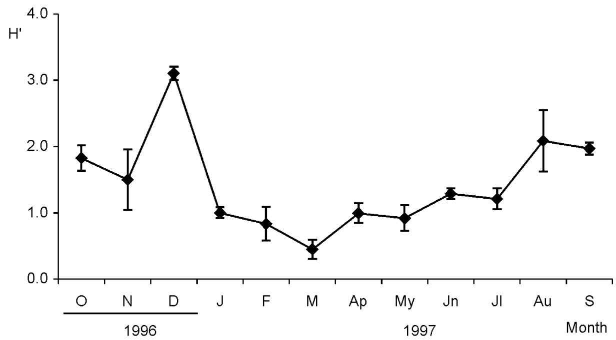

Fig. 4. Monthly values (average of the replicates ± SE) of Shannon–Wiener diversity index (H′) from October 1996 to September 1997.

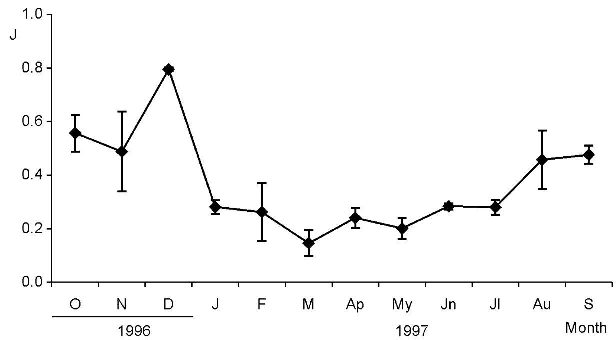

Fig. 5. Monthly values (average of the replicates ± SE) of evenness (J) from October 1996 to September 1997.

respect to the previous one (presence/absence). However, the autumn–winter samples still present a higher point scattering, while the spring and summer samples form a relatively compact group (Fig. 9). Although the separation among the monthly samples was not so distinct, when tested, spring and summer samples were significantly different from autumn and winter ones (one-way ANOSIM, Factor: warmer period *versus* colder period, $R = 0.527$, $P < 0.001$). Here again, SIMPER analysis shows that no more than ten species contribute 90% of the information regarding the similarity values among the autumn and winter samples (average similarity 51.6%). Eight of them, the same as for presence/absence data, are dominant species. In the spring–summer samples, 15 species are involved for contributing the same information (average similarity 61.3%) and nine of them, the same as for presence/absence data, are included among the 10 most dominant. Dissimilarity between spring–summer and autumn–winter samples is driven essentially by the same dominant species but through variation in their abundance: most species are more abundant in the warm months, except the epibiont *A. ephippium* which is more abundant in the cold months (Table 1).

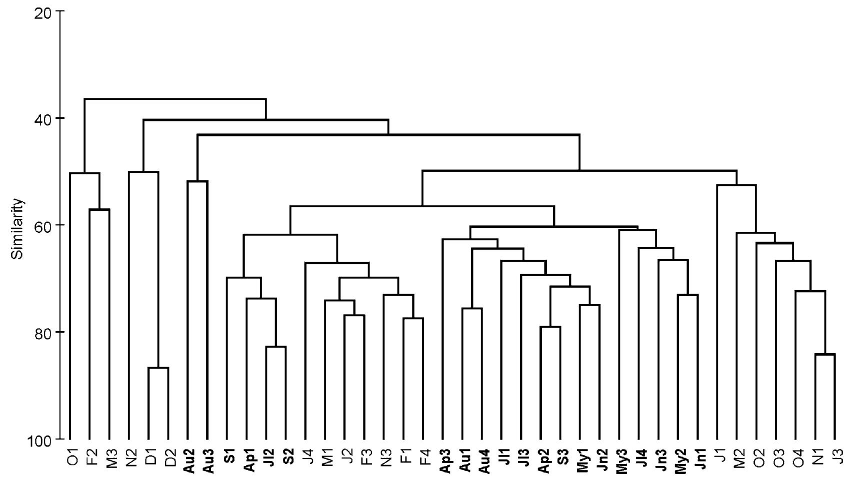

Fig. 6. Dendrogram of the 40 replicate samples of the molluscan assemblage using group-average clustering from Bray–Curtis similarities based on presence/absence of species.

