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Seasonal and diel changes in the structure of a crustacean decapod assemblage associated to a shallow *Cymodocea nodosa* meadow in northern Tunisia (Mediterranean Sea). An overview of Mediterranean decapod taxocoenoses

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Abstract

A study on the decapod assemblage inhabiting a shallow meadow of *Cymodocea nodosa* in the bay of La Goulette (Tunisia) was carried out from February 2009 to February 2010. Monthly samples (with replicates) were taken in the morning and at night, with a small Agassiz trawl. In total, 11699 specimens belonging to 41 species were caught. Significant day-night and seasonal changes are mainly related to movements (feeding) and recruitments. Higher abundance and richness were reported at night. Analyses did not reveal significant relationships between plant phenology, abundance and richness or between total abundance and temperature, but significant correlations with a time lag of 3 - 4 months between these factors exist, which could be related to hatching and larval development period. The nocturnal and diurnal values in the diversity and equitability indexes are quite similar throughout the year (peaks in spring - early summer, minimum in autumn - early winter). This pattern is due mainly to the strong dominance of a few species, with maximum abundances during their recruitment events, whose seasonal and day-night changes have been determined. Besides, an overview of the decapod assemblage associated to this seagrass has been carried out for the Mediterranean Sea. The assemblage can be divided into two groups (linked to the leaves and to the sediment). The differences in species composition among different Mediterranean areas must be related to different sampling methodologies, feeding and reproductive strategies, but also to the layout and influence of the surrounding habitats.

Keywords: Crustacea Decapoda, Cymodocea, Tunisia, Mediterranean Sea, temporal and day-night changes, diversity.

Introduction

Information on marine invertebrate biodiversity in Tunisia is rather poor and, although there are some relatively well-studied areas such as the Gulf of Gabès and the northern coast (Gulf of Tunis and the lagoons), further research is needed to gain good knowledge of the taxonomic groups and insights of the structure and dynamics of the different communities. Recent studies have focused on the latter but only about 120 Crustacean species have been mentioned (Afli, 2005; Ben Mustapha & Afli, 2007). In the northern lagoon of Tunis, Tlig-Zouari & Maamouri-Mokhtar (2008) and Tlig-Zouari *et al*. (2009) have recently cited 22 and 27 species of crustaceans, respectively (yet only 6 and 4 of these were decapods).

Regarding decapod studies in Tunisia we must highlight the comprehensive work contributed by Forest & Guinot (1956), who reported 60 species, mainly in the Gulf of Tunis, and from the Gulf of Gabes the report by El Lakhrach, *et al*. (2012) with 42 species.

General information on the animal communities associated to different seagrass species and their relationships with different factors have been reported from different geographical areas (see references in Lewis & Stoner, 1983; Mateo & García Raso, 2012). Studies on macrofaunal assemblage associated to small seagrass *Cymodocea nodosa* have been carried out in some Mediterranean areas and the adjacent Atlantic Ocean (e.g. Ledoyer, 1966, 1968; Scipione *et al*., 1996; Sánchez-Jerez *et al*., 1999; Guidetti & Bussotti, 2000; Reed & Manning, 2000; Barbera-Cebrián *et al*., 2002; Brito *et al*., 2005; Tuya *et al*., 2006; Schaffmeister *et al*., 2006; González *et al*., 2007; Como *et al*., 2008). Besides, very few studies have focused on Crustacean decapod assemblages (Ševčić, 1991; García Raso *et al*., 2006; Schaffmeister *et al*., 2006; Mateo & García Raso, 2012).

In Tunisia, knowledge of animal communities associated to marine habitats is scarce (Afli & Ben Mustapha, 2001; Ben Mustapha *et al*., 2002; De Gaillande, 1970 among others), and particularly of crustacean decapods associated to *Cymodocea nodosa* (Reed & Manning, 2000).

This study was designed on the basis of the previous considerations, and also due to: 1) the particular impor-

tance of this marine habitat, which hosts a rich plant and animal community; 2) because the knowledge of the invertebrate fauna associated to different habitats is a priority issue, not only in the European Union's, Marine Strategy Framework Directive (2008/56/EC), but also in other countries, as a basis for proper protection and sustainable management of marine resources; 3) the important role of these meadows in coastal food webs and chemical and physical processes (Duarte & Sand-Jensen, 1990); 4) their contribution to human welfare, with significant economic impact (Costanza *et al*., 1997); and 5) the declining of seagrasses due to increasing human pressures (Waycott *et al*., 1999; Zarranz *et al*., 2010).

The objective of this study is to: (1) determine the structure of the crustacean decapod assemblage associated to *Cymodocea nodosa* in Tunisia, and identify the influence of plant phenology and some environmental factors, (2) test seasonal and diel changes, and (3) provide a general overview of the crustacean decapod taxocoenosis, with special emphasis in the Mediterranean basin.

Hypotheses: (1) there is a high biodiversity due to the vegetated type of habitat, (2) there is an increase of species richness and abundance in the nocturnal samples, (3) there are significant variations between annual seasons and day-night, but higher in the latter and (4) the specific composition, in relation to that found in other European Mediterranean areas, shows differences mainly due to local factors.

Material and Methods

Study area

The sampling area is located in the bay of the La Goulette (36º49'06.78''N - 10º18'36.26''E), a popular beach used for tourism that undergoes human pressure, especially in the summer (Fig. 1). The whole area is influenced by the harbour of La Goulette and the canal of Khéreddine that communicates with the Tunis Lagoon and may drive up to ca. 950.000 m^3 / day of fresh water (Ministére de l'Environnement et de l'Aménagement du Territoire, 2000). This bay hosts a small shallow *Cymodocea nodosa* bed, at a depth range of 1 m to 10 m, surrounded by sandy bottoms, and near a rock barrier with extensive seaweed coverage.

Sampling

Sampling was carried out monthly, from February 2009 to February 2010, in the morning (at about 10:00 h) and at night (in moonless nights, 2-3 h after sunset, when an abundance peak of decapods has been reported (De Grave *et al*., 2006; García Raso *et al*., 2006). The samples were taken using a small Agassiz trawl, with a 70 cm-wide frame and a net mesh of 3 mm knot-to-knot. Each haul lasted 5 min. at a speed of 1 knot (1.85 km/h) and covered an area of ca. 108 m^2. Three monthly replicates were taken, at about 2 m depth, because random samples with low and very unequal densities can bias the results (Lewis & Stoner, 1983). Therefore, the monthly total sampling area was about 324 m^2.

