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Composition and structure of the molluscan assemblage associated with a *Cymodocea nodosa* bed in south-eastern Spain: seasonal and diel variation

Pablo Marina · Javier Urra · José L. Rueda · Carmen Salas

Abstract The molluscan taxocoenosis associated with a *Cymodocea nodosa* seagrass bed was studied throughout 1 year in Genoveses Bay, in the MPA "Parque Natural Cabo de Gata-Níjar" (south-eastern Spain). A total of 64,824 individuals were collected and 54 species identified. The molluscan fauna was mainly composed of gastropods (99.56% of individuals, 43 spp.). The families Rissoidae (72.98%, 11 spp.) and Trochidae (16.93%, 7 spp.) were the most abundant and diversified in terms of number of species. *Rissoa monodonta* (47.1% dominance), *Rissoa membranacea* (25.1%) and *Gibbula leucophaea* (11.6%) proved the top dominant species in both diurnal and nocturnal samples. Bivalves (0.41%, 10 species) and cephalopods (0.03%, 1 species) represented only a low percentage of the molluscan taxocoenosis. The molluscan assemblage was mainly composed of species with a wide geographical distribution in Europe, followed by strictly Mediterranean species. The abundance was significantly higher in the cold (December, March) than in the warm months (June, July). Species richness (S) was higher in nocturnal than in diurnal samples, reaching maximal values in diurnal samples of March and June. Shannon–Wiener diversity (H') values were generally higher in nocturnal samples than in diurnal ones, displaying minimum values in December and June, respectively. Evenness was similar in diurnal and nocturnal samples, with maximum values in July in both groups. S and H' were also significantly different between diurnal and nocturnal samples. Multivariate analyses based on both qualitative and quantitative data showed a significant seasonal and diel variation. Diel changes revealed to be more distinct than seasonal ones.

Keywords Molluscs · Seasonal dynamics · Diel dynamics · Mediterranean Sea · Seagrass

Introduction

Studies on different topics of seagrass beds have increased in the last decades, stimulated by their high ecological importance for coastal systems and the fact that they are among the most endangered coastal habitats, with a regression worldwide affecting biodiversity on both local and global scales (Short and Neckles 1999; Hemminga and Duarte 2000; Duarte 2002). In Europe, soft bottom seagrass beds have experienced a strong decline due to human impacts (e.g. eutrophication, intense illegal trawling activities) that have resulted in a significant loss of beds and their associated communities (Duarte 2002; Boström et al. 2006; Rueda et al. 2009b). Some of these beds even disappeared before their ecological role could be studied. Studies on the associated fauna, their spatial and temporal variation as well as their trophic interactions are of special interest to evaluate the importance of seagrass beds for the local biodiversity and to improve the management of local fisheries resources.

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Four true autochthonous seagrass species occur in the Mediterranean Sea, *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina* and *Nanozostera noltii* (Green and Short 2003). Other seagrass species are more restricted to estuaries and brackish-water lagoons (*Ruppia ssp.*) or have been introduced in the last century (*Halophila stipulacea*) (Green and Short 2003). The faunistic communities of *Posidonia oceanica* have been thoroughly studied over the last decades (Russo et al. 1984a, b; Templado 1984; Russo and Vinci 1991; Russo et al. 1991; Gambi et al. 1992; Sánchez-Jerez et al. 1999; Francour 1997), and the same applies to the communities associated with *Zostera marina* (Jacobs and Huisman 1982; Jacobs et al. 1983; Currás et al. 1993; Mattila et al. 1999; Rueda et al. 2008; 2009a, b; Rueda and Salas 2008). In contrast, the fauna of *C. nodosa* beds have scarcely been studied (García-Raso et al. 2006; Barberá et al. 2001; Guidetti and Bussotti 2000; Sánchez-Jerez et al. 1999; Ledoyer 1966; Sfriso et al. 2001; Brito et al. 2005), especially with regard to the temporal patterns of molluscan assemblages (Chemello et al. 1997; Terlizzi and Russo 1997; Tuya et al. 2001). In addition to seasonal changes, there is a diel variability related to short-term movements of the animals during the day–night cycle along the seagrass shoots or from adjacent habitats. There is some information on the diel variation in seagrass beds regarding organisms with high mobility such as fish (Gray et al. 1998; Griffiths 2001; Petrakis et al. 2001; Guest et al. 2003) and crustaceans (Vance 1992; Vance et al. 1994; Guest et al. 2003; García-Raso et al. 2006), but relevant information on molluscan taxocoenoses is scarce (Templado 1982; Le Loeuff and Intès 1999; Mattila et al. 1999; Sánchez-Jerez et al. 1999; Rueda et al. 2008).

The seagrass *Cymodocea nodosa* has a temperate–subtropical distribution including the Mediterranean Sea and the North-East Atlantic (from southern Portugal to Senegal, Madeira, Canary Islands) (Green and Short 2003). Together with *P. oceanica*, it probably represents one of the most important and abundant seagrasses in Mediterranean coastal systems (Mazzella et al. 1993). It has been treated as a pioneer species, capable of colonizing soft bottoms under a wide range of conditions and generally growing faster than other seagrass species in the Mediterranean Sea (Marbà et al. 2004). The aims of this study were to characterize the composition and structure of the molluscan assemblage of *C. nodosa* and to analyse the seasonal and diel changes throughout an annual cycle. The results should be compared to those from beds of other seagrass species with higher habitat complexity and lower growth rates, such as *Posidonia oceanica* or *Zostera marina* (Templado 1982; Rueda et al. 2008). The starting hypotheses were that (1) faunistic assemblages would be similar to those of other soft bottom seagrass species; (2) seasonal changes may occur as reported for other types of vegetated bottoms

(seagrass beds, macroalgae); and (3) there are diel changes of the assemblages due to the nocturnal feeding activities of some mollusc species.

Materials and methods

Study area

The sampling site is located off Genoveses beach, in the Natural Park of Cabo de Gata-Níjar, Almería, Spain. In this area, *Cymodocea nodosa* occurs patchily distributed at depths between 4 and 15 m (García-Raso et al. 2006). The sediment is mainly composed of clean fine sands with less than 5% of mud and 2% of organic matter (González et al. 2007, 2008). The studied seagrass bed has an extension of ca. 10,000 m^2 with coverage values between 40 and 70% and leaf biomass between 50 and 60 g DW m^{-2} (González et al. 2007, 2008). Leaf production in this bed is 135.6 mg DW shoot^{-1} year^{-1}, and herbivory loss has been estimated to be ca. 2 mg shoot^{-1} year^{-1} (Cebrián et al. 1996). Water temperature ranges from 15°C in winter to 24°C in summer. Salinity remains almost constant throughout the year due to the low rainfall (less than 200 mm per year) and fresh water input in the area (e.g. absence of rivers and streams). Nevertheless, it can reach 37.4 psu in summer, with similar values from the surface to 25 m depth.

