Study of a *Crustacea Decapoda* Taxocoenosis of *Posidonia oceanica* Beds from the Southeast of Spain

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With 8 figures and 3 tables

Abstract. During 1986 and 1987 a decapod crustacean taxocoenosis of *Posidonia oceanica* beds from the southeast of Spain has been studied.

Data on abundance-dominance of the 50 species found and other information such as reproduction and the selective use of gastropod shells by the dominant hermit crabs are given.

Differences in richness and equitability between shallow (3–4 m) and deeper (5–7 m) samples are also shown.

The taxocoenosis presents a geometrical distribution in which only 9 species have a relative abundance higher than 1 % and in which the structure is basically controlled by the two dominant hermit crabs, *Cestopagurus timidus* and *Calcinus tubularis,* and hydrodynamic conditions.

Problem

Infralittoral *Posidonia oceanica* beds represent an important nursery and shelter for many animals and seaweeds, and has been called an "oasis of life" (Boudouresque & Meinesz, 1982). It exhibits a complex biotic community (Pérès & Picard, 1964; Kikuchi & Pérès, 1977), with a high richness, in which many animals spend all or part of their lives. More than 1000 different species have been mentioned in the literature (*e. g.,* Harmelin, 1964; San Martin & Vieitez, 1984, on *Polychaeta;* Bourcier & Willsie, 1986, on *Sipunculida;* Templado, 1984 a, on *Mollusca;* Boero, 1981 a, b, on *Hydroidea;* Benito, 1987; Pansini & Pronzato, 1985, on *Porifera;* Harmelin, 1973, on *Bryozoa;* Bellan-Santini *et al.,* 1986, on *Amphipoda;* Lopez-Ibor *et al.,* 1982, on *Echinodermata;* Bell & Harmelin-Vivien, 1983, on fishes; and Mateu, 1970, on *Foraminifera*).

This community inhabits the two strata of *Posidonia,* the leaves (photophilous) and rhizomes (sciaphilous), in which two different epiphytic associations have been described (Molinier 1959–60; Ben, 1971; and Boudouresque, 1968: *Posidonietum oceanicae* or *Myrionema orbiculare – Giraudia sphacelarioides*

and *Peysonnelia squamaria* or *Udoteo-Peyssonnelietum,* respectively). The animal community here has been subdivided into four or five subunits according to microhabitat structure and mode of life (KIKUCHI & PÉRÈS, 1977; KIKUCHI, 1980). This high animal diversity results in a large number of inter- and intraspecific strategies, which are further governed by intrinsic and extrinsic factors such as light-dark periodicity, seasonal influences, hydrodynamic conditions, depth, and the influence of adjoining biotopes.

Also, *Posidonia* beds are very important in the infralittoral trophic chain, thus forming a key element of the latter (TRAER, 1980; NEDELEC et al., 1981; VERLAQUE, 1981; WITTMANN et al., 1981; CHESSA et al., 1983; ZUPI & FRESI, 1985; BELL & HARMELIN-VIVIEN, 1983).

This brief introduction aims at providing a general view of the importance and complexity of the studied seagrass. Although many published works exist, little is known about the quantitative structure of the faunal community and its temporal evolution. Also, the significance of the species, mainly the dominant ones, to community structure is unknown (as is also the case in other seagrasses such as *Zostera marina,* see THAYER et al., 1984).

Moreover, no specific papers on *Decapoda* exist; the best references are found in general studies (PÉRÈS & PICARD, 1964; LEDOYER, 1966 and 1968, in the foliar stratum; HARMELIN, 1964, in rhizomes; and TEMPLADO, 1984b, in the Spanish littoral).

Material and Methods

1. Study area

The study area is located in southeast Spain off the Genoveses beach in the Nature Park of Cabo de Gata, Almería.

The *Posidonia* bed is small, is located on a soft bottom with few rocks, and is in good condition. Its bathymetric range is between 1 and 10 m.

In comparison with the *Posidonia* beds from Ischia, Gulf of Naples (whose range is from 1 to 30 m and in which four different zones have been defined; SCIPIONE et al., 1983), the studied bathymetric area would correspond to the transition (2–4 m, characterized by a peak richness in groups such as *Isopoda*, LORENTI & FRESI, 1983) and typical (6–12 m) zones of the animal community.

2. Sampling

In 1986 and 1987, bi-monthly samples were always collected at approximately 11:00 a. m., using SCUBA equipment (except under bad weather conditions). The sampling depth during the first year was 3 to 4 m, in the second year 5 to 7 m.

The sample area was always greater than 900 cm^2 (30 × 30 cm) and the rhizome height always about 20 cm. The minimum area suggested by HARMELIN (1964) was somewhat larger, but his sieve mesh was wider (1.8 mm). DE METRIO et al. (1978) established a minimum area of 950 cm^2 for the total benthos, but they did not include crustaceans in the study, employed a different method (involving "aspiration" on leaves), and used a 5 mm mesh (thus loosing some of the smaller specimens and missing many of those hidden in the rhizomes). Other authors used a smaller area (20 × 20 cm) (ERGEN et al., 1988).

The rhizome height in our samples allows the capture of members of the few species that have a vertical distribution, since these are rarely found deeper than 10 cm and most inhabit the first 4 cm (WILLSIE, 1983; HARMELIN, 1964).

The samples (rhizomes with their leaves) were pulled out and immediately placed *(in situ)* in plastic bags by two divers. Thus, only the most rapidly swimming species which hide among the leaves, do not utilize the rhizomes as a refuge, and have a small population density could escape. To verify this a different sampling method was used: a 30 cm net (2 mm mesh) provided with a closing mechanism was dragged across the leaves in an adjoining 12 m² area for 10–15 min.

In the laboratory the leaves and rhizomes of each sample were separated and washed using a three sieve column (smallest mesh 0.5 mm). This method retained even postlarvae or megalopes, which were not included in the study but provided information on recruitment times.

After separating the fauna, the leaves and rhizomes were dried at 105 °C for 48 h. These dry weights served as a quantifying basis for the faunistic data.

In the numerical analysis the absolute and relative abundances of all species from all samples were calculated. For purposes of comparison, the absolute abundances of the dominant species were referred to 1000 g dry weight of the sample.

Diversity, using the SHANNON-WEAVER index, the equitability, and the dominance-diversity curves (GARCÍA-RASO & FERNANDEZ, 1987; GARCÍA-RASO, 1988) were also calculated. Finally, in order to detect the similarity between samples from quantitative data, an analysis of principal coordinates (Q mode) was carried out.