For the phenological study, five replicates of 50 x 50 cm quadrant were randomly selected every two months. These quadrants are further divided into four parts (25 x 25 cm), three of which were used to obtain shoot density (note: the 4th was reserved for further epifaunal and endofaunal studies). These samples were obtained at a depth of 1-2 m (according to the tidal cycle) by diving. A more complete phenological study is currently in preparation.

Sediment granulometry was analyzed with a column of standard sieves (Buchanan, 1984) and Trask's index was calculated (Trask, 1950). Organic matter in the sediment was measured by ignition at 500ºC for 1hour.

Water temperature was measured on site at the time of sampling, in the morning, using thermometers with 0.1ºC precision. Also, 1 l of sea water was collected and

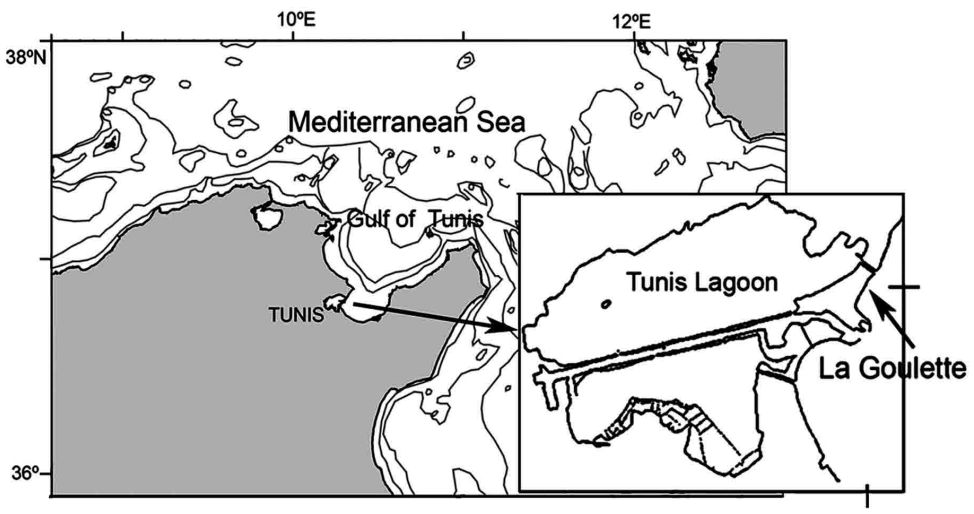


Fig. 1: Location of sampling area in La Goulette (indicated with an arrow in the lower right corner, coordinates: 36º49'06.78''N - 10º18'36.26''E).

transported in darkness to the laboratory for salinity determination. The measurements of salinity were made with a salinometer (WTWCOND315i/SET).

Data analysis

For decapod species identification taxonomic studies on the Atlantic Ocean (African and European) and Mediterranean Sea were used, including the classical and basic study of Zariquiey Álvarez (1968), as well as recent nomenclature revisions and checklists [Ng *et al*., 2008; De Grave & Fransen, 2011 and Worms Register of Marine (Appeltans *et al*., 2013)].

The relationship (Pearson correlation) between shoot density (number per square meter) and richness, total abundance, and abundance of the dominant species were determined using the SPSS software package; the relationships between richness, total abundance and environmental factors were also determined. Seasonality and day-night differences were analyzed with the PRIMER software package (Clarke & Warwick, 1994) using a fourth root transformation of quantitative data without standardization. Significance of differences between pre-established groups (day/night and different seasons) was assessed according to the ANOSIM (non-parametric permutation procedure applied to the similarity matrix) routine. To establish the relationships between samples, a similarity matrix (Bray-Curtis index) was used to construct bivariate MDS plots (MDS routine). The diversity values of the Shannon index and evenness values were calculated (DIVERSE routine). The relative abundance or dominance (Di, %), the frequency of occurrence (Fi, %), and the contribution of species to average within-group similarity were also determined (SIMPER routine).

Results

Abiotic variables

The sediment for most of the monthly samples corresponds to fine sand (0.125<Q50<0.250), but in May 2009, September 2009, January 2010 and March 2010 to very fine sand (0.063<Q50<0.125). Track's index was always 0.4 (well sorted). Organic matter values ranged between 0.109% and 0.29%, with a mean value of 0.171%, and a standard deviation of 0.064. Sea surface temperatures (Fig. 2) show monthly differences with maximum values in summer and early autumn (June to September), and minimum values in winter (February). Monthly salinity values (Fig. 2) ranged between 35.8 and 37.8 psu, being lower during the wet season (December to May).

Phenology of Cymodocea nodosa

The evolution of shoot density is shown in Figure 3. The maximum and minimum values were found in end spring - beginning of summer (June) and winter (December and February) respectively. Annual shoot density evolution follows a similar trend to that observed for temperature and salinity, although some monthly delay was observed for the latter two.

Crustacean decapod assemblages

A total number of 11699 specimens belonging to 41 species were captured. Total abundance (Nt), relative abundance (= dominance, D%) and frequency of occurrence (= presence, F and F%) of the species in day- and night-time samples are shown in Table 1. The diurnal faunal data in July were poorer (probably due to sampling problems).

The permanent or constant species, with presence values above 75% (all replicas, diurnal and nocturnal, considered separately), were *Hippolyte inermis* and *Palaemon xiphias*, followed by *H. leptocerus* (F% = 73.1). All these species show high diurnal and nocturnal values, overall during daytime (Table 1, Figs. 4A, B, C). Other species must be considered as permanent when the day and night samples are analyzed separately [this is the case of *Processa edulis* (night-time) (Table 1, Fig. 4D)] and monthly replicas are grouped (total: *P. xiphias*, *H. inermis*, *P. edulis*, *Carcinus aestuarii* and *H. leptocerus;* diurnal: *P. xiphias*, *H. inermis*, *Carcinus aestuarii*, *H. leptocerus* and *P. edulis*; and nocturnal: *P. xiphias*, *P.*

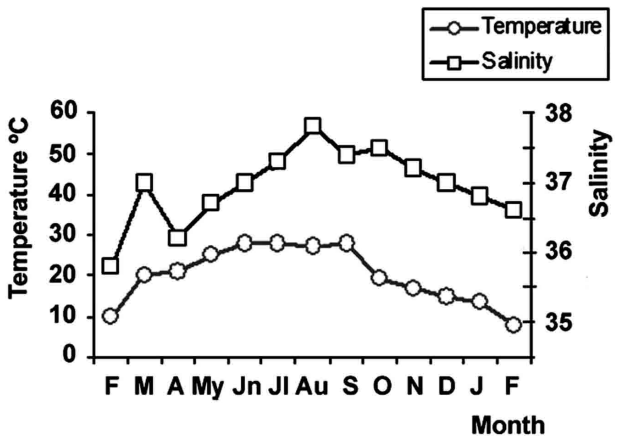


Fig. 2: Monthly evolution of temperature and salinity of surface seawater. February 2009 to February 2010.