Sample collection and laboratory procedures

Samples were taken in the *C. nodosa* bed at depths between 10 and 14 m in different seasons (July 1999, December 1999, March 2000 and June 2000), in the morning (always between 11.00 and 13.00) and in moonless nights (at least 2 h after sunset), using a small Agassiz trawl at a speed of 1 knot (1.85 km h^{-1}). This trawl has a dredge frame of 72 cm width and a net mesh of 3 mm (knot to knot). In spite of the relatively large mesh size, there was probably no significant underestimation of the abundance of juveniles as usually large amounts of material were collected which stretched the net and therefore clogged the mesh size. Each haul lasted for 10 min, thus covering an area of ca. 222 m^2. This area was larger than that normally sampled in studies on the macrofauna of seagrass communities (1 m^2 or less: Jacobs et al. 1983 and Currás et al. 1993; 6 m^2: Sánchez-Jerez et al. 1999), but similar to that used in some fish studies (243 m^2: Mattila et al. 1999). Such large areas were also sampled in studies of other benthic components such as decapods (García-Raso et al. 2006). At each sampling date, two or three replicates were normally taken during the day and also during the night, except in June 2000. In this month, only a single sample could be collected because the amount of material collected in the *C.*

nodosa bed (during both daytime and night) was more than twice as high as in previous samplings due to a massive proliferation of filamentous algae, mainly *Ectocarpus* s.l.

The fauna of each sample was sieved over mesh sizes of 10, 7, 5, 3 and 1 mm, and the different size fractions were stored separately in 70% ethanol. This was done in order to facilitate sorting at the species level, and to help to separate juveniles from adults of some species. Each mollusc species was identified and their individuals per sample were counted. The complete material has been deposited in the Departamento de Biología Animal from the Universidad de Málaga (Spain).

Data analyses

Each species was characterized by (1) its abundance or density (numbers per 222 m^2 sampled area), (2) the frequency index (%F) as the percentage of samples in which the species was present (Glémarec 1969) and (3) the dominance index (%D) as the percentage of individuals of one particular species in a sample (Glémarec 1969). The species were also characterized in terms of their preference for different microhabitats within the *C. nodosa* bed, their feeding guilds and their biogeographical distribution, following similar categories as used by Rueda et al. (2009a) for molluscan assemblages associated with eelgrass beds in the Alboran Sea (Table 1).

In relation to microhabitat preference, the following categories were considered: (1) soft bottom infauna (SI), mainly bivalves, that are permanently buried in the sediment colonized by *C. nodosa*; (2) epibionts and ectoparasites (EP), that is, species that live on or feed on other, generally larger animals; (3) epifauna on vegetated substrates (VE), that is, species that live on *C. nodosa* leaves or on macroalgae; (4) hard bottoms epifauna (HE), that is, species generally found on rocks or shells; (5) organisms that live partly buried in soft bottoms (SB); (6) demersal species that occasionally bury in the sediment (DE), including species with high mobility such as cephalopods; and (7) soft bottom epifauna (SE), including gastropod and bivalve species that generally inhabit the sediment layer covered by *C. nodosa*.

According to feeding guilds, the following categories were considered: (1) predators (P), feeding on other mobile organisms such as molluscs or polychaetes; (2) scavengers (SC), feeding on remains of dead organisms; (3) deposit feeders (D), feeding on organic particles contained in the sediment covered by *C. nodosa*; (4) ectoparasites and specialized predators (E), living and feeding on much larger organisms; (5) filter feeders (F), capturing the seston particles with their gills and/or with mucous strings; (6) macroalgae grazers (AG); (7) seagrass grazers (SG), ingesting seagrass tissues; (8) microalgae or periphyton

grazers (MG), feeding on microalgae (e.g. diatoms) that cover the *C. nodosa* leaves; and (9) oophagous feeders (O), that is, gastropods that feed on egg masses of other organisms.

Information on microhabitat preference and feeding guilds has been obtained from the literature on the molluscan fauna associated with seagrass beds (Ledoyer 1962, 1966; Templado 1982; Hergueta 1996; Luque and Templado 2004; Quintas 2005; Rueda and Salas 2007) or from the general literature on molluscs ecology (Fretter and Graham 1962; Tebble 1966; Morton 1967; Graham 1971; Bouchet et al. 1979; Nordsieck and García-Talavera 1979; Kohn 1983; Russell-Hunter 1983; Luque 1984, 1986; Templado et al. 1993; Hayward and Ryland 1995; Salas 1996: Gómez-Rodríguez and Pérez-Sánchez 1997; Beesley et al. 1998; Rueda et al. 2009a). Additional information on the preference of species for different microhabitats within

Table 1 Codes used in species characterization in relation to microhabitat preference, feeding guild and biogeographical distribution

Category	Code	Comments
Preferential substrate (microhabitat)	DE	Demersal that may bury
	EP	Epibionts & ectoparasites
	HE	Hard bottoms epifauna
	SB	Partly buried in soft bottoms
	SE	Soft bottoms epifauna
	SI	Soft bottoms infauna
	VE	Epifauna on vegetated substrates
Trophic group (feeding guild)	AG	Herbivores of macroalgae and epiphytes
	P	Predators on mobile preys
	D	Deposit feeders
	E	Ectoparasites and carnivores on preys without mobility
	F	Filter feeders
	MG	Microalgae herbivores
	SC	Scavengers
	SG	Seagrass-feeding herbivores
	O	Egg and spawn feeders
Biogeographical distribution	AF	Western Africa
	CN	Canary Islands
	IM	Ibero-Moroccan gulf
	ME	Mediterranean Sea (those species that occur only in the Alboran Sea are excluded from this sector)
	NE	Northern Europe
	WE	Western Europe

C. nodosa beds and feeding habits has been obtained during the present sampling and by laboratory observations.

The classification of the species with respect to their biogeographical distribution is problematic, due to the lack of consensus on geographical areas that have been established by different authors mainly on the basis of oceanographic characteristics (Ekman 1953; Briggs 1974; Longhurst 1998). In order to handle the geographical range in more detail, geographical areas were established on a finer scale as follows: (0) Alboran Sea, with all the species found in this study; (1) Mediterranean Sea beyond the Alboran Sea (ME); (2) Ibero-Moroccan Gulf (IM), including the southern coasts of Portugal and the Atlantic coasts of Andalusia (south-western Spain) and Morocco according to the faunistic lists given by Pallary (1920), Salas (1996), Rueda et al. (2000, 2001), Rueda and Salas (2003), Gofas et al. (2011) and to unpublished data of the Algarve 1988 expedition of the Muséum National d'Histoire Naturelle, Paris; (3) western Europe (WE), from Portugal to the southern coasts of the United Kingdom according to the data given by Nobre (1940), Tebble (1966), Graham (1971), Bouchet et al. (1979), Thompson and Brown (1976), Rolán (1983) and Rolán et al. (1990); (4) northern Europe (NE), from the southern coasts of the United Kingdom to Scandinavia based on data by Høisæter (1985) and Hansson (1998); (5) Canary Islands (CN), based on the works by Hernández et al. (2011) and Gómez-Rodríguez and Pérez-Sánchez (1997); and (6) western Africa (AF), from Mauritania to tropical western African coasts according to the information given by Gofas and Zenetos (2003) on western African species that also occur in the Alboran Sea. The presence of the species in the different geographical areas was noted and their chorotypes were established. For this purpose, a cluster was performed using the similarity index of Bray–Curtis (Bray and Curtis 1957), in which species with a similar biogeographical range were grouped. In this analysis, qualitative data (presence/absence of species in each area) were used without any further transformation and standardization. This multivariate analysis was carried out using the PRIMER from Plymouth Marine Laboratory, UK (Clarke and Warwick 1994).