Results

Taking constant rhizome height into account enables clear presentation of the relation between rhizome and leaf weight (Fig. 1); this represents the variation tendency in the foliar area over the study period. This evolution is of great interest since it governs epiphyte biomass during the cycle. Ephiphyte biomass in turn represents an important "step" in the trophic network of the system.

The minimum is apparent at the beginning of winter and the maximum in summer. However, the maximum foliar area is less marked in the shallower samples than in the deepest ones; these were found in May and August, respectively. Moreover, the foliar area shows a clear drop in shallower waters in summer and autumn when winds do the greatest damage to the studied area (pers. observ.).
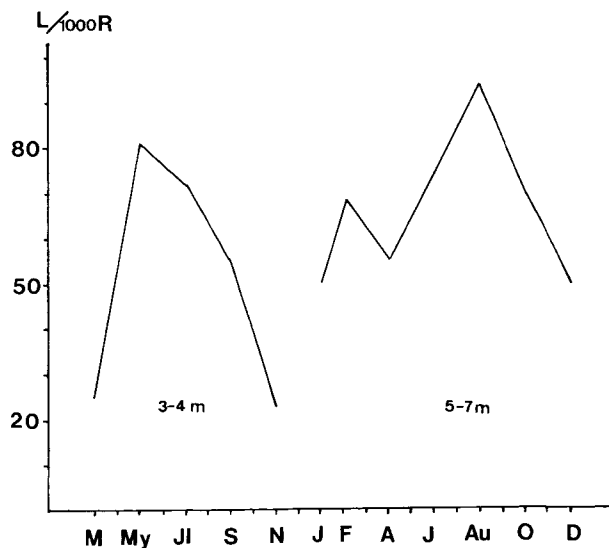

Fig. 1. Evolution of leaf dry weight/1000 g rhizomes, at 3–4 m (1986) and 5–7 m (1987) in the studied area.
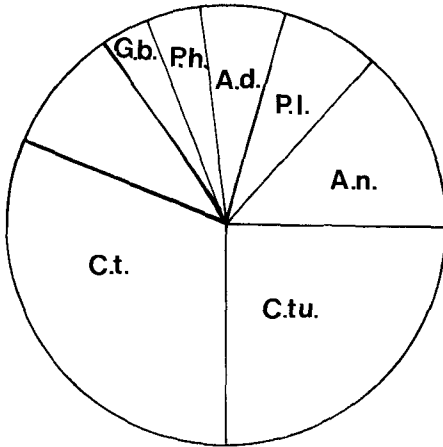
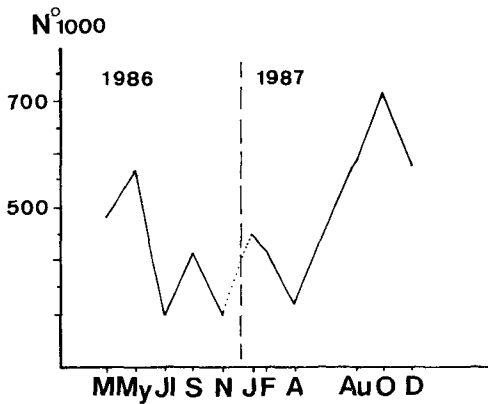Fig. 2. Abundance of the seven most dominant species.

Fig. 3. Evolution of the general abundance of decapods during 1986 (at 3–4 m) and 1987 (at 5–7 m), referred to 1000 g dry weight of sample (leaves and rhizomes).

1. Faunistic results

The monthly and annual faunistic information obtained and the relative and absolute abundance of the different species during the study period (1986–1987) is shown in Tables 1 and 2.

a. Composition, abundance, and dominance

A total of 6585 specimens belonging to 50 species were captured.

In spite of the high richness, the decapod taxocoenosis is dominated by few species. Only 9 have a relative abundance higher than 1 % and represent 95.4 % of the total individual numbers (Table 3). These are: *Cestopagurus timidus* (31. 6 %), *Calcinus tubularis* (25.3 %), *Athanas nitescens* (13.6 %), *Pisidia longicornis* (7.4 %), *Alpheus dentipes* (6.0 %), *Pilumnus hirtellus* (4.1 %), *Galathea bolivari* (3.9 %), *Thoralus cranchii* (2.5 %), and *Pilumnus villosissimus* (1.0 %).

Table 1. Faunistic survey of 1986. Absolute and relative abundances are given for each species and studied month. Asterisks denote the presence of ovigerous females. Total abundance is indicated in the right margin. At the bottom, volumes (rhizome and leaf dry weight) for each sample in grams, the absolute abundance total (No.), the amount referred to 1000 g of dry weight, richness (S), the diversity index (H'), and equitability (J') are given.

In the first month of study two samples were taken, one at 9 m and the normal one at 3–4 m.