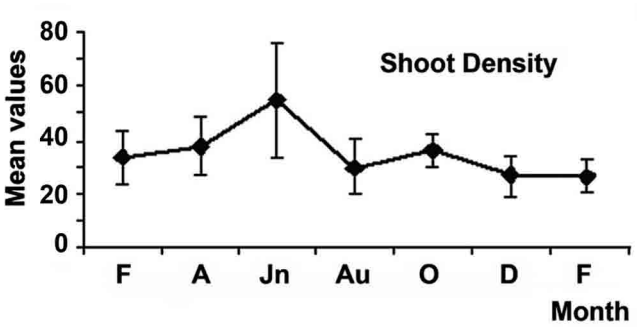


Fig. 3: Bimonthly shoot density, annual evolution of means with standard deviations. February 2009 to February 2010.

Table 1. Total number of specimens (Nt) and dominance (D%) of the species caught during daytime and night-time monthly samples (in all replicates: 39) and frequency of occurrence (F and F%) (replicates not grouped, all considered separately). February 2009 to February 2010.

	Total			Daytime				Night-time			
Species	Nt	Dt%	F%	Nt	D%	F	F%	Nt	D%	F	F%
Palaemon xiphias Risso, 1816	4719	40.34	**100.00**	2601	56.88	39	**100.00**	2118	29.72	39	**100.00**
Hippolyte inermis Leach, 1815	1303	11.14	**83.33**	612	13.38	33	**84.62**	691	9.70	32	**82.05**
Hippolyte leptocerus (Heller, 1863)	652	5.57	**73.08**	431	9.42	31	**79.49**	221	3.10	26	66.67
Processa edulis (Risso, 1816)	2913	24.90	69.23	45	0.98	15	38.46	2868	40.25	39	**100.00**
Carcinus aestuarii Nardo, 1847	335	2.86	64.10	110	2.41	28	71.79	225	3.16	22	56.41
Paguristes syrtensis De Saint Laurent, 1971	342	2.92	52.56	79	1.73	19	48.72	263	3.69	22	56.41
Palaemon serratus (Pennant, 1777)	228	1.95	42.31	148	3.24	17	43.59	80	1.12	16	41.03
Eualus cranchii (Leach, 1817)	163	1.39	38.46	39	0.85	12	30.77	124	1.74	18	46.15
Palaemon adspersus Rathke, 1837	81	0.69	34.62	35	0.77	11	28.21	46	0.65	16	41.03
Processa robusta Nouvel & Holthuis, 1957	105	0.90	33.33	6	0.13	4	10.26	99	1.39	22	56.41
Sicyonia carinata (Brünnich, 1768)	86	0.74	32.05	13	0.28	7	17.95	73	1.02	18	46.15
Palaemon longirostris H. Milne-Edwards, 1837	53	0.45	30.77	24	0.52	12	30.77	29	0.41	12	30.77
Eualus occultus (Lebour, 1936)	124	1.06	28.21	48	1.05	9	23.08	76	1.07	13	33.33
Hippolyte niezabitowskii D'Udekem d'Acoz, 1996	94	0.80	28.21	55	1.20	10	25.64	39	0.55	12	30.77
Palaemon elegans Rathke, 1837	52	0.44	28.21	41	0.90	13	33.33	11	0.15	9	23.08
Pisidia longimana (Risso, 1816)	150	1.28	20.51	141	3.08	8	20.51	9	0.13	8	20.51
Philocheras trispinosus (Hailstone, 1835)	36	0.31	16.67	22	0.48	7	17.95	14	0.20	6	15.38
Calcinus tubularis (Linnaeus, 1767)	19	0.16	16.67	6	0.13	6	15.38	13	0.18	7	17.95
Diogenes pugilator (Roux, 1829)	53	0.45	15.38	40	0.87	8	20.51	13	0.18	4	10.26
Pirimela denticulata (Montagu, 1808)	26	0.22	14.10	7	0.15	6	15.38	19	0.27	5	12.82
Liocarcinus vernalis (Risso, 1827)	25	0.21	14.10	14	0.31	6	15.38	11	0.15	5	12.82
Macropodia rostrata (Linnaeus, 1761)	15	0.13	12.82	6	0.13	4	10.26	9	0.13	6	15.38
Inachus phalangium (Fabricius, 1775)	11	0.09	10.26	3	0.07	2	5.13	8	0.11	6	15.38
Philocheras monacanthus (Holthuis, 1961)	21	0.18	8.97	16	0.35	3	7.69	5	0.07	4	10.26
Macropodia longirostris (Fabricius, 1775)	12	0.10	8.97	1	0.02	1	2.56	11	0.15	6	15.38
Processa elegantula Nouvel & Holthuis, 1957	10	0.09	8.97	3	0.07	2	5.13	7	0.10	5	12.82
Processa acutirostris Nouvel & Holthuis, 1957	7	0.06	7.69	2	0.04	1	2.56	5	0.07	5	12.82
Athanas nitescens (Leach, 1814)	13	0.11	6.41	0	0.00	0	0.00	13	0.18	5	12.82
Clibanarius erythropus (Latreille, 1818)	6	0.05	5.13	1	0.02	1	2.56	5	0.07	3	7.69
Liocarcinus navigator (Herbst, 1794)	6	0.05	5.13	0	0.00	0	0.00	6	0.08	4	10.26
Portunus hastatus (Linnaeus, 1767)	4	0.03	5.13	1	0.02	1	2.56	3	0.04	3	7.69
Brachynotus sexdentatus (Risso, 1827)	11	0.09	3.85	10	0.22	2	5.13	1	0.01	1	2.56
Pilumnus hirtellus (Linnaeus, 1761)	8	0.07	3.85	6	0.13	1	2.56	2	0.03	2	5.13
Pagurus anachoretus Risso, 1827	4	0.03	2.56	0	0.00	0	0.00	4	0.06	2	5.13
Melicertus kerathurus (Forskål, 1775)	2	0.02	2.56	2	0.04	2	5.13	0	0.00	0	0.00
Maja squinado (Herbst, 1788)	2	0.02	2.56	1	0.02	1	2.56	1	0.01	1	2.56
Macropodia czernjawskii (Brandt, 1880)	2	0.02	2.56	1	0.02	1	2.56	1	0.01	1	2.56
Acanthonyx lunulatus (Risso, 1816)	2	0.02	2.56	0	0.00	0	0.00	2	0.03	2	5.13
Alpheus dentipes Guérin-Méneville, 1832	2	0.02	1.28	2	0.04	1	2.56	0	0.00	0	0.00
Philocheras fasciatus (Risso, 1816)	1	0.01	1.28	1	0.02	1	2.56	0	0.00	0	0.00
Trachysalambria palaestinensis (Steinitz, 1932)	1	0.01	1.28	0	0.00	0	0.00	1	0.01	1	2.56
Total number of specimens	11699			4573				7126			
Total species	41			36				38			