The taxocoenosis was characterized by its species richness (S) (number of species per sample), the Shannon–Wiener diversity index (Krebs 1989) and the evenness index (Pielou 1969). Abundance values and ecological indexes were tested for statistically significant changes over the diel and seasonal cycles using one-factor ANOVA (Underwood 1997) and non-parametric analysis of Mann–Whitney if data were not homoscedastic. The tests included comparisons of the diurnal samples ($n = 8$) *vs* nocturnal ones ($n = 8$) and seasonal samples of cold months (autumn and winter) ($n = 10$) *vs* those of warm months (spring and summer) ($n = 6$). A Barlett test was carried out in order to verify the homogeneity of variances prior to ANOVA analyses. These statistical procedures were performed using the software SYSTAT 9 (SPSS).

The similarity between samples was evaluated using both qualitative (presence/absence) and quantitative data (fourth-root-transformed abundance data) of species per sample. The similarity index of Bray and Curtis (1957) was used as a meaningful and robust measure (Clarke 1993) for obtaining a cluster analysis (UPGMA method) and a MDS ordination with both qualitative and quantitative data (fourth-root-transformed data). Molluscan assemblages were also compared using an analysis of similarities (ANOSIM, Clarke and Green 1988), in relation to (a) diurnal ($n = 8$) *vs* nocturnal samples ($n = 8$) and (b) cold months (autumn and winter, $n = 10$) *vs* warm months samples (spring and summer, $n = 6$). This analysis is a non-parametric analogue to a multivariate analysis of variance (MANOVA) and compares ranked similarities between and within groups, which were selected a priori according to the studied factors (day *vs* night samples, cold season *vs* warm season samples). Finally, a SIMPER (SIMilarity PERcentage) analysis was done in order to know the contribution of the species to the similarity/dissimilarity within and between the same groups of samples. All these multivariate analyses were executed using the PRIMER software from Plymouth Marine Laboratory, UK (Clarke and Warwick 1994).

Results

Characterization of species and assemblages

A total of 54 species were identified, of which 30 spp. were collected in the diurnal samples and 52 spp. in the nocturnal ones. Gastopods represented the main group (43 spp.), followed by bivalves (10 spp.) and cephalopods (1 spp.) (Table 2). Two species (3.7% of the total species number), *Dosinia lupinus* and *Doto sp.,* were restricted to the diurnal samples, while 24 species, (44.4%) such as *Mitrella minor*, *Mangelia attenuata* and *Nassarius reticulatus*, were restricted to the nocturnal samples. A total of 68,155 individuals were collected, with 28,154 in the diurnal and 40,001 in the nocturnal samples. In both diurnal and nocturnal samples, the molluscan fauna was mainly composed of gastropods (99.6% of the total number of individuals collected). The family Rissoidae was the most abundant family (73.7% of individuals and 11 spp.), followed by Trochidae (16.7% of individuals and 7 spp.), Nassariidae (4.2% and 5 spp.), Phasianellidae (3.0% and 1 sp.) and Neritidae (2.1% and 1 sp.). Bivalves with 10 spp. represented only ca. 0.4% of the individuals. Finally,

Table 2 Mollusc species found in the studied *Cymodocea nodosa* bed in south-eastern Spain

Species	N	%D	%FR	MH	FG	Biogeographical range					
						NE	WE	CN	AF	IM	ME
Gastropods											
Calliostoma granulatum (Born, 1778)	3	<0.01	12.5	SE	E	+	+	+		+	+
Calliostoma planatum Pollary, 1900*	379	0.58	87.5	SE	E					+	+
Calliostoma zyziphinum (Linnaeus, 1758)	5	0.01	12.5	SE	E	+	+			+	+
Gibbula ardens (von Salis, 1793)	594	0.92	87.5	VE	MG						+
Gibbula leucophaea (Philippi, 1836)*	7,524	11.61	100	VE	MG						+
Jujubinus exasperatus (Pennant, 1777)	7	0.01	25	HI	MG		+	+		+	+
Jujubinus striatus (Linnaeus, 1767)*	2,465	3.80	100	VE	MG		+	+		+	+
Tricolia tenuis (Michaud, 1828)*	1,900	2.93	100	VE	AG					+	+
Smaragdia viridis (Linnaeus, 1758)*	1,339	2.07	100	VE	SG			+		+	+
Pusillina inconspicua (Alder, 1844)	11	0.02	25	VE	MG	+	+			+	+
Pusillina philippi (Aradas & Maggiore, 1844)	161	0.25	12.5	VE	MG						+
Pusillina marginata (Michaud, 1830)	2	<0.01	6.25	VE	MG	+	+			+	+
Rissoa guerinii Récluz, 1843*	106	0.16	81.25	VE	MG		+			+	+
Rissoa monodonta Philippi, 1836*	29,827	46.01	100	VE	MG						+
Rissoa membranacea (J. Adams, 1800)*	16,676	25.73	100	VE	MG	+	+			+	
Rissoa similis Scacchi, 1836	19	0.03	12.5	VE	MG					+	+
Rissoa variabilis (von Mühlfeldt, 1824)	1	<0.01	6.25	VE	MG						+
Rissoa ventricosa Desmarest, 1814*	74	0.11	68.75	VE	MG						+
Rissoa violacea Desmarest, 1814*	428	0.66	100	VE	MG						+
Alvania rudis (Philippi, 1844)	1	<0.01	6.25	VE	MG					+	+
Crepidula unguiformis Lamarck, 1822	1	<0.01	6.25	SE	F						+
Bittium latreilli (Payraudeau, 1826)	23	0.04	75	SE	MG		+	+		+	+
Bittium reticulatum (da Costa, 1778)*	37	0.06	43.75	SE	MG	+	+			+	+
Cerithium lividulum Risso, 1826	1	<0.01	6.25	HE	D			+		+	+
Tectonatica filosa (Philippi, 1844)	10	0.02	43.75	SB	P		+	+		+	+
Lunatia pulchella (Risso, 1826)	11	0.02	25	SB	P	+	+			+	+
Bolinus brandaris (Linnaeus, 1758)	2	<0.01	12.5	SE	P					+	+
Mitrella minor (Scacchi, 1836)	4	0.01	18.75	VE	O		+		+	+	+
Nassarius cuvieri (Payraudeau, 1826)*	2,618	4.04	87.5	SE	SC			+		+	+
Nassarius incrassatus (Strom, 1768)	23	0.04	43.75	SE	SC	+	+	+		+	+
Nassarius mutabilis (Linnaeus, 1758)	136	0.21	43.75	SE	SC						+
Nassarius pygmaeus (Lamarck, 1822)*	60	0.09	81.25	SE	SC	+	+			+	+
Nassarius reticulatus (Linnaeus, 1758)	30	0.05	25	SE	SC		+	+		+	+
Philine aperta (Linnaeus, 1767)	1	<0.01	6.25	SB	P	+	+			+	+
Cancellaria cancellata (Linnaeus, 1767)	10	0.02	18.75	SE	P		+	+	+		
Mangelia attenuata (Montagu, 1803)	1	<0.01	6.25	SE	P	+	+			+	+
Bela laevigata (Philippi, 1836)	1	<0.01	6.25	SE	P					+	+
Ringicula auriculata (Menard, 1811)	1	<0.01	6.25	SB	P			+	+	+	+
Bulla striata Bruguière, 1792	1	<0.01	6.25	SB	P			+	+	+	+
Aplysia fasciata Poiret, 1789	2	<0.01	12.5	SE	AG						
Aplysia punctata Cuvier, 1803	38	0.06	12.5	SE	AG	+	+	+		+	+
Doto sp.	1	<0.01	6.25	VE	E						
Pleurobranchaea meckelii (Leue, 1813)	4	0.01	12.5	SE	P				+	+	+
Bivalves											
Musculus costulatus (Risso, 1826)	3	<0.01	12.5	SE	F	+	+	+		+	+
Musculus subpictus (Cantraine, 1835)*	66	0.10	68.75	SE	F	+	+	+		+	+