1986	day/month	9 m 26/3	3–4 m 26/3	23/5	21/7	17/9	13/11	Total 3–4 m
2	*Processa macrophthalma*	–	–	1 0.2	–	3 0.6	–	4 0.20
5	*Hippolyte longirostris*	–	–	1 0.2	–	–	–	1 0.05
6	*Thoralus cranchii*	3* 0.3	11 2.4	18* 4.2	17 6.2	17* 3.4	1 0.3	64 3.25
7	*Eualus occultus*	–	5 1.1	–	2* 0.2	–	–	7 0.36
8	*Lysmata seticaudata*	3 0.3	1 0.2	4 0.9	1 0.1	8 1.6	–	14 0.71
9	*Gnathophyllum elegans*	1 0.1	–	1 0.2	–	–	3 1.0	4 0.20
10	*Brachycarpus biunguiculatus*	–	–	1 0.2	–	1 0.2	–	2 0.10
12	*Athanas nitescens*	86 9.3	13 2.8	24* 5.6	23 8.3	52* 10.3	76 24.7	188 9.54
13	*Alpheus macrocheles*	1 0.1	–	2* 0.5	1 0.1	2 0.4	5 1.6	10 0.51
14	*A. dentipes*	54* 5.9	24* 5.3	10* 2.3	35* 12.7	52* 10.3	23* 7.5	144 7.31
15	*Synalpheus hululensis*	–	5* 1.1	–	–	–	–	5 0.25
16	*S. gambarelloides*	–	2 0.4	–	–	–	–	2 0.10
19	*Galathea squamifera*	–	–	–	–	1 0.2	–	1 0.05
20	*G. bolivari*	35* 3.8	15* 3.3	11* 2.6	13* 4.7	15* 3.0	11 3.6	65 3.30
21	*Porcellana platycheles*	–	15* 3.3	–	–	–	–	15 0.76
22	*Pisidia longicornis*	49* 5.3	23* 5.0	23* 5.4	19 6.9	30 6.0	24 7.8	119 6.04
23	*Pagurus anachoretus*	5 0.5	1 0.2	3 0.7	1 0.1	2 0.4	1 0.3	8 0.41
24	*Cestopagurus timidus*	172* 18.7	198* 43.3	164* 38.5	112* 40.6	218* 43.3	78* 25.3	770 39.09
25	*Calcinus tubularis*	453 49.2	104 22.8	146 34.3	43* 15.6	60 11.9	51 16.6	404 20.51
26	*Upogebia deltaura*	–	–	–	–	–	2 0.6	2 0.10
27	*Dromia personata*	–	1 0.2	–	–	–	–	1 0.05
29	*Ebalia edwardsi*	–	–	–	1 0.1	–	–	1 0.05
31	*Sirpus zariquieyi*	–	2* 0.4	–	1 0.1	1 0.2	2 0.6	6 0.30
32	*Xantho incisus*	4 0.4	–	1 0.2	–	–	–	1 0.05
35	*Pilumnus hirtellus*	35 3.8	21 4.6	8* 1.9	3* 1.1	13* 2.6	23 7.5	68 3.45
36	*P. villosissimus*	5 0.5	8 1.8	–	1 0.1	19 3.8	4 1.3	32 1.62
37	*Paractaea monodi*	–	–	1 0.2	–	–	–	1 0.05
38	*Herbstia condyliata*	2 0.2	6 1.3	1 0.2	–	4 0.8	1 0.3	12 0.61
39	*Eurynome spinosa*	–	–	–	–	–	1 0.3	1 0.05
40	*Acanthonyx lunulatus*	–	2 0.4	4 0.9	1 0.1	2 0.4	–	9 0.46
41	*Pisa nodipes*	–	–	–	1 0.1	1 0.2	–	2 0.10
42	*P. tetraodon*	–	–	–	1 0.1	–	–	1 0.05
46	*Achaeus cranchii*	9* 1.0	–	–	–	1 0.2	2 0.6	3 0.15
47	*Maja crispata*	–	–	–	–	1 0.2	–	1 0.05
48	*Inachus phalangium*	–	–	1* 0.2	–	–	–	1 0.05
49	*Macrocopia czerniavskii*	3 0.3	–	–	–	–	–	–
50	*M. longirostris*	–	–	1 0.2	–	–	–	1 0.05
	Total dry weight *Posidonia* (g)	1102.3	949.7	753.8	925.6	1223.8	1051.6	4904.5
	N total	920	457	426	276	503	308	1970
	N in 1000 g	835	481	565	298	411	293	402
	Richness (S)	17	19	21	18	21	17	36
	Diversity (H')	2.40	2.74	2.48	2.73	2.84	2.94	
	Equitability (J')	0.59	0.65	0.56	0.65	0.65	0.72	

Table 2. Faunistic survey of 1987. For explanations see Table 1.

1987 day/month	8/1		5/2		10/4		5-7 m 25/8		7/10		15/12		Total 3-4 m	
1 *Processa edulis*	–		–		1	0.2	–		–		–		1	0.03
3 *P. nouveli*	–		–		1	0.2	–		–		–		1	0.03
4 *Hippolyte inermis*	–		–		–		–		1	0.1	–		1	0.03
5 *H. longirostris*	–		1	0.2	–		–		–		–		1	0.03
6 *Thoralus cranchii*	12	1.6	23	4.0	24*	5.6	21*	3.8	–		18	2.6	98	2.65
7 *Eualus occultus*	1	0.1	–		–		–		–		–		1	0.03
8 *Lysmata seticaudata*	2	0.3	–		1	0.2	4	0.7	1	0.1	2	0.3	10	0.27
9 *Gnathophyllum elegans*	–		2	0.4	–		–		1	0.1	–		3	0.08
10 *Brachycarpus biunguiculatus*	2	0.3	1	0.2	1	0.2	–		–		–		4	0.11
11 *Typton spongicola*	–		1	0.2	–		–		–		–		1	0.03
12 *Athanas nitescens*	191	26.2	106	18.6	65*	15.0	75*	13.6	64*	8.9	118	17.0	619	16.75
13 *Alpheus macrocheles*	7	1.0	6	1.1	–		1	0.2	3*	0.4	9	1.3	26	0.70
14 *A. dentipes*	25*	3.4	29*	5.1	30*	6.9	37*	6.7	28*	3.9	46	6.6	195	5.28
17 *Pontonia pinnophylax*	–		–		–		–		1	0.1	–		1	0.03
18 *Scyllarus pygmaeus*	–		1	0.2	–		1	0.2	1	0.1	–		2	0.05
19 *Galathea squamifera*	1	0.1	2	0.4	–		1	0.2	8	1.1	1	0.1	13	0.35
20 *G. bolivari*	18	2.5	15*	2.6	31*	7.2	48*	8.7	15*	2.1	30	4.3	157	4.25
22 *Pisidia longicornis*	34	4.7	45	7.9	47*	10.9	54*	9.8	84*	11.7	53	7.6	317	8.58
23 *Pagurus anachoretus*	9	1.2	3	0.5	3	0.7	–		5*	0.7	7	1.0	27	0.73
24 *Cestopagurus timidus*	215	29.5	214*	37.6	115*	26.6	154*	27.8	256*	35.6	188	27.1	1142	30.91
25 *Calcinus tubularis*	155	21.3	83	14.6	79	18.3	134*	24.2	199*	27.7	161	23.2	811	21.95
26 *Upogebia deltaura*	1	0.1	–		–		–		–		–		1	0.03
27 *Dromia personata*	–		1	0.2	–		–		1	0.1	–		2	0.05
28 *Ebalia deshayesi*	1	0.1	1	0.2	–		–		–		–		2	0.05
29 *E. edwardsi*	–		–		–		–		1	0.1	–		1	0.03
30 *Ilia nucleus*	–		1r	0.2	–		–		1r	0.1	–		2	0.05
31 *Sirpus zariquieyi*	1	0.1	–		–		–		–		–		1	0.03
32 *Xantho incisus*	–		1	0.2	–		–		1	0.1	4	0.6	6	0.16
33 *X. pilipes*	–		–		1	0.2	–		–		–		1	0.03
34 *Pinnotheres pisum*	–		–		–		–		1*	0.1	–		1	0.03
35 *Pilumnus hirtellus*	43	5.9	28	4.9	22	5.1	18*	3.2	30*	4.2	25	3.6	166	4.49
36 *P. villosissimus*	2	0.3	1	0.2	7	1.6	4	0.7	4	0.6	11	1.6	29	0.78
37 *Paractaea monodi*	1	0.1	2	0.4	–		–		–		–		3	0.08
38 *Herbstia condyliata*	–		–		1	0.2	–		4	0.6	–		5	0.14
40 *Acanthonyx lunulatus*	1	0.1	–		1	0.2	–		3	0.4	–		5	0.14
41 *Pisa nodipes*	–		–		–		–		–		1	0.1	1	0.03
42 *P. tetraodon*	–		–		–		1	0.2	–		1	0.1	2	0.05
43 *P. cf. carinimama*	3	0.4	–		–		–		1	0.1	–		4	0.11
44 *P. muscosa*	–		–		–		–		–		1	0.1	1	0.03
45 *Achaeus gracilis*	–		2	0.4	2	0.5	–		1*	0.1	1	0.1	6	0.16
46 *A. cranchii*	4	0.5	–		–		1	0.2	4*	0.6	16	2.3	25	0.68
Total dry weight *Posidonia* (g)	1643.6		1371.9		1372.7		953.3		1013.6		1204.3		7559.3	
N total	729		569		432		553		719		693		3695	
N in 1000 g	444		415		315		580		709		575		489	
Richness (S)	22		23		18		14		26		19		41	
Diversity (H')	2.72		2.80		3.03		2.80		2.68		2.99			
Equitability (J')	0.61		0.62		0.73		0.74		0.57		0.70			