edulis, *H. inermis*, *Processa robusta*, *Carcinus aestuarii*, *H. leptocerus* and *Eualus cranchii*).

The evolution of nocturnal and diurnal abundance values (Fig. 5A) follow a similar trend throughout the year, with maximum values in November and October respectively. They are due mainly to the incorporation of specimens of *P. xiphias*, *Hippolyte* species (Fig. 4A, B, C), and *P. edulis* (Fig. 4, D, dominant species in night-time sampling). The mean abundance values (replicates grouped) were: 352.8 (diurnal) and 482.5 (nocturnal).

Monthly mean richness values, with replicates (not grouped and grouped), were respectively: 8.3 - 13.9 (diurnal) and 10.5 - 16.2 (nocturnal). Throughout the year, monthly values of diurnal species richness are quite similar (monthly grouped replicates, Table 2). The evolution of abundance and species richness in nocturnal samples (Figs. 5A, B) fluctuates slightly more, due to increased activity caused partly by the incorporation of specimens and species (Table 1), some originating from neighbouring bottoms (sandy, rocky and seaweeds).

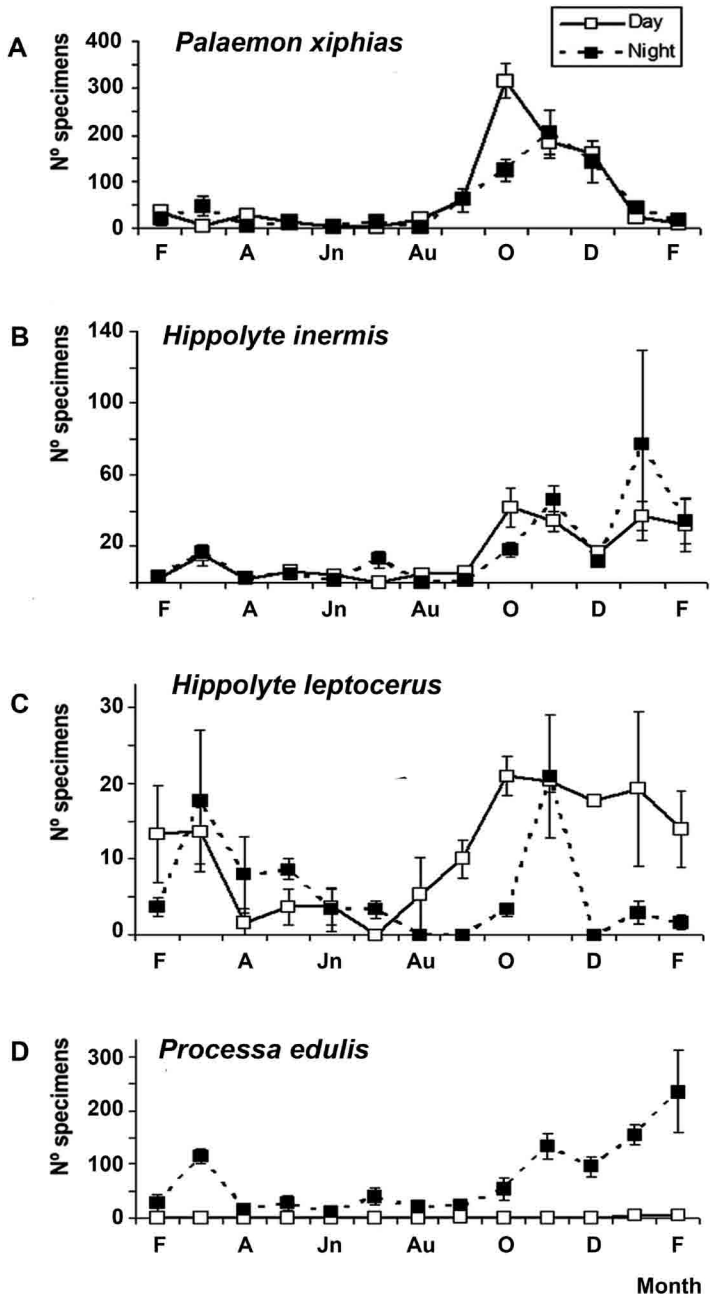


Fig. 4: Monthly evolution of the number of specimens of the species: (A) *Palaemon xiphias*, (B) *Hippolyte inermis*, (C) *Hippolyte leptocerus* and (D) *Processa edulis*, with standard error, in daytime and night-time samples. February 2009 to February 2010. The diurnal results of the July faunal study were lower because of some sampling problems (the same for Figures 5, 7 and 8).

The species with values of relative abundance (dominance) over 1% are shown in Table 1. There are only 9 species in the daytime and 11 in the night-time samples (10 in total). The values provided in Table 2 show the mentioned night effect, with increased richness and abundance, and slightly decreased equitability values: The dominance curves in nocturnal samples are somewhat less geometric than in diurnal ones (Fig. 6).

