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Polychaete communities associated with gastropod shells inhabited by the hermit crabs *Clibanarius erythropus* and *Calcinus tubularis* from Ibiza, Mediterranean Sea

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Shells inhabited by hermit crabs are unique microhabitats with an abundant epi- and endofauna. Using polychaetes as an example, communities associated with the whelk *Stramonita haemastoma*, the hermit crabs *Clibanarius erythropus* and *Calcinus tubularis*, as well as empty, damaged shells were investigated. No polychaete community was associated with live *S. haemastoma*: only 30% of the investigated gastropods harboured polychaetes. Hermit crab-occupied shells supported polychaete communities dominated by Spirorbidae in the case of *Clibanarius erythropus* and by small Sabellidae, *Spirobranchus polytrema* and *Dipolydora armata* in *Calcinus tubularis*. The polychaete fauna associated with empty shells was similar to that on shells previously inhabited by one of the hermit crab species but different from those of the surrounding hard bottom. The reproductive strategy of the some polychaetes species is adapted to life on this small-sized habitat.

INTRODUCTION

Shells of gastropods, particularly those inhabited by hermit crabs, are unique microhabitats because their epifauna often differs from the surrounding benthic fauna or from those of other adjacent organisms, e.g. algae, sponges, ascidians and bryozoans. Associations of epifaunal organisms with hermit crabs are well-known examples of different types of symbioses. A recent review of the diversity and natural history of hermit crab associates listed about 550 invertebrates from 16 phyla allied with about 180 hermit crab species (Williams & McDermott, 2004). With nearly 100 species associated with about 50 hermit crab species, the polychaetes are one of the most diverse groups in that analysis (Williams & McDermott, 2004).

Shells from gastropod assemblages vary by species, by size, by state of preservation and by whether they are occupied by a live gastropod or by one of multiple species of hermit crabs. These attributes all influence the epibiotic assemblages occurring on shells (Karlson & Shenk, 1983; McDermott, 2001). The observed differences in the composition of the epifauna have also been ascribed to competition, negative associations, hermit crab interactions and physical factors (e.g. Karlson & Shenk, 1983). Most experiments examining the significance of particular factors in controlling species abundance and richness patterns on hermit crab shells were conducted in estuaries or protected sounds, typically on sandy to muddy bottoms (e.g. Karlson & Shenk, 1983; McDermott, 2001).

Two studies have documented the epifaunal assemblages associated with hermit crab species in the Mediterranean Sea (Cuadras & Pereira, 1977; Stachowitsch, 1980). They investigated *Dardanus arrosor* (Herbst, 1796) (inhabiting shells of 11 gastropod species) as well as *Paguristes eremita* (Linnaeus, 1767) (as *P. oculatus* Milne-Edwards, 1863) and *Pagurus cuanensis* Bell, 1845 (inhabited shells of eight gastropod species). These hermit crab species were collected from muddy bottoms.

The associates of the hermit crab species *Clibanarius erythropus* (Latreille, 1818) and *Calcinus tubularis* (Linnaeus, 1767) have never been investigated before. Both species occur parapatrically or sympatrically in sublittoral hard bottom communities in the Mediterranean Sea. These shells and the surrounding hard bottom as a substrate are more similar to each other than shells and sandy or muddy bottoms, where most comparable studies have been conducted. Both hermit crab species occupied shells of the prosobranch gastropod *Stramonita heamastoma* (Linnaeus, 1767). When a hermit crab enters an empty gastropod shell, the shell comes 'back to life' (Williams & McDermott, 2004). The newly founded association is possibly more attractive to potential associated species or symbionts (Samuelsen, 1970). When the shells become damaged (e.g. by endolithic species or erosion) hermit crabs desert them. The gastropod shell is deposited and ultimately becomes part of the surrounding hard bottom.