Table 3. General composition of the *Posidonia – Decapoda* community. Absolute and relative abundances of all species in the samples.

		N°	%			N°	%
1	*Processa edulis* (Risso, 1816)	1	0.02	2	*P. macrophthalma* Nouvel & Holthuis, 1957	4	0.06
3	*P. nouveli* Al-Adhub & Williamson, 1975	1	0.02	4	*Hippolyte inermis* Leach, 1815	1	0.02
5	*H. longirostris* (Czerniavsky, 1868)	2	0.03	6	*Thoralus cranchii* (Leach, 1817)	165	2.5
7	*Eualus occultus* (Lebour, 1936)	8	0.1	8	*Lysmata seticaudata* (Risso, 1816)	27	0.4
9	*Gnathophyllum elegans* (Risso, 1816)	8	0.1	10	*Brachycarpus biunguiculatus* (Lucas, 1846)	6	0.09
11	*Typton spongicola* Costa, 1844	1	0.02	12	*Athanas nitescens* (Leach, 1814)	893	13.6
13	*Alpheus macrocheles* (Halistone, 1835)	37	0.6	14	*A. dentipes* Guérin, 1832	393	6.0
15	*Synalpheus hululensis* Coutière, 1908	5	0.07	16	*S. gambarelloides* (Nardo, 1847)	2	0.03
17	*Pontonia pinnophylax* (Otto, 1821)	1	0.02	18	*Scyllarus pygmaeus* (Bate, 1888)	2	0.03
26	*Upogebia deltaura* (Leach, 1815)	3	0.05	19	*Galathea squamifera* Leach, 1814	14	0.2
20	*G. bolivari* Zariquiey A., 1950	257	3.9	21	*Porcellana platycheles* (Pennant, 1777)	15	0.2
22	*Pisidia longicornis* (Linnaeus, 1767)	485	7.4	23	*Pagurus anachoretus* Risso, 1827	40	0.6
24	*Cestopagurus timidus* (Roux, 1830)	2084	31.6	25	*Calcinus tubularis* (Linnaeus, 1767)	1668	25.3
27	*Dromia personata* (Linnaeus, 1758)	3	0.05	28	*Ebalia deshayesi* Lucas, 1846	2	0.03
29	*E. edwardsi* Costa, 1838	2	0.03	30	*Ilia nucleus* (Linnaeus, 1758)	2	0.03
31	*Sirpus zariquieyi* Gordon, 1953	7	0.1	32	*Xantho incisus* (Leach, 1814)	11	0.2
33	*X. pilipes* A. Milne Edwards, 1867	1	0.02	34	*Pinnotheres pisum* (Linnaeus, 1767)	1	0.02
35	*Pilumnus hirtellus* (Linnaeus, 1761)	269	4.1	36	*P. villosissimus* (Rafinesque, 1814)	66	1.0
37	*Paractaea monodi* Guinot, 1969	4	0.06	38	*Herbstia condyliata* (Fabricius, 1787)	19	0.3
39	*Eurynome spinosa* Hailstone, 1835	1	0.02	40	*Acanthonyx lunulatus* (Risso, 1816)	14	0.2
41	*Pisa nodipes* (Leach, 1815)	3	0.05	42	*P. tetraodon* (Pennant, 1777)	3	0.05
43	*P. cf. carinimana* Miers, 1879	4	0.06	44	*P. muscosa* (Linnaeus, 1758)	1	0.02
45	*Achaeus gracilis* (Costa, 1839)	6	0.09	46	*A. cranchii* Leach, 1817	37	0.6
47	*Maja crispata* Risso, 1827	1	0.02	48	*Inachus phalangium* (Fabricius, 1775)	1	0.02
49	*Macrocopia czerniavskii* (Brandt, 1880)	3	0.05	50	*M. longirostris* (Fabricius, 1775)	1	0.02