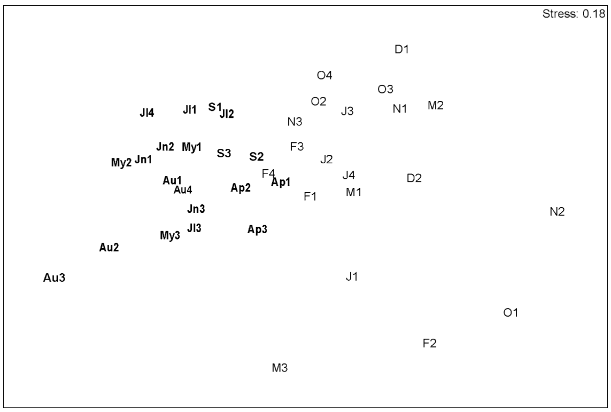

Fig. 7. Multi-dimensional Scaling ordination plot of the monthly samples of the molluscan assemblage based on the presence/absence of species.

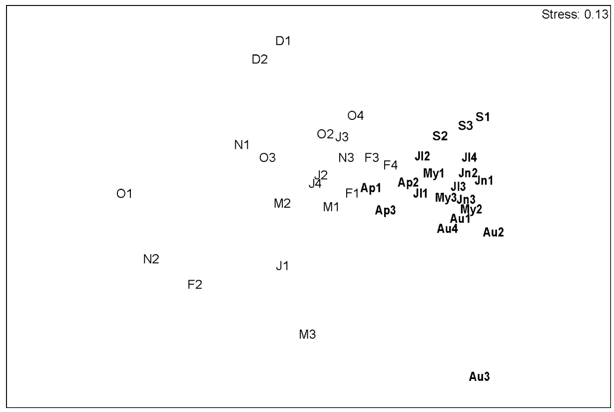

Fig. 9. Multi-dimensional Scaling ordination plot of the monthly samples of the molluscan assemblage based on the fourth root transformed quantitative data.

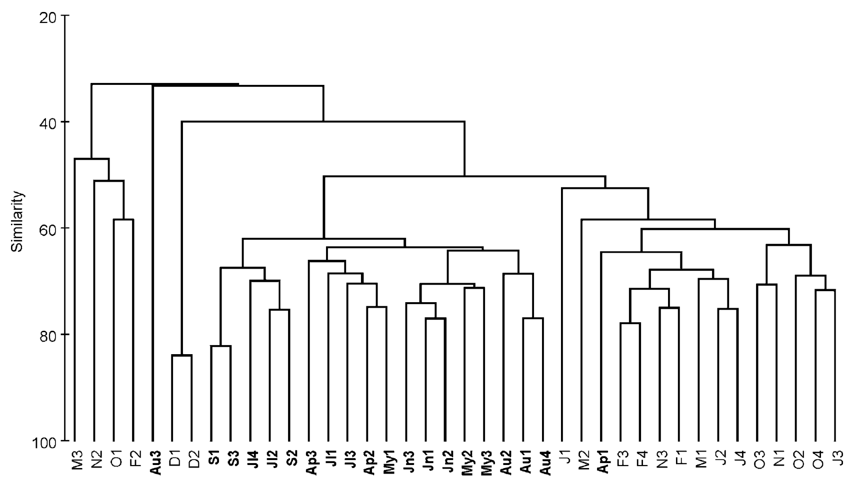

Fig. 8. Dendrogram of the 40 replicate samples of the molluscan assemblage using group-average clustering from Bray–Curtis similarities based on the fourth root transformed quantitative data.

Discussion

Mollusc assemblages and their biogeographical affinities

The mollusc fauna associated with the *Zostera marina* bed from Cantarriján bay, with 80 species, is the most diverse from the studied *Z. marina* beds, in the Atlantic (Jacobs & Huisman 1982; Jacobs *et al.* 1983; Currás *et al.* 1993; Boström & Bonsdorff 1997; Frost *et al.* 1999; Hily & Bouteille 1999; Blanchet *et al.* 2005; Quintas 2005), and in the Mediterranean (Ledoyer 1962, 1964; Çinar *et al.* 1998; Sfriso *et al.* 2001).

Several circumstances could be related with this high species richness:

(1) *Sampling procedures*, such as: (i) the relatively high number of replicates; (ii) the extended period of sampling allowing to collect also occasional species (some of them probably ephemeral species, and others that use the bed only for feeding or breeding); (iii) the relatively large sampling area considered (several replicates of 222 m^2) (*i.e.* in a study on mollusc epifauna of *Posidonia oceanica*, Russo & Terlizzi (1998) sampled with a hand-towed net an area of about 20 m^2; (iv) the efficiency of the type of trawls (small Agassiz) for epifauna.