No significant correlations were found between shoot density and richness (diurnal and nocturnal samples), total abundance (total monthly mean values), and the abundances of dominant species (*P. xiphias* and *H. leptocerus* and *H. inermis*). This could be due to the fact that the greatest shoot density was found in spring (March-June), while maximum abundances of specimens appear at the end and the beginning of the year (October to February). And no significant correlations were found between total abundance and temperature; but significant correlations with a time lag of 3 (Rho = 0.6, $p < 0.03$) and 4 (Rho = 0.76, $p < 0.003$) months exist, which would be related to hatching and larval development periods of dominant species. On the other hand, there are no significant cor-

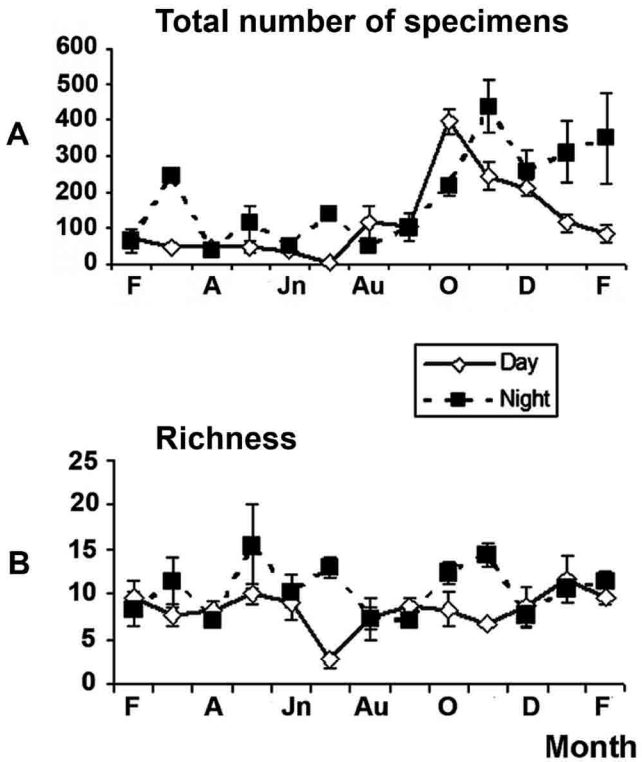


Fig. 5: Daytime and night-time monthly evolution of mean values of (A) the total number of specimens and (B) richness, with standard error, in the *Cymodocea nodosa* meadow. February 2009 to February 2010.

relations between monthly salinity and specific richness (whether diurnal or nocturnal).

Concerning dominant species and total abundance, significant correlations were found between the abundance of *P. edulis* (nocturnal (PEn) and total (day+nigh PEt)), and total abundance of the assemblage (nocturnal (TN) and total (T)) (PEn-TN and PEt-TN, both with $R = 0.964$, $p < 0.0005$; PEn-T and PEt-T, both with $R = 0.786$, $p < 0.036$), but especially at night. These results show the nocturnal dominant behaviour of this species.

On the other hand, significant correlations between the daytime (HId), night-time (HIn) and total (HIt) abundances of *H. inermis* (always linked to leaves stratum), and the total (T), total diurnal (TD), and total nocturnal

Table 2. Monthly values of richness (S), number of specimens (N), Shannon diversity (H' $\log_2$) and evenness indexes (J') obtained with grouped monthly replicates.

	S		N		J'		H'(log2)	
	Day	**Night**	**Day**	**Night**	**Day**	**Night**	**Day**	**Night**
F09	16	13	222	193	0.64	0.60	2.58	2.22
M09	13	20	136	738	0.70	0.61	2.58	2.62
A09	15	12	141	110	0.60	0.67	2.34	2.38
My09	17	24	135	341	0.74	0.77	3.02	3.51
Jn09	15	17	115	146	0.86	0.82	3.35	3.35
Jl09*	6*	15	12*	409	0.75*	0.77	1.95*	3.00
Au09	15	14	350	154	0.72	0.55	2.82	2.09
S09	12	10	312	311	0.57	0.53	2.04	1.76
O09	15	22	1184	645	0.29	0.42	1.12	1.89
N09	10	25	738	1318	0.36	0.46	1.21	2.15
D09	15	12	635	782	0.38	0.42	1.47	1.52
J10	17	14	342	932	0.71	0.54	2.92	2.06
F10	15	13	251	193	0.72	0.60	2.80	2.22

(*) The diurnal results of July were lower because of sampling problems

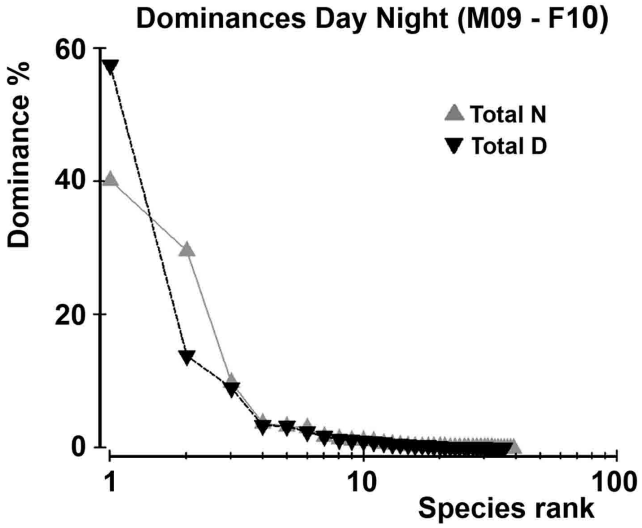


Fig. 6: Annual dominance curves of the decapod assemblage from nocturnal (N) and diurnal (D) sampling (March 2009 to February 2010).

(TN) abundances of the assemblage were also found (HId-T: R = 0.929 $p < 0.003$; HId-TN: R = 0.786 $p < 0.036$; HId-TD: R = 0.786 $p < 0.036$; HIn-TN: R = 0.821 $p < 0.023$; Ht-T: R = 0.786, $p < 0.036$; HIt-TN: R = 0.929, $p < 0.003$). These results show the importance of this species in the meadows.

Conversely, no significant correlations were obtained between the abundances of the dominant species *P. xiphias* (mainly diurnal) and total abundances (whether diurnal, nocturnal and total).