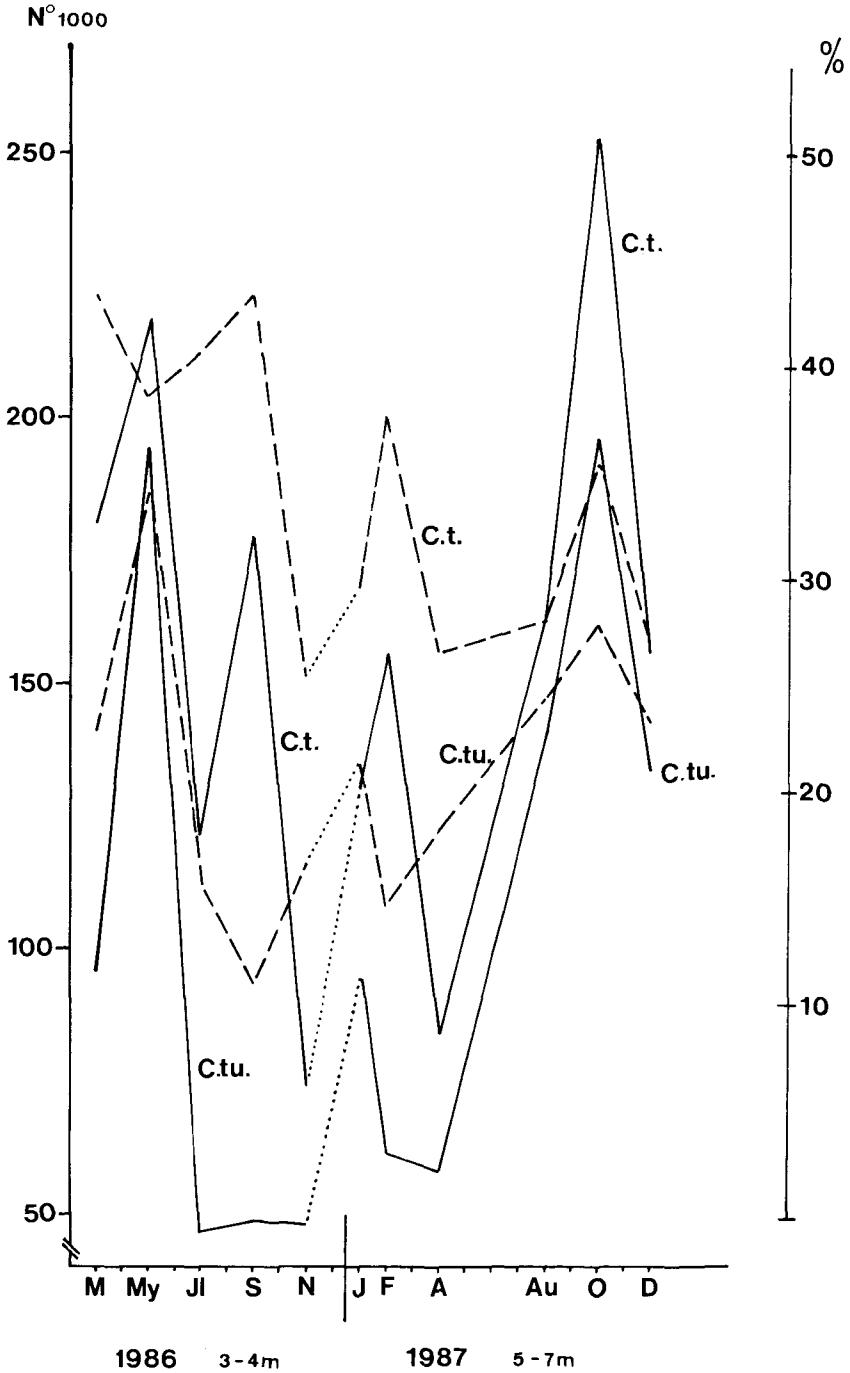Total: Caridea + Palinuridea 23.6%   Anomura + Thalassinidea 69.3%   Brachyura 7.0%

Fig. 4. Evolution of abundance of the two dominant hermit crabs, *Cestopagurus timidus* (C. t.) and *Calcinus tubularis* (C. tu.). Continuous lines: absolute abundances (referred to 1000 g dry weight of sample); broken lines: relative abundances.

Of these, only the first 7 (Fig. 2) are present in all the samples; the last two species, together with *Pagurus anachoretus,* are absent in one sample.

The hermit crabs *Cestopagurus timidus* and *Calcinus tubularis* clearly dominate (Fig. 2, Tables 1, 2). Thus, the variations in their abundances (Fig. 4) determine variation of the entire taxocoenosis (Fig. 3).

The absolute abundances of both species follow the same pattern, except for shallower samples during the minimum foliar period (summer and autumn), in which an apparently closer relationship between *C. tubularis* and dry weight of leaf exists. However, the correlation between both is low (0.46) and not significant.

C. timidus is slightly more dominant on shallow bottoms, while *C. tubularis* increases in abundance with depth, where the hydrodynamism is less pronounced. This is most obvious in the two March 1986 samples, which were taken near the minimum (3 m) and maximum depth (9 m) of the meadow; it is somewhat less clear in the overall two year study since the difference in depth (3–4 m and 5–7 m, respectively) was less.

With respect to other species represented in all samples and having a relative abundance higher than 5 %:

A. nitescens (together with *C. tubularis*) seems to prefer less hydrodynamic bottoms. Nevertheless, this species increases in number in autumn (more obvious at 3–4 m) and winter (especially at 5–7 m) after the reproductive period. This coincides with the data obtained from calcareous bottoms (GARCÍA-RASO & FERNANDEZ, 1987). The number of *P. longicornis* specimens increases in summer and autumn and is slightly higher at 5–7 m (for taxonomic considerations see GARCÍA-RASO, 1987). *A. dentipes* has a somewhat lower relative abundance than on shallow calcareous bottoms.

b. Reproduction

In the more abundant species such as *C. timidus, A. dentipes,* and *G. bolivari,* ovigerous females are present nearly throughout the year. However, they seem to be lacking or are reduced in number at the end and at the beginning of each year; this is more pronounced in *A. nitescens* (April–October) and even more so in *C. tubularis* (from July to October).

On the other hand, the greater abundance of minute specimens, in certain months, allows us to detect maximum recruitment of the different species. For *C. timidus* this appears to be September and for *G. bolivari* July–August. With regard to species with lower population densities, very small specimens of *Sirpus zariquieyi* and *Acanthonyx lunulatus* appear in July, while *Achaeus cranchii* appears in December and *Paractaea monodi* in January–February (the carapace areas were not well defined in the smallest).

As is the case for the seaweed *M. lichenoides* in shallow calcareous bottoms, the studied *Posidonia* bed is a habitat essentially functioning as a nursery and for early development (GARCÍA-RASO, 1988). The vast majority of decapods are thus young or small specimens.

c. Other biological data

On the use of gastropod shells by hermit crabs: The dominant species, *C. timidus*, chooses medium-sized *Bittium* shells, mainly *B. reticulatum* (DA COSTA, 1778). Living *B. reticulatum* are fairly scarce in the studied samples. For this reason, either horizontal or vertical movement in search of suitable shells is probable. ZUPI *et al.* (1985) conclude that vertical migration takes place. However, *B. reticulatum* has a wide bathymetric range and inhabits various biotopes, preferably *Cymodocea* (TEMPLADO, 1982) and calcareous bottoms (HERGUETA, pers. comm.).