(2) *The deeper situation of the studied bed* (between 14 and 16 m depth), which implies a certain stability in time moderating environmental variability, such as wave action, storms, desiccation, *etc.* Hemminga & Duarte (2000) discussed the role of the depth in the stability of the seagrasses formations. Jacobs & Huisman (1982) found an increment of diversity with depth in *Z. marina* and *Zostera noltii* meadows that they consider correlated with environmental stability.

(3) *The patchy distribution* of the *Z. marina* bed from Cantarriján bay, with a sandy bottom surrounding the fragmented bed. Actually most *Z. marina* beds are somehow patchy at different scales (*i.e.* square meters, or tens of square meters), and the influence of such fragmentation in seagrass beds for the macrofauna has been largely discussed (Robbins & Bell 1994; Bologna & Heck 1999; Frost *et al.* 1999; Sánchez-Jerez *et al.* 1999; Bell *et al.* 2001; Bologna 2006). According to Bologna (2006), the edges in a fragmented *Z. marina* bed, have a significantly greater density of benthic organisms than the interior and the unvegetated zones. Consequently, the edges of *Z. marina* formations may actively and passively accumulate food resources and organisms, which would lead to increased secondary production and potentially elevate trophic transfer to the higher level consumers (Bologna & Heck 1999; Bologna 2006). Moreover, the edges of a seagrass bed would be the first available refuge for organisms moving between habitat patches or an active refuge for organisms living in nearby unvegetated bottoms. However, Frost *et al.* (1999) did not find significant differences between the species of the macrofauna from fragmented and continuous *Z. marina* beds in Salcombe Estuary, Devon (UK), the differences found were related with differences in density of some species.

The transition from the unvegetated to vegetated bottom in *Z. marina* beds is less abrupt than in patchy *P. oceanica* beds. The bottom inside the bed is sandy and similar to the nearby soft bottom and in fact many species typical of soft bottoms have been collected inside the bed by SCUBA diving and digging (J.L. Rueda and C. Salas, unpublished data). Nevertheless, only eight species (with only 21 individuals) can be considered typical of the unvegetated sandy bottom, and were not collected in other *Z. marina* beds from Southern Spain. The influence of the nearby soft bottom on the composition of the mollusc assemblage from the studied *Z. marina* bed can thus be considered quite limited. The similarity of the infauna in the *Zostera* bed and in unvegetated surrounding sediments was likewise explicitly stated by Mars (1966, p. 53) in the French Mediterranean lagoons.

Some of these soft-bottom species are gastropods and may use the bed as a feeding ground, such as the carnivorous *Orania fusulus* (2 ind.) and *Crassopleura maravignae* (3 ind.) or the scavengers *Nassarius heynemanni* (1 ind.) and *Gibberula miliaria* (3 ind.). The other four species are filter feeders, such as the gastropod *Turritella communis* (1 ind.), and the three bivalves, *Digitaria digitaria* (2 ind.), *Acanthocardia aculetata* (1 ind.) and *Clausinella fasciata* (4 ind.). These bivalves are typically associated with bioclastic bottoms that occur at the deeper edge of the bed.

(4) *The latitudinal location*, in the Alborán Sea, near the Strait of Gibraltar and in front of the African coast. This marine zone has probably the highest species richness from the littoral of Europe (Gofas 1999). From a biogeographical point of view, most of the molluscs (65%) found in the *Z. marina* bed from Cantarriján have a Lusitanian–Mediterranean distribution (*sensu* Ekman 1953). About 22% show a Mediterranean distribution, although some of them can be found up to the South of Portugal and a few of them have been collected around the Canary Islands, such as *Smaragdia viridis* or *Bolma rugosa*. The proximity to Africa is shown by the presence of four species with a mainly West African distribution, which have a Northern limit in the Western Mediterranean, such as *Cancellaria cancellata*, *Tectonatica filosa*, *O. fusulus* and *N. heynemanni* (Table 1). Only *Rissoa membranacea* has a typical Atlantic distribution associated with *Z. marina* or *Caulerpa prolifera* meadows (Rueda & Salas 2003). This relationship is reflected by its high abundance (9.8% of total molluscs), and frequency (95% of the samples) (Table 1). Taking into account the dominance and the frequency, only a few species can be considered frequent and typically