Table 2 continued

Species	N	%D	%FR	MH	FG	Biogeographical range					
						NE	WE	CN	AF	IM	ME
Mytilaster minimus (Poli. 1795)	1	<0.01	6.25	SE	F		+	+		+	+
Flexopecten flexuosus (Poli, 1975)	2	<0.01	6.25	SE	F			+		+	+
Anomia ephippium Linnaeus, 1758	118	0.18	62.5	EP	F	+	+	+		+	+
Parvicardium vroomi van Artsen, Moolenbeek y Gittenberger, 1984	2	<0.01	6.25	VE	F					+	+
Spisula subtruncata (da Costa, 1778)	7	0.01	12.5	SI	F	+	+	+		+	+
Ervilia castanea (Montagu, 1803)	61	0.94	18.75	SI	F		+	+		+	+
Chamelea gallina (Linnaeus, 1758)	8	0.01	31.25	SI	F					+	+
Dosinia lupinus (Linnaeus, 1758)	1	<0.01	6.25	SI	F	+	+	+		+	+
Cephalopods											
Sepietta oweniana (d'Orbigny 1840)	17	0.03	37.5	DE	P	+	+			+	+

For each species are indicated total numbers of individuals collected (*N*), frequency values (%*F*), dominance values (%*D*), preferred microhabitat (*MH*), feeding guild (*FG*) and biogeographical range. * represents those species illustrated in figures of the supplementary material. For codes, see Table 1

cephalopods with 17 individuals of a single species (*Sepietta oweniana*) made the smallest contribution (<0.1%) to the molluscan taxocoenosis.

The top ten dominant species of the diurnal and nocturnal samples are indicated in Table 3. In both assemblages, the dominant species were the rissoids *Rissoa monodonta* (53.4% in diurnal and 41.4% in nocturnal assemblages, %D) and *Rissoa membranacea* (20.2 and 29.1%, respectively), followed by *Gibbula leucophaea* (11.1%), *Jujubinus striatus* (3.7%) and *Tricolia tenuis* (3.5%) during the day and by *G. leucophaea* (11.9), *N. cuvierii* (4.7%) and *J. striatus* (3.8%) during the night. Due to the high dominance of these 7 gastropod species, the other 47 spp. showed dominance values of less than 1% (Table 2). A total of 7 spp. were found in all diurnal samples (%F = 100%): *Gibbula leucophaea*, *Jujubinus striatus*, *Tricolia tenuis*, *Smaragdia viridis*, *Rissoa monodonta*, *Rissoa membranacea* and *Rissoa violacea* (Table 3). These species plus *Calliostoma planatum*, *Nassarius cuvierii* and *Nassarius pymaeus* were also found in all nocturnal samples. Thus, there were a high number of species that were not highly dominant but nevertheless occurred in most or even all samples from the *Cymodocea nodosa* bed, independent of time and season.

Microhabitat preference and feeding guilds

Regarding microhabitat preference, the studied molluscan assemblage was dominated by epifaunal species of soft bottoms (40.7%), followed by species associated with seagrass or macroalgae (35.2%), soft bottom infauna and species that live partly buried in the sediment (both < 10%). In the diurnal samples, species associated with seagrass and macroalgae were the dominant group in

number of species (46.67%), followed by epifaunal species of soft bottoms (26.67%) (Table 4). In the nocturnal samples, in contrast, epifaunal species of soft bottoms were dominant (42.31%), followed by those of seagrass and macroalgae (34.62%). In relation to abundance values, species associated with seagrass and macroalgae dominated in both diurnal (96.3%) and nocturnal samples (93.1%).

Microalgal grazers (31.5% of the species), predators (20.4%) and filter feeders (20.4%) were the most frequent feeding guilds. In terms of abundance, microalgal grazers were highly dominant (>90% individuals), followed by macroalgal grazers and scavengers (each < 5%). Other feeding guilds such as egg feeders (*Mitrella minor*) and seagrass feeders (*Smaragdia viridis*) were less abundant (<2%). In the diurnal samples, microalgal grazers and filter feeders dominated in species number, while nocturnal samples showed an increase in the number of predators (from 2 to 11 spp.) and scavengers (from 3 to 5 spp.) (Table 4). In terms of abundance, microalgal grazers dominated in both diurnal and nocturnal samples (ca. 90%), with an increase in predators and scavengers in the nocturnal samples.

Biogeographical remarks

The recorded molluscan species display different patterns of biogeographical distribution. These were obtained in a cluster using the Bray–Curtis similarity index and qualitative data on the presence/absence of the species in different biogeographical areas (Fig. 1). Information on the biogeographical distribution could not be obtained for 4 spp., which were thus excluded from the analyses. The main groups are (1) strictly Mediterranean species (ME) (9 spp., 17.3%) such as the dominant *Rissoa monodonta* and

Table 3 Top dominant (%D) and frequent (%F) molluscan species in the global (diurnal + nocturnal), diurnal and nocturnal assemblages associated with a *C. nodosa* bed (10–14 m depth)