C. tubularis, like *C. timidus*, seems to prefer shells of *Bittium* and *Hinia;* however, it appears to be less selective because it also frequently occupies other shells. Two interesting examples are *Columbella rustica* (whose interior can be shared with living specimens of *Crepidula*) and *Vermetus* sp. (two specimens with hermit crab occupants); neither were ever occupied in the study area by *C. timidus*.

With regard to parasitism, rhizocephalans and bopyrids were rare. Bopyrids infested only 3 species: *G. bolivari* (7 specimens: March 1986, January 1987, April 1987, and August 1987), *P. longicornis* (1 specimen from August 1987), and *H. longirostris* (1 specimen). Rhizocephalans parasitized 3 specimens of *C. timidus*.

2. Taxocoenosis structure

Diversity ranged from 2.40 to 3.03, depending more on equitability than on richness (Tables 1, 2 and Fig. 5). In fact, the hermit crabs' maximum (representing 56.9%) coincides with minimum diversity and equitability.

Richness varied from 17 to 26, being higher than on calcareous bottoms (GARCÍA-RASO & FERNANDEZ, 1987; GARCÍA-RASO, 1988) with a similar taxacoenosis. Richness and equitability are higher and fluctuate more at 5–7 m.

The dominance-diversity curves (Fig. 6a, b) are more or less similar to the coralligenous curves (GARCÍA-RASO, 1988), although perhaps somewhat less geometrical.

Similarity between samples. Samples could be arranged into four groups (Fig. 7). These are related to variations both in diversity and in equitability (see Fig. 5 and Tables 1 and 2), which, as has been shown, largely depend on the abundances or the recruitment of the dominant species. Therefore, the first "quadrant" includes the two months (group A) of maximum recruitment of the two dominant hermit crabs of both studied cycles (Fig. 4), which present the minimum diversity and equitability (Fig. 5). The opposite "quadrant" contains group B – the months of both years which have the opposite characteristics (maximum equitability and diversity), *i. e.*, minima or average abundances in both dominant species. Groups C and D show middle values. Nevertheless, C shares (together with A) the positive side of the "axis", since this group contains the months having a maximum abundance of one of the two dominant hermit crab species and of *A. nitescens* (the third dominant species).

If the same analysis is carried out for the 7 dominant species alone (Fig. 8) –
the ones controlling the system – and the samples are studied seasonally, a clear
seasonality is evident in 1986. This is less obvious in 1987. This seasonality
mainly pertains to the set of shallower samples in which the external ambient
variations and especially hydrodynamism have a greater influence. This influence
is higher in summer and autumn and appears to affect the shallower leaves
(Fig. 1) and *C. tubularis* abundance (Fig. 4).
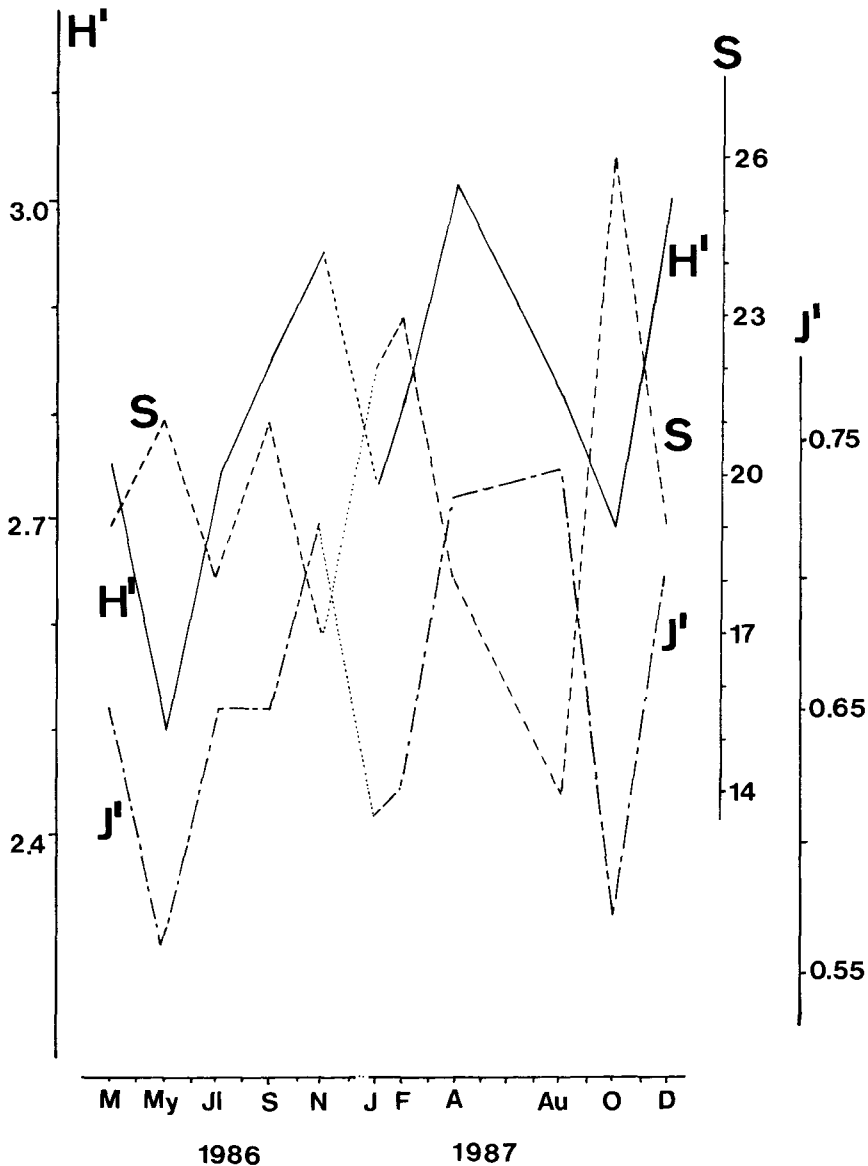
Fig. 5. Evolution of diversity (H′), equitability (J′), and richness (S) during the studied years.
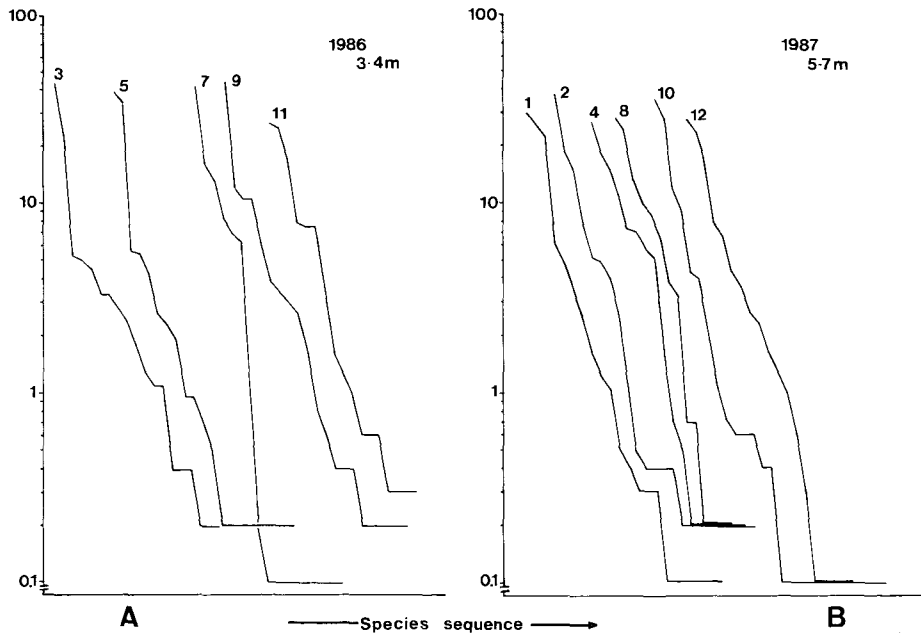
Fig. 6. Monthly dominance-diversity curves during: A. 1986 at 3–4 m, and B. 1987 at 5–7 m (1: January, ..., 12: December).