The evolution of nocturnal and diurnal diversity (H') and equitability (J') values (Figs. 7A, B, and Table 2) are quite similar and show a parallel evolution, with peaks at the end of spring and beginning of summer (H' = May-June, J' = June), and minimum values in autumn and early winter (October to December). The latter is especially due to the strong dominance of a few species (Tables 1 and 3). The maximum values of diversity and evenness, when replicates are analyzed independently, were found in May 2009 (H' = 2.467, J' = 0.882, both in the replicate 2). The maximum and minimum values when monthly replicates are pooled are shown in Table 4, and the annual mean values were: H' = 2.32 (day) - 2.37 (night), J' = 0.62 (day) - 0.60 (night).

There are significant differences between diurnal and nocturnal assemblages (all replicas) (global test: $p < 0.001$, R = 0.236; across all seasons groups $p < 0.001$, R = 0.332). The ordination analysis (MDS) (Fig. 8) shows these groups. A total of 23 species contribute to explaining 90.52% of the dissimilarity (SIMPER, dissimilarity average = 58.37%), and only 8 species (Table 3) explain 52.05%. However, when untransformed data are analyzed, to highlight the strong influence of the abundances, the average dissimilarity value increases to 76.92 and only 10 species explain 90.16% of cumulative contribution (indeed *P. xiphias* and *P. edulis* explain 59.87%). This is obvious evidence of the strong dominance of both species in this biotope.

Significant seasonality was also found (yet with low R values), both globally ($p < 0.001$, R = 0.227) and between "pairs" of seasons in the year (p value < 0.001 in all, except in winter and spring: $p < 0.006$). The greatest R value was found between winter and summer (R = 0.343). Average dissimilarity values between seasons (SIMPER) were: W-Sp = 52.15; W-Su = 61.57; W-Au = 50.99; Sp-Su = 62.07; Sp-Au = 55.59 and Au-Su = 60.72.

Discussion

Phenology

The annual trend of shoot density in the studied *Cymodocea nodosa* meadow from Tunisia is similar to that observed in its entire distribution area. Thus, in the Mediterranean Sea, the maximum and minimum values were found in spring-summer and winter respectively (data from Spain: Mateo & García Raso, 2012; Tunisia: present study; Ischia - Tyrrhenian Sea: Cancemi *et al*., 2002; and Greece (leaf biomass): Malea & Zikidou, 2011), and the same happens in the adjacent Atlantic Ocean areas (Canary Islands: Tuya *et al*., 2006) with maximum in May and minimum in December. However, differences in the values were observed in these areas, which are very probably related to changes or differences in the environmental conditions (Buia & Mazzela, 1991; Terrados & Ros, 1992; Cancemi *et al*., 2002).

Crustacean decapod assemblages from Tunisia

The strength of this study and the high richness of this biotope are demonstrated by comparing our data (a single biotope, at about 2 m depth, with 41 species) with other, such as those from the Gulf of Gabes (El Lakhrach *et al*., 2012, all biotopes, between 20 to 260 m depth, with 42 decapod species).

Table 3. SIMPER Similarity Percentages - species contributions. One-Way Analysis. Bray Curtis similarity. Groups daytime & night-time (with transform abundance data√√). Average dissimilarity = 58.37.

Species	Av.Abund	Av.Abund	Av.Diss	Diss./SD	Contrib.%	Cum.%
Processa edulis	0.48	2.65	7.73	2.12	13.25	13.25
Palaemon xiphias	2.36	2.32	3.76	1.22	6.43	19.68
Hippolyte leptocerus	1.47	1.04	3.62	1.17	6.20	25.88
Hippolyte inermis	1.62	1.57	3.60	1.07	6.16	32.04
Paguristes syrtensis	0.64	0.96	3.32	1.06	5.70	37.74
Carcinus aestuarii	0.96	0.85	3.02	1.14	5.18	42.92
Palaemon serratus	0.69	0.57	2.92	0.96	5.00	47.92
Eualus cranchii	0.39	0.67	2.41	1.01	4.13	52.05
...	...	...	...	...	....	....

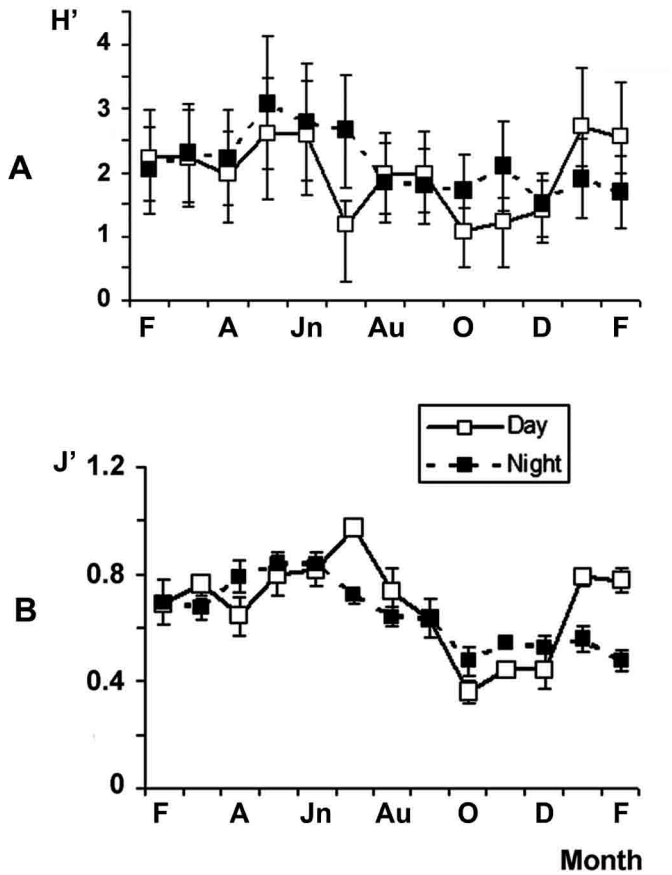


Fig. 7: Daytime and night-time monthly evolution of (A) the diversity (H', Shannon-Wiener) and (B) evenness (J', Pielou index) mean values, with the standard error, of the decapod assemblage in the *Cymodocea nodosa* meadow. February 2009 to February 2010.