This paper describes the structure of the shell-associated polychaete fauna, beginning with the species associated with the live gastropod *S. haemastoma*, continuing with those species on shells inhabited by the two above-mentioned hermit crab species, and then those growing on damaged, empty shells formerly inhabited by hermit crabs. These associates are compared with those on pebbles of comparable size, as part of the surrounding hard bottom, and found in the same habitat. As the highest proportion of taxa found in these communities are polychaetes, only this taxon is investigated here.

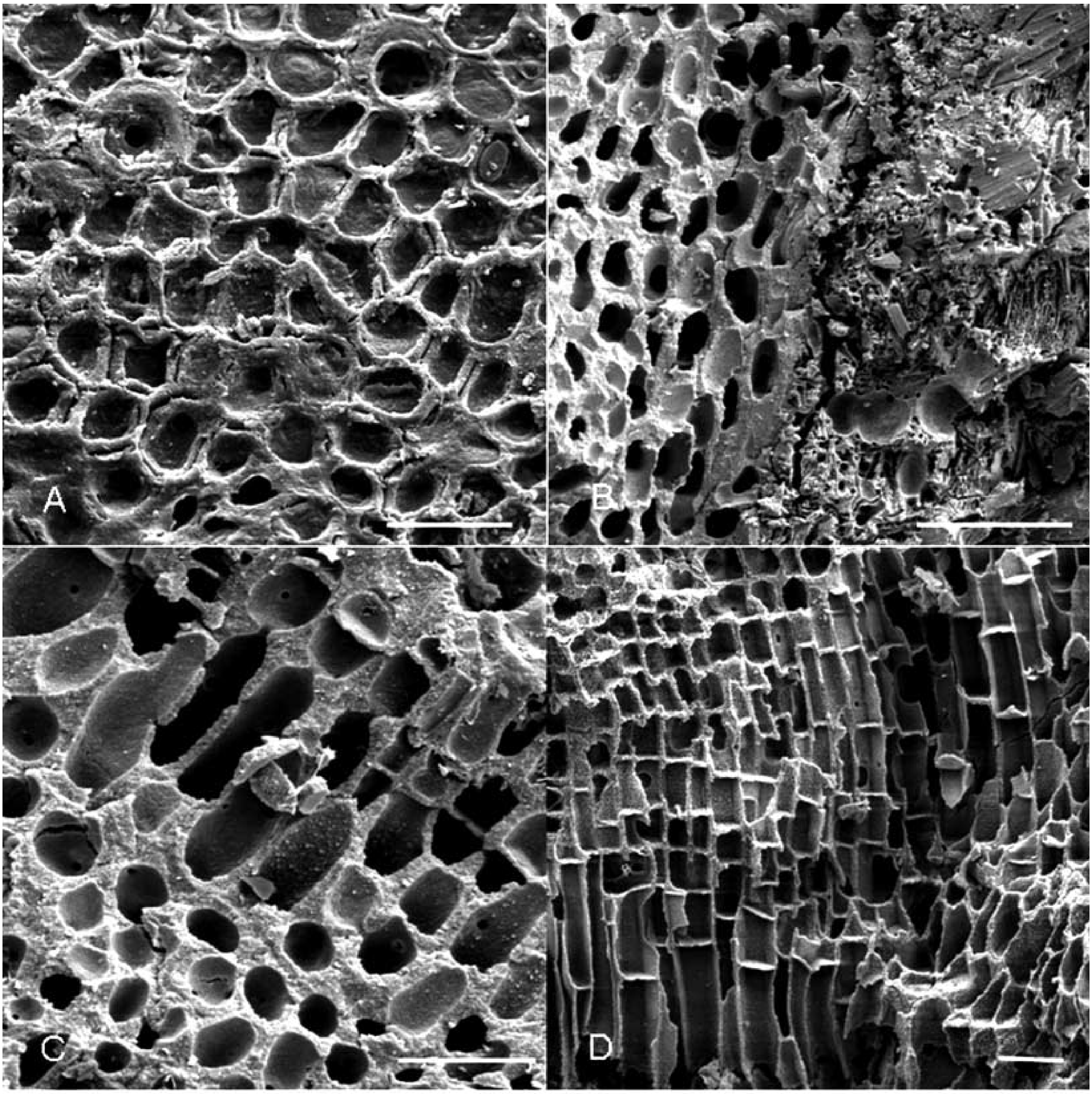

Figure 1. Scanning electron microscopy micrographs of calcareous algae on a gastropod shell. (A) View from above; (B) boundary between calcareous algae (left) and gastropod shell (right) (cross-section); (C) calcareous algae (cross-section); and (D) calcareous algae (cross-section). Scale bars: A, C, D, 20 μm; B, 50 μm.

MATERIALS AND METHODS

Samples of shells of *Stramonita haemastoma* were randomly collected in April and September 1999 by diving at 1–5 m depth in the Cala Olivera (38°56′10″N 1°30′10″E) a small cove on the south-east coast of Ibiza (north-western Mediterranean Sea). Both live *S. heamastoma*, and shells occupied by the hermit crabs *Calcinus tubularis* and *Clibanarius erythropus* (N=20 individuals for each species and sampling period), were sampled. Fourteen empty shells (ten in April and four in September), which were partially damaged and therefore currently unsuitable for hermit crabs, were also collected. The number of empty shells determines the abundance of hermit crabs at the study site. We could never find empty shells suitable for occupation by hermit crabs in the Cala Olivera, and all empty shells without hermit crabs were damaged. Finally, seven pebbles (five in April and two in September) comparable to the shells in size were collected. Empty shells and pebbles were difficult to find: they were rapidly removed by hydrodynamic processes or their surfaces were quickly fouled by encrusting algae, camouflaging these small objects. Shells and pebbles were placed separately in a 0.05% phenol–seawater solution for several hours to drive the associated fauna out. This method functions very well with most polychaetes, but not with Spirorbidae. To determine which of the Spirorbidae tubes were inhabited, the tubes were scraped off from the