Discussion

The comparison of our foliar area data with those obtained from other *Posidonia* studies (Romero, 1985), shows coinciding tendencies.

The differences found between the two cycles are probably due, at least in part, to depth, since in the most superficial area, hydrodynamism can affect leaf development or increase leaf loss. In fact our observations indicate that strong Levante winds do the most harm in the area in summer and autumn.

Faunistically, our sample data differed from those reported in other studies (Harmelin, 1964; Ledoyer, 1966; Carbonell, 1984; Templado, 1984 b) in that:

1. Our samples were characterized by greater specific richness and abundance. This, we believe, is due to (a) the investigations covering annual cycles, (b) the method of sampling, and (c) the use of a fine mesh in the separation of specimens in the laboratory. This approach enabled us to capture all the species that spend all or part of their lives in the rhizomes, and to retain the majority (if not all) of the specimens in the samples. Thus, while densities of 500–700 indivs. · m^{-2} have been reported (Kikuchi, 1980) for the rhizome layer of *Posidonia oceanica* from the Gulf of Naples, our samples contained up to more than 900 indivs. · 0.09 m^{2}.

2. The decapod species considered to be characteristic of *Posidonia*, i. e., those able to rest on leaves such as *Hippolyte inermis* and *H. longirostris*, have little quantitative importance in the overall decapod community in the meadow
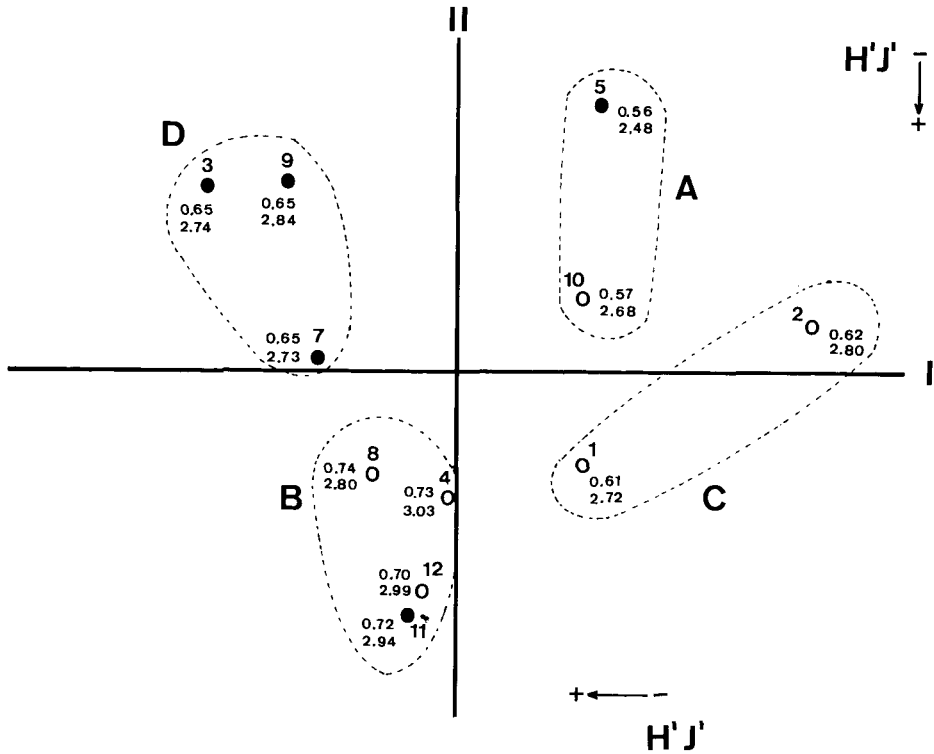
Fig. 7. Similarity between monthly samples (1: January, ..., 12: December; black circles: 1986, white circles: 1987). Analysis of principal coordinates (Q mode). Percentage residual 68.8.

and are restricted to the foliar stratum. In fact, the number of specimens captured in 12 m^2 (using a net, at a depth of 6–9 m), was: 16 specimens of *H. inermis* and 1 of *H. longirostris*. In comparison, a much smaller sample (0.09 m^2) may contain more than 400 hermit crabs.

The same holds true for other Natantia belonging to genera *Palaemon* and *Processa*, although their abundances are even lower (see Tables) and no specimens were caught on the leaves during the day. Other studies show that the latter are only found, or are found at least in greater numbers, at night (LEDOYER, 1966; KIKUCHI, 1980) (day-night differences are also known in other groups, TEMPLADO, 1982; RUSSO *et al.*, 1983). These natantians must originate either from (a) deeper bottoms, which we have not studied, or (b) adjacent habitats (as demonstrated for other groups, SPADA, 1971; PEREIRA, 1981). The above species would thus use the meadow as a hunting or feeding ground in their phase of nocturnal activity (CHESSA *et al.*, 1985; ZUPI & FRESI, 1985).

The taxocoenosis of the studied *Posidonia* beds and that of the seaweed *M. lichenoides* (ELLIS & SOL.) LEMOINE (GARCÍA-RASO & FERNANDEZ, 1987; GARCÍA-RASO, 1988) are qualitatively very similar. The dominant species are the same; only the order of dominance changes, the dominant species being the two hermit crabs *C. timidus* and *C. tubularis*.