In the studied decapod assemblage of *Cymodocea nodosa* from Tunisia, neither the global abundance, nor species richness, nor the abundances of dominant species (*P. xiphias* and *H. leptocerus* and *H. inermis*) showed a significant relationship with plant phenology. This is due to the fact that the greatest shoot density was found in spring (March-June), while maximum specimen abundances appear at the end and the beginning of the year (October to February). Conversely, other studies found a relationship between species abundance and seagrass density (Lewis & Stoner, 1983). In Queensland, Mellors & Marsh (1993) found a correlation between the density of specimens of the Processidae, Palaemonidae and Hippolytidae families and seagrass biotic parameters (analyzing bimonthly samples). Mateo & García Raso (2012) observed a correlation between the shoot density of *Cymodocea* and the decapod assemblage in Malaga (with seasonal samples). Worthington *et al*. (1992) concluded that the density of seagrass shoots explains very little of the large-scale variation observed in the abundances

Table 4. Permanent, common and the most dominant decapod species (day, night, total) in the Mediterranean *Cymodocea* beds (as a whole). These data have been deduced from the main quantitative studies on the subject (Ledoyer, 1966, 1968; Števčić, 1991; García Raso et al., 2006; Mateo & García Raso 2012). (*) the species *H. niezabitowskii* was probably identified as *H. inermis* in some older studies.

Permanent species	**Common species**	**Dominant species**		
Presence >75%	**Presence 75 - >50%**	**Daytime - %**	**Night-time - %**	**Total - %**
H. inermis	*P. edulis*	*P. xiphias* - 30.1	*P. edulis* - 25.8	*P. xiphias* - 21.3
E. cranchii	*L. navigator*	*H. niezabitowskii* - 12.5	*P. xiphias* - 18.4	*P. edulis* - 13.2
H. leptocerus	*S. carinata*	*H. inermis* - 12.4	*H. niezabitowskii* - 10.9	*H. inermis* - 10.4
	P. trispinosus	*H. leptocerus* - 12.3	*H. inermis* - 7.8	*H. niezabitowskii* - 10.4
	P. fasciatus			*H. leptocerus* - 6.2
	C. erythropus			*P. robusta* - 4.2
	M. longirostris			
	M. czernjawskii			
	M. rostrata			
	P. xiphias			
	P. serratus			
	P. adspersus			
	C. tubularis			
	A. nitescens			

of associated fish and decapods, although some species showed significant variations with the density of seagrass shoots in some sampling periods (thus indicating that more individuals were found in denser beds). These different results between areas could be related to the life cycle - recruitment time of the dominant species (which could be different), but also to the sampling methodology. The abundance peaks can be more correctly detected when large sampling areas and monthly samples are studied. Maximum decapod abundance in La Goulette (global and those of the dominant species) was found at the end of the year (October to December), coinciding with the maximum abundance and recruitment period of the dominant species (see López de la Rosa *et al*., 2002; 2006; Manjón-Cabeza *et al*., 2009, for *H. inermis*; see Guerao *et al*., 1994, for *P. xiphias*; see Chessa *et al*., 1989; López de la Rosa *et al*., 2002, for *P. edulis*). Also, the life cycles might be related to water temperature, because this latter is higher 3-4 months before recruitments - maximum abundance values, when spawning and larval development periods happen (significant correlations with a time lag of 3 - 4 months exist). Perhaps these conditions are most favourable for the egg and/or larval development of shallow species. Environmental variables, such as temperature, play important roles in regulating crustacean physiology, including reproduction and de-

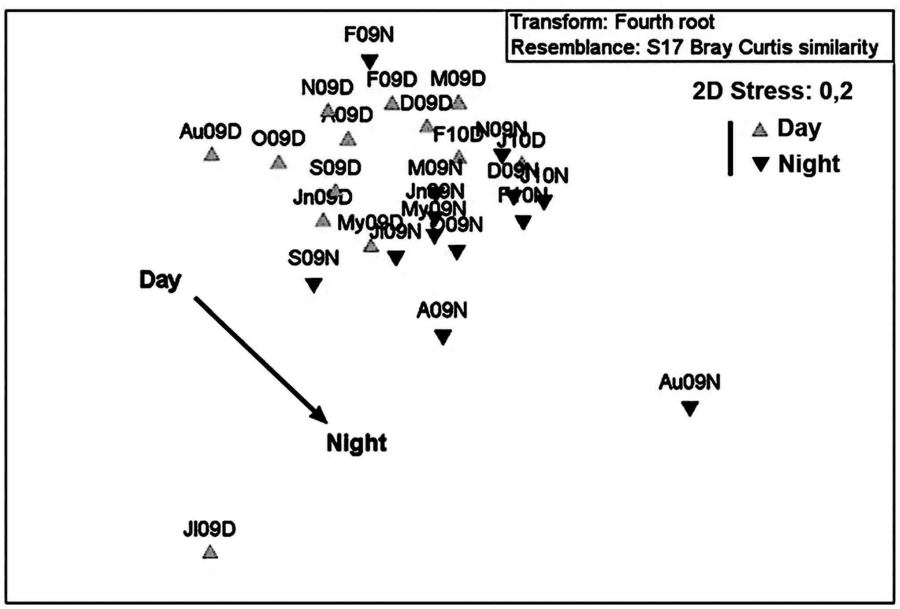


Fig. 8: MDS ordination analysis, with monthly replicates grouped.

velopment (Wear, 1974; Grabe, 2003; Nagaraju, 201Furthermore, there are no significant correlations between species richness (either diurnal or nocturnal) and salinity, at the level described. Although this is a factor in the distribution of some species (e.g. *Palaemon* spp., Guerao *et al*., 1993), it is relatively unimportant in determining the numbers of intertidal-subtidal species (Abele, 1974).

As regards the species, the significant correlations between the daytime, night-time and total abundances of *H. inermis* (always linked to leave stratum), and the total, total diurnal and total nocturnal abundances of the assemblage support the suggestion that this species must be considered as permanent (day and night) and as characteristic in the meadows. On the other hand, day-night and seasonal changes are significant and related to movements and recruitments of dominant species. In the Mollusca taxocoenosis of *Zostera marina* significant day-night changes were found, and related to feeding strategies (with a significant increase of the abundance of scavengers and carnivorous species in nocturnal samples) (Rueda *el al*., 2008). In our study, in nocturnal samples, there is an increase of activity derived from the incorporation of some specimens, some of them coming from neighbouring bottoms (sandy, rocky and seaweeds) and other, such as *Processa* spp., seeking food in the *Cymodocea nodosa* meadow. Species of *Processa* are known to burry in the sediment in day-time and, thus, are not vulnerable to a sampling gear like the Agassiz trawl. Different abundances in day and night catches are the result of vulnerability to the sampling gear used.