Total			Diurnal			Nocturnal		
Species	N	%D	Species	N	%D	Species	N	%D
Dominant species								
Rissoa monodonta	30,961	47.1	*Rissoa monodonta*	13,247	53.4	*Rissoa monodonta*	16,580	41.4
Rissoa membranacea	16,531	25.1	*Rissoa membranacea*	5,023	20.2	*Rissoa membranacea*	11,653	29.1
Gibbula leucophaea	7,646	11.6	*Gibbula leucophaea*	2,755	11.1	*Gibbula leucophaea*	4,769	11.9
Nassarius cuvierii	2,617	4.0	*Jujubinus striatus*	926	3.7	*Nassarius cuvierii*	1,882	4.7
Jujubinus striatus	2,270	3.4	*Tricolia tenuis*	867	3.5	*Jujubinus striatus*	1,539	3.8
Tricolia tenuis	1,980	3.0	*Nassarius cuvierii*	736	3.0	*Tricolia tenuis*	1,033	2.6
Smaragdia viridis	1,367	2.1	*Smaragdia viridis*	462	1.9	*Smaragdia viridis*	877	2.2
Gibbula ardens	502	0.8	*Gibbula ardens*	289	1.2	*Calliostoma planatum*	358	0.9
Rissoa violacea	415	0.6	*Rissoa violacea*	150	0.6	*Gibbula ardens*	305	0.8
Calliostoma planatum	395	0.6	*Pusillina philippi*	74	0.3	*Rissoa violacea*	278	0.7
Total			Diurnal			Nocturnal		
Species	%FR		Species	%FR		Species	%FR	
Frequent species								
Tricolia tenuis	100		*Gibbula leucophaea*	100		*Calliostoma planatum*	100	
Smaragdia viridis	100		*Jujubinus striatus*	100		*Gibbula leucophaea*	100	
Gibbula leucophaea	100		*Tricolia tenuis*	100		*Jujubinus striatus*	100	
Jujubinus striatus	100		*Smaragdia viridis*	100		*Tricolia tenuis*	100	
Rissoa monodonta	100		*Rissoa monodonta*	100		*Smaragdia viridis*	100	
Rissoa membranacea	100		*Rissoa membranacea*	100		*Rissoa monodonta*	100	
Rissoa violacea	100		*Rissoa violacea*	100		*Rissoa membranacea*	100	
Nassarius cuvieri	87.5		*Gibbula ardens*	87.5		*Rissoa violacea*	100	
Calliostoma planatum	87.5		*Musculus subpictus*	87.5		*Nassarius cuvieri*	100	
Gibbula ardens	87.5		*Calliostoma planatum*	75		*Nassarius pygmaeus*	100	
Nassarius pygmaeus	81.2		*Rissoa guerinii*	75		*Gibbula ardens*	87.5	
Rissoa guerinii	81.2		*Bittium latreilli*	75		*Rissoa guerinii*	87.5	
Bittium latreilli	75		*Nassarius cuvieri*	75		*Nassarius mutabilis*	87.5	
Musculus subpictus	68.7		*Rissoa ventricosa*	62.5		*Rissoa ventricosa*	75	
Rissoa ventricosa	68.7		*Nassarius pygmaeus*	62.5		*Bittium latreilli*	75	

Gibbula leucophaea; (2) species with a wide distribution in Europe but absent from the Canary Islands (NE, WE, IM, ME) (9 spp., 17.3%), such as *Nassarius pygmaeus* and *Bittium reticulatum;* (3) species with a wide distribution including northern and western Europe, the Ibero-Moroccan Gulf, the Mediterranean Sea and the Canary Islands (NE, WE, IM, ME, CN) (8 spp., 15.4%), such as *Anomia ephippium* and *Nassarius incrassatus*; (4) species that mainly occur in the Mediterranean Sea and the Ibero-Moroccan Gulf (ME, IM) (8 spp., 15.4%), such as *Tricolia tenuis* and *Calliostoma planatum*, which ranked among the top ten dominant species; (5) species occurring in western Europe, the Ibero-Moroccan Gulf, the Mediterranean Sea and at the Canary Islands (WE, IM, ME, CN) (6 spp.,

11.5%), such as the highly dominant *Jujubinus striatus* which is also associated with other seagrass species (e.g. *Zostera marina*); and (6) species occurring in the Mediterranean Sea, the Ibero-Moroccan Gulf and at the Canary Islands (ME, IM and CN) (4 spp., 7.7%), such as *Nassarius cuvierii* and *Smaragdia viridis* that feed on epidermal tissues of *C. nodosa*. Other interesting groups were represented by (1) Atlantic species from northern Europe (1 spp., 1.9%), such as *Rissoa membranacea* that was the second dominant species and is also highly dominant in other seagrass species in this area (e.g. *Zostera marina*), and (2) species that also occur in western Africa, such as *Cancellaria cancellata*, *Bulla striata*, *Tectonatica filosa* or *Ringicula auriculata*.

Table 4 Percentages of species and individuals in relation to their microhabitat preference and feeding guild affinity in diurnal and nocturnal samples

	Number of species			Number of individuals	
	Day	Night		Day	Night
Microhabitat preference					
VE	46.67	34.62	VE	96.32	93.06
SE	26.67	42.31	SE	3.36	6.53
EP	3.33	1.92	EP	0.23	0.15
SI	13.33	5.77	SI	0.05	0.16
DE	3.33	1.92	DE	0	0.04
SB	3.33	9.62	SB	0.01	0.05
HE	3.33	3.85	HE	0.02	0.01
Feeding guilds					
MG	46.67	32.69	MG	91.08	88.36
F	23.33	19.23	AG	3.49	2.68
SC	10.00	9.62	SC	3.07	5.26
E	6.67	5.77	SG	1.86	2.19
P	6.67	21.15	F	0.39	0.43
AG	3.33	5.77	E	0.09	0.91
SG	3.33	1.92	P	0.02	0.14
O	0	1.92	O	0	0.01
D	0	1.92	D	0	0

For codes, see Table 1

In summary, the molluscan species spectrum was mainly composed of species with a wide biogeographical distribution along the European Atlantic and the Mediterranean coasts (24 spp.). Strictly Mediterranean species (9 spp.) and species also occurring in the Ibero-Moroccan Gulf (8 spp.) represented the second group regarding the number of species. Species reaching the coasts of western Africa (6 spp.) were less represented than those occurring in northern Europe (18 spp.).

Seasonal and diel changes

Abundance values (N, individuals m^{-2}) displayed seasonal changes with maxima during autumn and winter months (Mann–Whitney; factor 'cold–warm': $U = 10.00$, $p < 0.05$), but diurnal and nocturnal values were not significantly different (factor 'diel': $U = 21.00$, $p > 0.05$) (Fig. 2). S displayed higher values in cold (December–March) than in warm months, but these differences were statistically not significant (one-factor ANOVA: factor 'cold–warm': $F = 0.356$, $p > 0.05$). Significant differences were found, however, in S values between day and night, with higher number of species in the nocturnal than in the diurnal samples (Fig. 2) (one-factor ANOVA: factor 'diel': $F = 13.410$, $p < 0.005$). The evenness (J') was rather stable throughout the year, with similar values in day and night samples between 0.4 and 0.6 (Fig. 2). No significant differences were found in relation to the diel (one-factor ANOVA: factor 'diel': $F = 0.052$, $p > 0.05$) nor to the seasonal variation