In comparison with calcareous bottoms, the higher richness in *Posidonia* is perhaps not surprising: it is a much more open system, with less limitations (space, food resources), and in which at least two different strata (leaves and rhizomes) can be defined.

The superficial calcareous bottoms cited above have more limitations and are more uniform. This results in higher competitive pressure for the resources in general and subsequently a repartition of these (more obvious in the samples from Málaga; GARCÍA-RASO & FERNANDEZ, 1987). Thus, the dominant species that spend their lives in this biotope show different morphologies and adaptations; a synchronization probably exists. More or less the same happens between the dominant species in the studied *Posidonia* meadows, only the two abundant hermit crabs being anatomically similar. Perhaps they utilize different
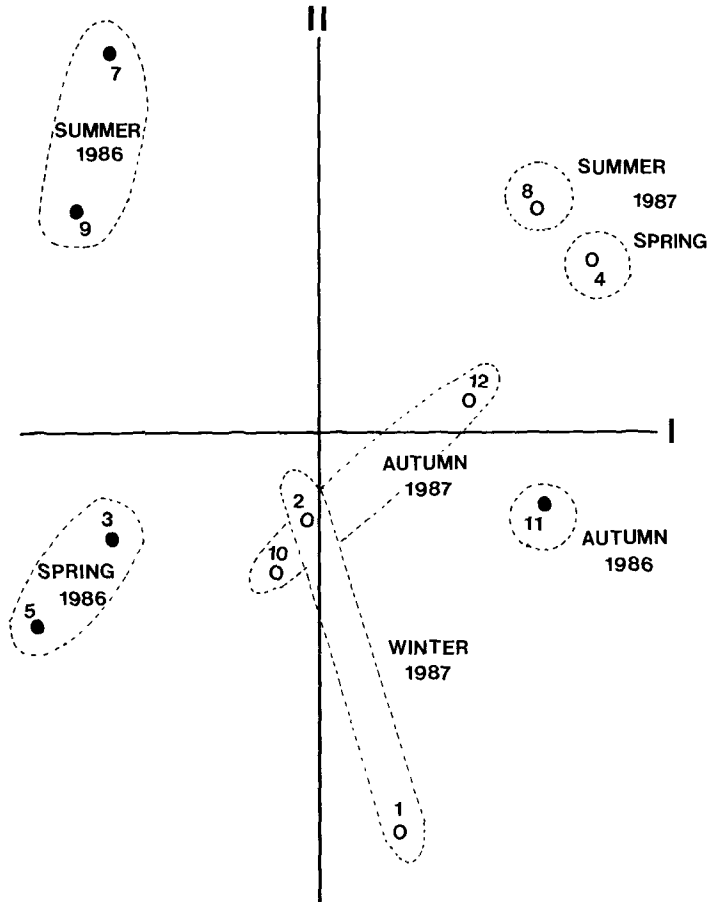

Fig. 8. Similarity between monthly samples (1: January, ..., 12: December; black circles: 1986, white circles: 1987). Analysis of principal coordinates (Q mode) with the seven dominant species (percentage residual 52.1). The different seasons in both years are indicated.

resources or occupy different "niches". So, when the MacArthur broken stick model (MacArthur, 1957; Colinvaux, 1973) is applied to the dominant species, and the distances that separate the monthly samples of stable equilibrium (the differences between the chi square and the obtained values) are correlated against species abundance, the higher value (r = 0.6) is found in a dominant hermit crab, *C. tubularis*.

This species prefers deeper bottoms (Table 1: March samples at 3 and 9 m; and Tables 1 and 2: total abundances) and seems to have a closer relationship with the foliar surface. However, the decrease of both *C. tubularis* (Fig. 4) and the foliar area (Fig. 1) may be completely or partly independant of each other; both may be due to hydrodynamism, which is more pronounced in shallower waters, especially in summer.

The greater and fluctuating richness and equitability at 5–7 m is probably due to the position towards the centre of the studied meadow where: (a) *Posidonia* is better developed, (b) the typical community exists (Scipione *et al.*, 1983), and (c) the depth represents a "border" (Margalef, 1974) between a shallow and a deep "zone" with different characteristics (hydrodynamism, leaf density, adjacent biotope influence) and, above all, with different relative species abundances. Nevertheless, the differences in richness are minimal and are based (Tables 1 and 2) on species with low population densities.

Differences due to different depth and hydrodynamic conditions have also been found in other groups (Ledoyer, 1966; Pronzato & Belloni, 1981; Boero, 1981 a, b; Boero *et al.*, 1985; Russo *et al.*, 1984; Lorenti & Fresi, 1983; Scipione *et al.*, 1983).

The study of the similarity between monthly samples shows the characteristics of the habitat and the decapod community: an open and shallow system with a high dominance of a few species in which two different strata (leaves and rhizomes) may be defined. The structure of the decapod community, both overall and monthly, is thus controlled by many factors, of which the strongly dominant species and the hydrodynamic conditions (directly or indirectly through the leaves) are most important.

Summary

A total of 6585 specimens belonging to 50 species were found. However, only 9: *Cestopagurus timidus, Calcinus tubularis, Athanas nitescens, Alpheus dentipes, Pisidia longicornis, Pilumnus hirtellus, Galathea bolivari, Thoralus cranchii,* and *Pilumnus villosissimus* have a relative abundance higher than 1 % (totalling 95.4 %); only the first seven are always present.

In the entire taxocoenosis, the species of the genera *Hippolyte* and *Processa* – generally considered to be "typical" for this habitat – have very little quantitative importance. The structure and evolution of the taxocoenosis over time is basically controlled by the two dominant hermit crabs. Their abundances follow the same pattern of development, although this is less obvious in shallower waters in summer and autumn, during which a decrease of *C. tubularis* coincides with a decrease in the foliar area and with stronger hydrodynamic conditions.

The dominance-diversity curves show a geometrical distribution. The diversity (between 2.4 and 3.03) depends on the equitability. The richness (between 17 to 21) and equitability fluctuate more at 5–7 m, perhaps because this depth lies in the middle of the studied meadow where the typical animal community exists and where a boundary effect might be present. In the study of samples (Q mode), the defined groups show, at least in part, a dependence on the diversity-equitability; these are strongly related to the maximum recruitment of the 2 or 3 dominant species and the external environmental fluctuations (hydrodynamic conditions), the latter mainly in the shallower samples.

Acknowledgements

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