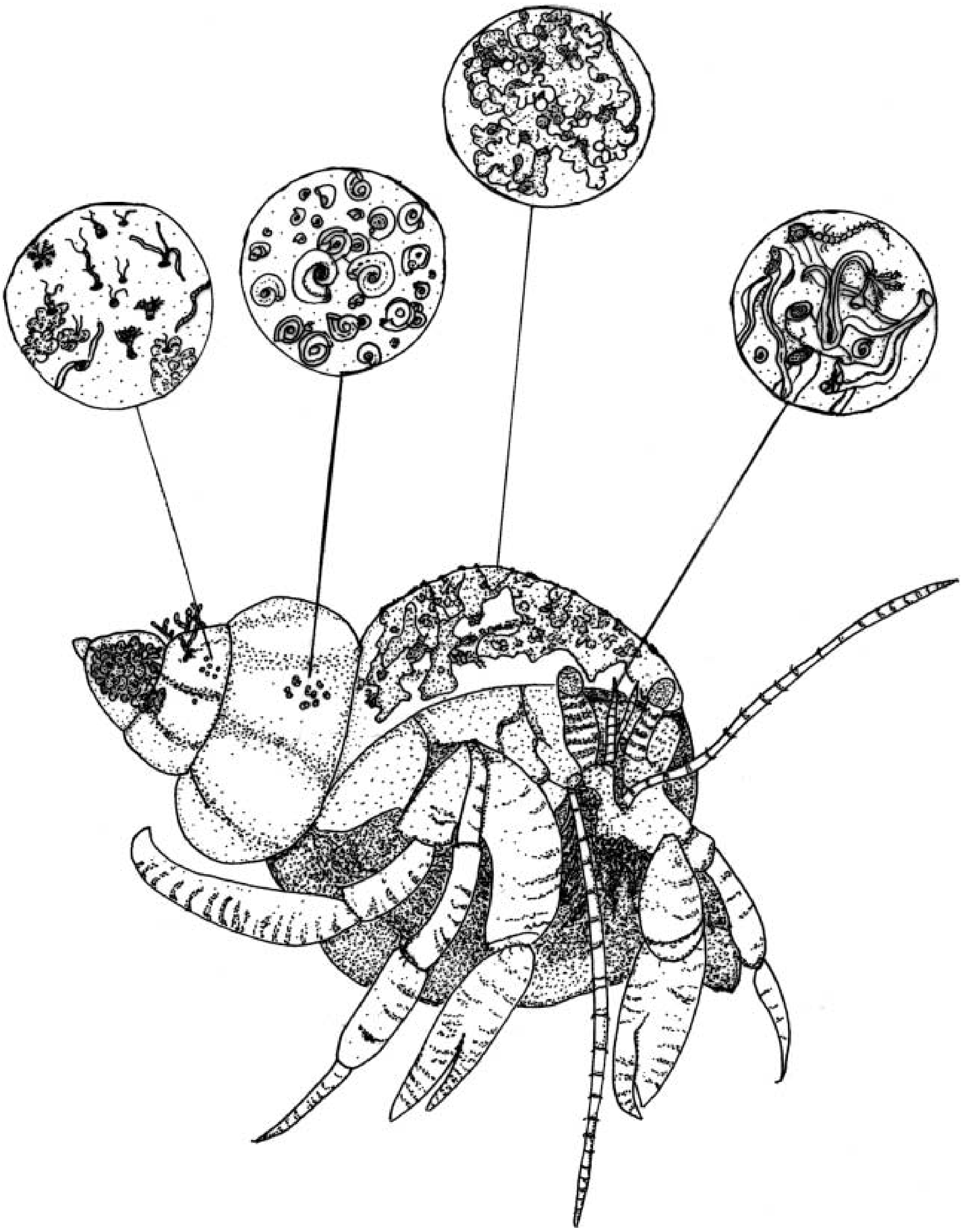

Figure 2. Epibiotic community on a gastropod shell inhabited by a hermit crab with discretely motile filter- (Fabriciinae) and surface-deposit-feeders (*Dipolydora armata*), sessile deposit feeders (Spirorbidae), motile herbivores (e.g. Syllidae) and sessile filter feeders (Serpulidae) (from left to right).

substrate. Many of these tubes along with the spirorbids themselves were destroyed during this process: such specimens were impossible to identify but they were counted. All other polychaetes were collected, identified to species or to the lowest possible taxonomic level and counted. After identification, the specimens were preserved in 75% ethanol, and most of them were stored in the collection of the University of Rostock (ZSRO).

The statistical package PRIMER 5.0 was used to compute the following univariate indices: number of individuals and species in the samples, species diversity (Shannon–Wiener, H′) and evenness (E_s). Bray–Curtis similarities were calculated using the mean abundances of species from all substrates. Principal component analyses (PCAs) were carried out based on a correlation matrix between species and samples using the statistical package CANOCO 4.5. For these analyses the number of individuals was not transformed. The significance of samples from different substrates was tested using the Monte Carlo permutation test with 1000 permutations and a significance level of 1%.

RESULTS

The collected shells were of similar size; shells inhabited by hermit crabs: length 40.7 ±6.0 mm, width

Table 1. *Mean abundance (ind shell^{-1}) and standard deviation (in parentheses), number of taxa and univariate summary statistics (H′ species diversity, E_s evenness) of polychaetes of each substrate in April and September 1999.*