Overview of the decapod assemblages of Cymodocea nodosa in the Mediterranean Sea

Data on species composition and richness of decapod crustaceans in *Cymodocea nodosa* beds are found in general studies (Sánchez-Jerez *et al*., 1999; Tuya *et al*., 2001; Albayrak *et al*., 2007; Como *et al*., 2008), but these data are generally poor, because the goals are either too general and/or not specifically targeted to the study of decapod assemblages. The most extensive and/or specific studies on this group show that diurnal assemblage richness ranged between 9 and 32 species (Ledoyer, 1968; Ševčić, 1991; García Raso *et al*., 2006; Mateo & García Raso, 2012) and between 16 and 46 for nocturnal ones (Ledoyer, 1968; García Raso *et al*., 2006). Schaffmeister *et al*. (2006) reported 11 shrimp species in a subtidal mixed habitat (*Cymodocea nodosa* with *Zostera noltii*) in Mauritania. Reed & Manning (2000) studied two beds of *Cymodocea nodosa* in Tunisia (Salammbô & Sidi Bou Said), during an annual cycle, although they reported only 18 decapod species (no separate diurnal and nocturnal data were provided), while in this study (La Goulette, near Salammbô) 41 species were caught, 36 diurnal and 38 nocturnal. These high values are more or less similar to the ones found in the two most exhaustively studied areas in Southern Spain (García Raso *et al*., 2006; Mateo & García Raso, 2012).

Taking into account the above mentioned studies, a total of 90 decapod species have been reported from this biotope in the Mediterranean Sea. Of these species, 81 were caught during daytime sampling but only 14 (17.3%) were present in more than half (62.5%) of the surveyed sites (1 in Tunisia, 3 in Spain, 2 in Croatia and 2 in France). A similar analysis cannot be provided for nocturnal samples, because only 3 sites/countries (1 in Tunisia, La Goulette, 1 in Spain, Almería and 1 in France, Villefranche) provide more or less suitable data, yet with differences in sampling methodology and intensity; therefore, comparison could be considered questionable.

This relatively high global richness is a consequence of the "sink" function of the seagrasses. Many species, both adults and/or juveniles, look for shelter for various reasons: reproduction, nursery area, and predation (usually during night). Thus, for species that inhabit this and adjacent biotopes, and are predators on benthic invertebrates (crustaceans, molluscs, polychaetes, etc), the meadows are an important food resource. This could apply to species belonging to the genera *Processa* and *Palaemon*, such as *Processa edulis*, *Palaemon adspersus* and *P. xiphias* (Zupi & Fresi, 1985; Chessa *et al*., 1989; Guerao, 1994).

Three species of Hippolytidae (*H. inermis, H. leptocerus* and *E. cranchii*) can be considered permanent in the *Cymodocea nodosa* beds of the Mediterranean Sea, with presence values exceeding 75% (diurnal and nocturnal samples, even if the replicates are considered independent samples) (Table 4). The hippolytids are usually associated to seagrasses (linked to leaf stratum) and algae (d'Udekem d'Acoz, 1996), and they are considered "characteristic" of these biotopes (Ledoyer, 1966; 1968; 1969; 1984; Kikuchi & Pérès, 1977; Scipione *et al*., 1996; Mateo & García Raso, 2012). The genus *Hippolyte* is well adapted to the leaves, by shape, colour and behaviour, thus reducing their vulnerability to predation by visual hunters (Main, 1987) and are considered a mesograzer (Douglass *et al*., 2011), feeding on detritus and diatoms (Zupi & Fresi, 1985; Zupo, 2001). *Eualus cranchii* is abundant in shallow habitats (rhizomes of *Posidonia,* rhizomes-associated calcareous concretions, etc) (García Raso, 1990; López de la Rosa & García Raso, 1992) and algae (López de la Rosa *et al*., 2002; 2006). Another 13 species, with presence values ranging between 75 and 50%, can be considered "common" in the Mediterranean area (Table 4); the first five species associated to sediments (*P. edulis, L. navigator, S. carinata, P. trispinosus, P. fasciatus*) (often buried), bare or with seagrasses.

As regards dominance, five species can be considered dominant in the *Cymodocea nodosa* beds of the Mediterranean Sea, with values exceeding 5% of total abundance, but the order changes when only diurnal or nocturnal samples are considered (Table 4). These belong to three shrimp genera: *Hippolyte* (with *H. inermis*, *H. leptocerus* and *H. niezabitowskii*; also *H. holthuisi* in Almería, García Raso *et al.*, 2006), *Palaemon* (with *P. xiphias*, *P. adspersus* and *P. serratus*) and *Processa*, the latter mostly at night

(Ledoyer, 1968; García Raso *et al*., 2006; and this study), with *P. edulis* as the most abundant within this genus.

The different abundances or dominances between sites (as it happens with the genus *Palaemon*) seems to be determined by the environmental characteristics and the biology of the species (feeding strategies - predation, reproduction cycle - recruitments, and ability to adapt to changes) (Forster, 1959; Guerao *et al*., 1994; Guerao, 1995; Guerao & Ribera, 1995; 1996; Felicio *et al*., 2002; Manent & Abella-Gutiérrez, 2006; Bilgin *et al*., 2008). In this way, movements - migrations of *P. adspersus* have been related to water temperature (Hagerman & Østrup, 1980; Bilgin *et al*., 2008) but not always (Bilgin *et al*., 2009). Anthropogenic pressure (Douglass *et al*., 2010), stronger during summer, should not be forgotten either. Furthermore, the location of the meadows (depth, emplacement) and the influence of the different surrounding habitats are important factors in the decapod assemblage structure, and they are responsible for the differences between geographic areas and sites (species composition and dominance). Como *et al*. (2008) confirmed the role played by living seagrasses on the successful colonization of numerous species from different substrates. Also, the layout, organization and influence of the surrounding habitats, could modify patterns through changes in the incorporation of different species, recruitment, predation intensity and mortality (Tuya *et al*., 2010; Mateo & García Raso, 2012). For example, the high abundance of the hermit crab *Clibanarius erythropus* mentioned by Reed & Manning (2000) was most probably due to the existence of pebbles associated or adjacent to the studied shallow meadows, as it happened with the samples from the Punta de Calaburras, in Spain (Málaga) (Mateo & García Raso, 2012).

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