associated with the *Zostera* bed (Table 2): *Jujubinus striatus*, *R. membranacea*, *Nassarius pygmaeus*, *Mitrella minor*, *S. viridis*, *Rissoa monodonta*, *Bittium reticulatum*, *Calliostoma* cf. *planatum*, among the gastropods; and *Anomia ephippium*, *Musculus subpictus*, among the bivalves. Most of these species were also collected in a *C. prolifera* bed from the Bay of Cádiz, in which were not found *S. viridis* strictly associated with *Z. marina* and *Cymodocea nodosa* nor *R. monodonta*, a typical Mediterranean species (Rueda & Salas 2003). This pattern of dominance by a few species was also found in other studies on macrofauna associated with *Z. marina*: Thayer *et al.* 1975 in Newport River estuary (North Carolina, USA), Turner & Kendall 1999 in the River Yealm (UK).

In *P. oceanica* meadows from five western Mediterranean sites Russo & Terlizzi (1998) found a wide variability in the composition of the molluscan assemblages. Each seagrass meadow was well characterized by the high dominance of a few particular species; among them *J. striatus*, *B. reticulatum* and *Nassarius incrassatus* are also dominant in the mollusc assemblage of *Z. marina* from Cantarriján bay. Templado (1984), nevertheless, found similar molluscan assemblages in different *P. oceanica* beds from Cabo de Palos (Eastern Spain), with a few characteristic (dominant) species, which were different from those found in the Cantarriján *Z. marina* bed. Scipione *et al.* (1996) also found a few dominant species in *P. oceanica* and *C. nodosa*, from which only *B. reticulatum* is shared by *C. nodosa* (from Ischia) and *Z. marina* (from Cantarriján). Actually the *Posidonia* meadow differs so much from *Zostera* because its rhizome stratum is edificating an equivalent to a hard substrate, whereas the rhizomes of *Zostera* remain within the sediment.

The mollusc assemblage of our study differs from those found in the lagoon of Venice (Sfriso *et al.* 2001) and in the Turkish coast (Çinar *et al.* 1998). In these areas the *Zostera* spp. studied were shallow, between 0.5 and 2 m, and influenced by fresh water inputs. Most of the fauna collected in these studies was infauna, due mainly to the use of sampling methods such as corers or small quadrates. Moreover, in these areas and shallow depths, the winter water temperatures are similar to those registered in Northern Europe.

The most similar mollusc assemblage from a *Zostera* bed has been found by Quintas (2005) in Galicia (NW Spain), in the mixed meadows of *Z. marina* and *Z. noltii*, with 68 species of molluscs identified, among which *J. striatus*, *R. membranacea*, *B. reticulatum* and *Nassarius reticulatus* were the most common species.

From a trophic point of view, most of the dominant mollusc species (gastropods) from *Z. marina* bed are grazers, such as rissoids or trochids. These feed on diatoms and other periphyton, as it has been indicated in other seagrasses (Peduzzi 1987; Lepoint *et al.* 2000; Fredriksen *et al.* 2004; Hily *et al.* 2004). *Nassarius pygmaeus* is a scavenger, feeding among others on dead animals. The presence of *M. minor* is very interesting from a trophic point of view; because this species is a specialized predator feeding on eggs of various species, generally other molluscs, but probably also other taxa such as fishes (García Raso *et al.* 2004). Its frequency (82.5%) and abundance (1799 individuals collected and an average density of about 20 ind. per 100 m^2) point out the role as a spawning site and a nursery of *Z. marina* (Hemminga & Duarte 2000). Thayer *et al.* (1975) found also *Mitrella lunata* as the third most abundant species in a Western Atlantic *Z. marina* bed, where 45 species of macrofauna were identified, among which 33 were fishes.

The two most frequent and abundant bivalves are suspension-feeders (*A. ephippium*, *M. subpictus*), that seem to find a sufficient source of particles, considering their abundance values.

Temporal changes in the mollusc assemblages

Seagrasses in temperate areas generally show large temporal variations in shoot density, canopy morphological features and epiphyte biomass, although mainly observed in the temperate northern seagrass meadows, most of them distributed in the intertidal zone (Hemminga & Duarte 2000). Consequently, there is a temporal variation in densities of seagrass-associated animals that often coincides with that of the macrophyte biomass (*Z. marina*: Thayer *et al.* 1975; Toyohara *et al.* 1999; Sfriso *et al.* 2001; *C. nodosa*: Scipione *et al.* 1996; Sfriso *et al.* 2001).