(one-factor ANOVA: factor 'cold–warm': $F = 4.077$, $p > 0.05$). The Shannon–Wiener diversity index (H', log$_2$) was also rather constant throughout the year, with maximum values in June (2.5 bits) and July (2.4 bits), but without significant differences among cold and warm months (one-factor ANOVA: factor 'cold–warm': $F = 1.922$, $p = 0.215$, $p > 0.05$). Nevertheless, H' values were significantly higher in nocturnal than in diurnal samples (one-factor ANOVA: factor 'diel': $F = 10.5$, $p < 0.01$). This difference was maximal in June, due to low S and J' values of the diurnal sample.
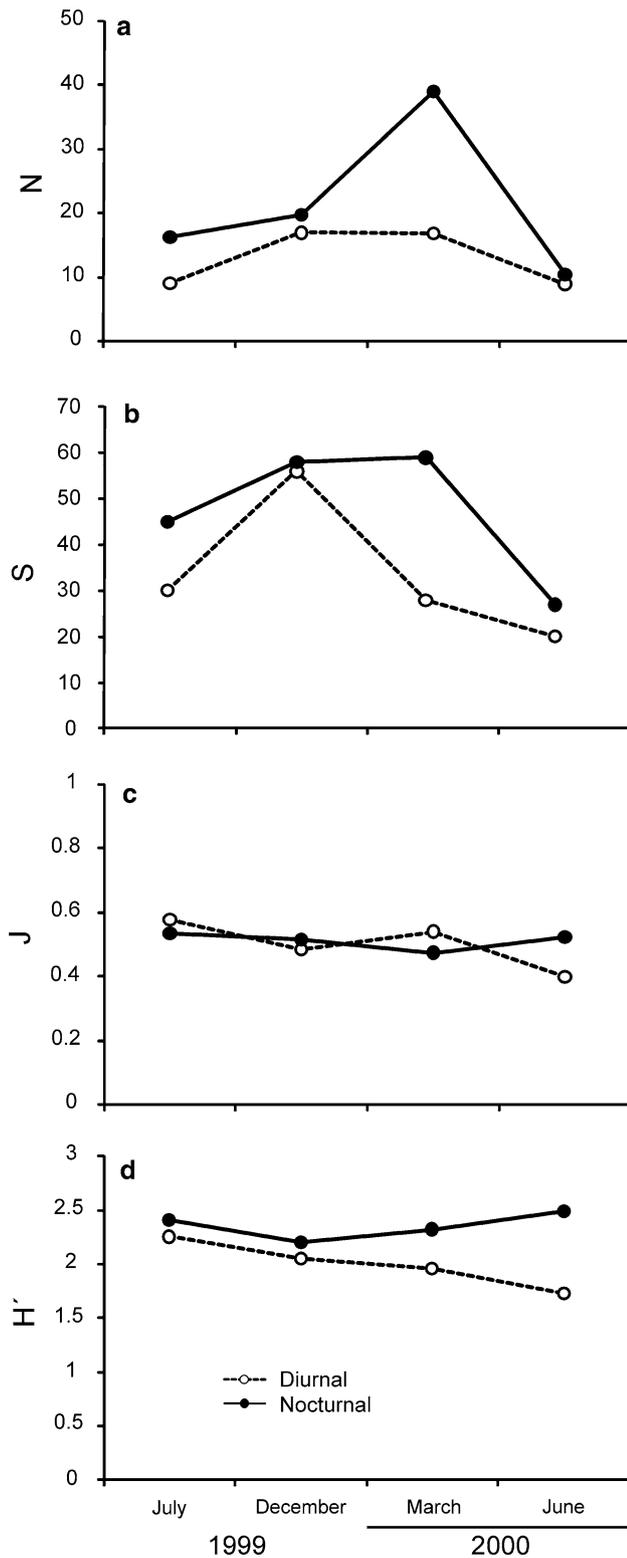
The MDS (based on Bray–Curtis similarity index) using qualitative (presence/absence of species) and quantitative data (fourth root of abundance) reflected a seasonal (cold–warm) and a diurnal–nocturnal grouping of samples (Fig. 3). One-factor ANOSIM analysis resulted in significant differences between diurnal and nocturnal samples when using qualitative or quantitative data (in both cases $R_{\text{ANOSIM}} = 0.28$, $p < 0.05$). Significant differences were also obtained when comparing samples from cold and warm months using qualitative ($R_{\text{ANOSIM}} = 0.61$, $p < 0.005$) and quantitative data ($R_{\text{ANOSIM}} = 0.64$, $p < 0.005$). SIMPER analyses showed that the highest contribution for the diel variation was made by the absence of the predator species *Nassarius mutabilis*, *Nassarius reticulatus* and *Lunatia pulchella* from the diurnal samples and by the higher abundance of *Nassarius cuvierii*, *Rissoa membranacea*, *Gibbula ardens*, *Calliostoma planatum* and *Jujubinus striatus* in the nocturnal samples. Regarding seasonal

Fig. 1 Cluster displaying faunistic groupings in relation to their presence in different geographical sectors using qualitative data (presence/absence) and the similarity index of Bray–Curtis (for codes, see "Materials and methods" and Table 1)
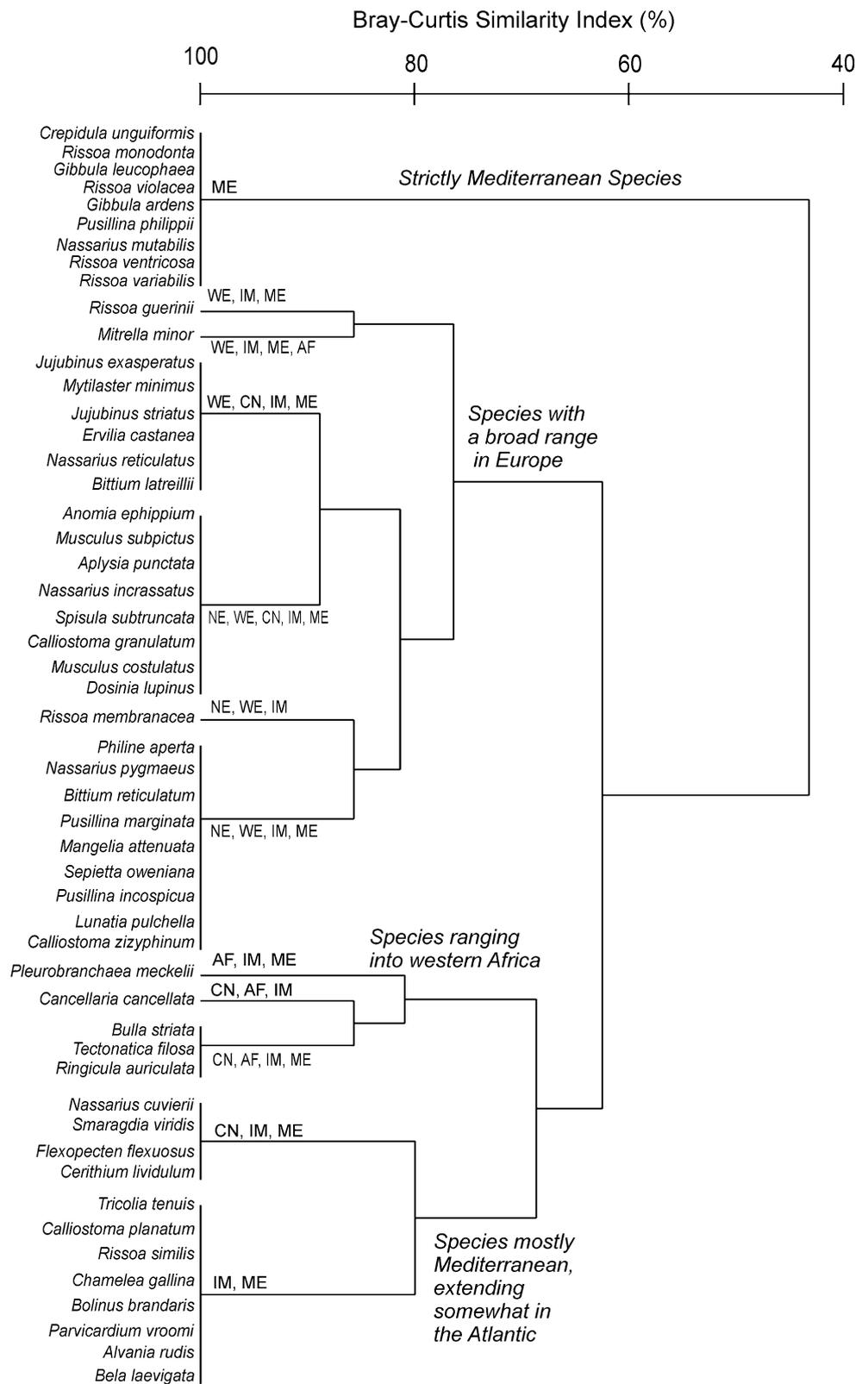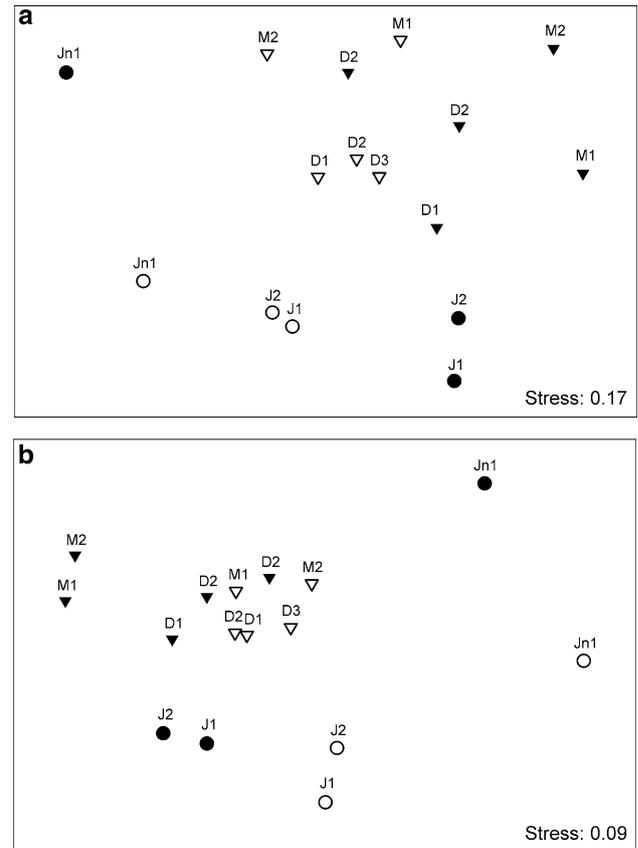