The structure of the mollusc taxocoenosis here studied changed over time (Figs 2–5), although with a relatively high variability especially in the autumn and winter months. This pattern is probably related to the different degree of patchiness in mollusc populations, and variability also of the *Z. marina* bed features, which seem stronger during the autumn–winter months due also to more variable and unstable environmental conditions.

High abundance and species richness values were found in the spring and summer in coincidence with the increment of seagrass canopy height and shoot density. Similar temporal patterns in relation with biomass or shoot/frond density of seagrass and seaweed beds were found in studies of mollusc assemblages from other vegetated bottoms off Southern Spain (Rueda *et al.* 2001; Sánchez-Moyano *et al.* 2001; Rueda & Salas 2003) and also in other locations within the Mediterranean Sea (Terlizzi & Russo 1998; Sfriso *et al.* 2001). In *C. nodosa* beds from Ischia (Scipione *et al.* 1996) and from the Canary Islands (Brito *et al.* 2005), maximum abundance is found in September for molluscs and polychaetes, respectively.

As most of the species of molluscs associated with seagrasses are grazers that feed on the periphyton living on the leaves, the increments in abundance during the warm period could be related with the increment of leaf surface and likely of epiphyte colonizaton. In contrast during the autumn and winter, when the leaves fall and shoot density is reduced, the abundance also decreases. Another factor related with changes in the abundance of the species is recruitment (Rueda *et al.* 2001; Rueda & Salas 2003), which in the studied *Zostera* bed is responsible for the density increments for some of the dominant species, such as *B. reticulatum*, *N. pygmaeus* or *J. striatus*. The latter is responsible for the increase in abundance observed in February, and in the various spring and summer months (Table 1). The peak of September is related with recruitment events [during the summer months there is an increment of juveniles (1–3 mm) of some dominant species, such as *Rissoa* spp., *Nassarius* spp., *J. striatus*, *M. minor*].

The temporal trend of species richness values (Fig. 3) was mainly related with the presence in the bed of occasional species during the warm period (Table 1). Some of these occasional species use the bed for feeding (*Sepia officinalis*) or for breeding (opistobranchs); they may have a short life cycle but no detailed information is available. It is interesting to note the increment of carnivorous gastropods and cephalopods in the bed, probably attracted by the increment in animal densities during the summer. Diversity and evenness values show also a temporal trend (Fig. 4). The relatively low values of these indices in various months were related with the high abundance of *J. striatus* (Table 1, Fig. 2). These values are similar to those found in Newport River (North Carolina) (Thayer *et al.* 1975). These authors suggested that these low values reflect a young and evolving eelgrass-bed community. In fact the studied patchy bed from Cantarriján bay can be considered somehow unstable, because of the small size of the patches, which make it very sensitive to environmental (*i.e.* sea storms or torrential rains) or antropogenic influences (*i.e.* frequent fishery activity). In fact, after completing this study, there were torrential rains, which smothered the bed under sediments; and ever more illegal trawling in the protected area is damaging these beds.

Conclusions

The *Zostera marina* seagrass bed from Cantarriján Bay (Southern Spain) represents a habitat of high biodiversity and abundance for the mollusc fauna, with confluence of species from different biogeographical regions.

This molluscan assemblage is characterized by the high dominance of a few species (eight gastropods). Among these species it is interesting to note the high abundance and frequency of *Mitrella minor*, a specialized predator feeding on the eggs of other species that point out the role as spawning site and nursery of the studied *Z. marina* bed.

The spring and summer months were characterized by higher species richness and abundance, probably in relation with the higher development of the seagrass canopy and high shoot density. December is characterized by strong decreases in species richness and abundance, probably related with the reduction in canopy development in *Zostera*, but still with high evenness and diversity values. The temporal changes in the mollusc assemblage structure are revealed with the analysis of both the presence/absence and the abundance data (Cluster and MDS multivariate analyses). The pattern observed in the studied *Z. marina* bed pointed out a high variability (and possibly higher patchiness) during the autumn–winter months and more homogeneous assemblages in the spring–summer periods. This could be related once again to the meadow and canopy features and their annual dynamics, with general environmental conditions, and not the least with the life history and autoecology of the individual species.

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