differences, the highest contribution to the variation was given by the low abundance of *Nassarius cuvierii, Anomia ephippium, Rissoa ventricosa, Gibbula leucophaea* and *Rissoa membranacea* in warms months (spring and summer) and of *Gibbula ardens, Bittium reticulatum* and *Pusillina philippi* in cold months (autumn and winter).

Fig. 3 MDS based on **a** qualitative (presence/absence) and **b** quantitative similarities (Bray–Curtis index) among the molluscan assemblages of different seasons (July 1999 to June 2000) and times of day in a *Cymodocea nodosa* bed (10–14 m depth); *empty symbols* = diurnal samples, *solid symbols* = nocturnal samples, *triangles* = cold month samples (*D* December, *M* March), *circles* = warm month samples (*J* July, *Jn* June)

Fig. 2 Molluscan seasonal dynamics in **a** abundance (*N* individuals m^{-2}), **b** species richness (*S* species sample^{-1}), **c** evenness (*J*) and **d** Shannon–Wiener diversity index (*H'*) in a *Cymodocea nodosa* seagrass bed (10–14 m depth); diurnal samples (*dashed line* and *empty symbols*) and nocturnal samples (*continuous line* and *solid symbols*); means *without error bars*

Discussion

Composition and structure of the molluscan assemblage

As in some other studies on seagrass-associated molluscs (Arroyo et al. 2006; Rueda et al. 2008) and decapods (García-Raso et al. 2006), an Agassiz trawl was chosen for sampling in the present study. The sampling area (about 222 m^2 per transect) was thus much larger than in previous studies on molluscan biocoenoses of *Cymodocea nodosa* beds using corers or hand-towed nets (sampling areas of less than 10 m^2 per sample; Chemello et al. 1997; Terlizzi and Russo 1997; Tuya et al. 2001). On the one hand, sampling by corers or quadrats may be more representative of the complete (epifaunal and infaunal) assemblage (González et al. 2007; Rueda and Salas 2008), but on the other hand, due to the small sampling area in relation to the overall seagrass bed, rare species may easily escape notice,

resulting in an underestimation of the total number of species. This may have happened in the study of González et al. (2007), who sampled the same *C. nodosa* bed using corers and listed only 21 species (compared to 54 in the present study). Nevertheless, sampling with the Agassiz trawl could underestimate those species of the infauna that live burrowed deeply in the sediment, such as the bivalves *Loripes lacteus* or *Spisula subtruncata* (Ballesteros et al. 2004).

The composition and structure of the sampled molluscan assemblage was rather similar to those of C*ymodocea nodosa* beds in other parts of the Mediterranean Sea (Chemello et al. 1997; Terlizzi and Russo 1997). Gastropods were the dominant group in all cases, mainly the families Rissoidae and Trochidae, followed by bivalves and cephalopods. The number of species was similar to that of *C. nodosa* beds in Italy, where 53 spp. (Chemello et al. (1997) and 42 spp. (Terlizzi and Russo 1997) were recorded. Nevertheless, the faunistic composition varied differently. Only 5 species (*Pusillina marginata, Gibbula ardens, Rissoa similis, Bittium latreilii* and *Jujubinus striatus*) occurring in the *C. nodosa* bed of Genoveses were also reported by Chemello et al. (1997). Eight of the ten most dominant molluscs of the *C. nodosa* bed of Genoveses belong to the group of epifaunal species associated with vegetated bottoms; out of these, *Smaragdia viridis* and *Rissoa membranacea* are strictly associated with seagrasses (Rueda and Salas 2007; Rueda et al. 2009a), and other species such as *Rissoa monodonta, Jujubinus striatus, Gibbula leucophaea* and *Tricolia tenuis* are generally found in macroalgae or seagrass beds in southern Spain (Rueda and Salas 2003; Rueda et al. 2009a).

In beds of other seagrass species (e.g. *Posidonia oceanica, Zostera marina, Nanozostera noltii*), molluscs are also a dominant group, displaying normally higher densities than other abundant groups such as polychaetes (Sfriso et al. 2001) and crustaceans (e.g. amphipods: Sánchez-Jerez et al. 1999). The studied molluscan assemblage associated with *C. nodosa* shared some similarities with those of *Zostera marina* beds in the Alboran Sea (Arroyo et al. 2006; Rueda et al. 2008). In both assemblages, gastropods were the dominant group in number of species, with five of the top ten dominant species (*Jujubinus striatus, Calliostoma planatum, Rissoa membranacea, Smaragdia viridis* and *Rissoa monodonta*) of *Z. marina* beds showing high dominance values also in the studied *C. nodosa* bed. Nevertheless, the *S* values in *C. nodosa* beds were lower than in *Z. marina* and *P. oceanica* beds (Rueda et al. 2008; Como et al. 2008). This might be related to differences in sampling effort or to a lower habitat complexity of *C. nodosa* beds compared with those of *Z. marina* and *P. oceanica* with shoots that are generally longer and wider, and displaying higher numbers of leaves

as well as (in the case of *P. oceanica*) a complex rhizome stratum (Green and Short 2003). This less complexity in habitat could also affect other faunistic groups, such as echinoderms, sponges and anthozoans, which are the preferred food of some molluscan species (e.g. eulimids, triphorids and epitonids, respectively) that were not found in the studied *C. nodosa* bed.

The dominant feeding guild in the *C. nodosa* bed of Genoveses was represented by microalgal grazers associated with the leaf stratum as it was also found for the epifauna associated with *C. nodosa* in Italy (Terlizzi and Russo 1997; Chemello et al. 1997) or with *Z. marina* (Mattila et al. 1999; Nakaoka et al. 2001; Rueda et al. 2009a). In these beds, predators represent another important group indicating high prey availability as it was reported for *Z. marina* beds of the Alboran Sea (García-Raso et al. 2004; Rueda et al. 2009a). The presence of the egg feeder *Mitrella minor* may point out the importance of this habitat as a spawning and nursery site for different species as found in *Z. marina* beds (Arroyo et al. 2006, Rueda et al. 2009a). The presence of seagrass feeders such as *Smaragdia viridis* is also of interest as in this way seagrass carbon might be allocated to higher trophic levels such as fish (Rueda and Salas 2007).

There is an increasing trend in the number of mollusc species from northern Europe to the south, with 380 spp. in the English Channel (Cornet and Marche-Marchad 1951), 660 spp. in Galicia (Rolán 1983; Rolán et al. 1990) and ca. 1,000 spp. in the Alboran Sea (Gofas et al. 2011). In *C. nodosa* beds of other parts of the Mediterranean, molluscan assemblages seem to have similar numbers of species as in southern Spain, with a high contribution of the families Rissoidae, Phasianellidae, Trochidae and Nassariidae (Terlizzi and Russo 1997; Chemello et al. 1997). Nevertheless, highly diverse molluscan assemblages associated with *C. nodosa* beds could also occur in more southern locations (western Africa, Canary Islands), where relevant studies are still very scarce and generally did not include intensive sampling efforts (Tuya et al. 2001).

The studied molluscan fauna was mainly composed of species with a wide biogeographical distribution, but also included species that are strictly Mediterranean (16.6%) and Mediterranean species that also occur in the Ibero-Moroccan Gulf (14.8%). The location close to the Alboran Sea and the Almeria-Oran front may influence the faunistic composition because of the presence of Mediterranean species not present in Atlantic *C. nodosa* beds. This oceanic front represents a natural barrier to dispersal and gene flow of many species from different groups (Galarza et al. 2009; Patarnello et al. 2007). On the other hand, there are also Atlantic species that do not occur in Mediterranean *C. nodosa* beds. This applies to *Rissoa membranacea*, which was supposed to reach the Ibero-Moroccan Gulf and

was recently also found in *Zostera marina* beds of the Alboran Sea (Rueda et al. 2008). This species also occurred at high densities in the *C. nodosa* bed of Genoveses, so this is possibly its first record in the Mediterranean Sea (except of the Alboran Sea). Nevertheless, it is unknown whether *R. membranacea* is synonymous with *R. elata, R. venusta, R. fragilis* or *R. grossa* occurring in *Zostera marina* beds of Italy and France, as there are serious taxonomic difficulties regarding this species complex.

According to García-Raso et al. (1992) and Ballesteros et al. (2004), there are two types of communities (inhabited by different species assemblages) associated with *C. nodosa* meadows, one type characteristic of shallow meadows (0–2 m deep between *P. oceanica* meadows and the coastline) in calm waters and on muddy-sandy bottoms and another one associated with meadows in more open waters on deeper sandy bottoms (more than 8–10 m deep, normally below the belt of *P. oceanica*). The molluscan assemblage of the present study seems to belong to the latter type of community.

Intra-annual and diel variation

Significant differences between cold and warm months were only found for abundance values, which were maximal in cold months (December and March). This agrees with the findings on other Mediterranean *C. nodosa* beds by Sfriso et al. (2001), whereas Terlizzi and Russo (1997) registered maximal values in spring and summer months, concurring with the maximum development of the *C. nodosa* bed. The low spring/summer abundance values in the present study could be related to the high availability of the macroalga *Ectocarpus* sp. that was collected extensively during those months, or to a lower probability of capturing molluscs with the trawl in warm months when the *C. nodosa* bed was also more developed.

Species richness values differed significantly between the day and night samples. A total of 24 species were only found during the night; most of them are predators such as *Nassarius mutabilis*, *Nassarius reticulatus* and *Lunatia pulchella*. H' and J' values were rather constant throughout the year, as was also found by Chemello et al. (1997) for molluscs from *C. nodosa* beds in Italy, and in nocturnal molluscan assemblages of *Z. marina* of the Alboran Sea (Rueda et al. 2008). By contrast, a seasonal trend with maximum values in summer was found for molluscan assemblages associated with *C. nodosa* beds of the Canary Islands (Tuya et al. 2001). In the present study, most of the significant differences were found between the diurnal and nocturnal assemblages, with higher values of S and H' in the nocturnal samples (Fig. 2).

Studies on diel changes in the molluscan fauna associated with seagrass meadows have revealed that these seem to be less acute than in other taxonomic groups such as decapods, amphipods and fishes (Templado 1982; Mattila et al. 1999; Le Loeuff and Intès 1999; Sánchez-Jerez et al. 1999; Rueda et al. 2008). The diurnal/nocturnal changes in the abundance of molluscs of *C. nodosa* were less marked than the seasonal ones. These findings differ from those on decapods in the same *C. nodosa* bed (García-Raso et al. 2006) and on molluscs of *Z. marina* (Rueda et al. 2008). Nevertheless, some significant diurnal/nocturnal changes were observed, mainly related to S and H', which were both higher during the night. Abundance values were also higher during the night, but this difference was statistically not significant. The absence of a strong diel pattern in abundance values could be due to the large contribution of some dominant species such as some rissoids (e.g. *R. monodonta*), which generally do not display diel movements (Templado 1982; Rueda et al. 2008). In *C. nodosa* beds, a high percentage of the species in nocturnal samples (45.8%) were sediment-linked predators or scavengers, which may forage at night-time as also found for other seagrass beds (Rueda et al. 2008). Nevertheless, the diel variation observed in the present study was less marked than those found for *Z. marina* and *P. oceanica*. This might relate to the lower habitat complexity and species diversity of *C. nodosa* meadows compared with those of other seagrass species (see above) as well as to a low differentiation between the sediment and the leaf stratum when compared with *Posidonia oceanica* beds (Templado 1982; Rueda et al. 2008).

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