	April 1999					September 1999				
Species/substratum	*S. haemastoma* mean (SD)	*C. erythropus* mean (SD)	*C. tubularis* mean (SD)	Empty shells mean (SD)	Pebbles mean (SD)	*S. haemastoma* mean (SD)	C. erythropus mean (SD)	*C. tubularis* mean (SD)	Empty shells mean (SD)	Pebbles mean (SD)
Harmothoe sp. juv.[†]	0	0	0	0	0	0	0	0	0	0.5 (0.71)
Chrysopetalum debile[†]	0	0	0	0	0.2 (0.45)	0	0	0	0	1.5 (2.12)
Eulalia viridis	0	0	0	0	0	0	0	0.05 (0.22)	0	0
Notophyllum foliosum	0	0	0	0	0	0	0	0	0.25 (0.5)	0
*Ophiodromus pallidus**	0	0	0	0.3 (0.48)	0	0	0	0.05 (0.22)	0	0
Autolytus cf. *quinquedecimdentata*	0	0	0	0.1 (0.31)	0.2 (0.45)	0	0	0	0	0
*Brania pusilla**	0	0	0.1 (0.44)	0.3 (0.48)	0.2 (0.45)	0	0	0.05 (0.22)	0	0.5 (0.71)
Brania sp. 1	0	0	0.05 (0.22)	1.3 (1.89)	0.4 (0.55)	0	0	0	0	0
*Sphaerosyllis hystrix**	0	0	0	0	0	0	0	0.05 (0.22)	0	0
*Sphaerosyllis pirifera**	0	0	0	0	0	0	0	0.1 (0.45)	0	0
Eusyllis sp. juv.	0	0	0	0	0.4 (0.89)	0	0	0	0	0
*Pionosyllis lamelligera**	0	0	0	0.1 (0.32)	0.8 (0.89)	0	0	0.05 (0.22)	0	0.5 (0.71)
Haplosyllis spongicola	0	0	0	0	0.2 (0.45)	0	0	0	0	0
Syllis gracilis	0	0.05 (0.22)	0.15 (0.67)	0	0.2 (0.45)	0	0	0	0	0.5 (0.71)
Typosyllis armillaris	0	0	0	0	0	0	0	0	0.5 (0.58)	0
Typosyllis cornuta[†]	0	0	0	0	0	0	0	0	0	0.5 (0.71)
Typosyllis hyalina	0	0	0	0	0	0	0	0.05 (0.22)	0	0
*Typosyllis prolifera**	0	0	0	0	0	0	0	0.05 (0.22)	0	0.5 (0.71)
Typosyllis sp. juv.	0	0	0.05 (0.22)	0	0.4 (0.55)	0	0	0	0	0.5 (0.71)
Syllidae juv.	0	0	0.05 (0.22)	0.1 (0.32)	0.2 (0.45)	0	0	0.2 (0.52)	0	0.5 (0.71)
*Perinereis cultrifera**	0	0	0.05 (0.22)	0.1 (0.32)	0	0	0	0	0.25 (0.5)	0
Websterinereis glauca	0	0	0	0	0.2 (0.45)	0	0	0	0	0
Nereis sp. juv.	0	0	0	0.1 (0.32)	0	0	0	0	0	0
Nematonereis unicornis[†]	0	0	0	0	0.4 (0.55)	0	0	0	0	1.0 (1.41)
Lysarete ninetta[†]	0	0	0	0	0	0	0	0	0	1.5 (2.12)
Eunicidae juv.	0	0	0	0	0	0	0	0.1 (0.31)	0	0
*Schistomeringos rudolphi**	0	0	0	0	0	0	0	0.5 (0.76)	0	4.0 (5.66)
Ophryotrocha sp.	0	0	0	0.1 (0.32)	0	0	0	0	0	0
Dipolydora armata	0.05 (0.22)	7.3 (19.35)	6.6 (12.64)	16.9 (42.76)	0	0.95 (4.25)	0.6 (1.76)	7.7 (14.96)	1.25 (1.89)	0
Aphelochaeta marioni	0	0	0	0	0	0	0	0	0.25 (0.5)	0

Caulleriella sp. juv.	0	0	0	0.1 (0.32)	0	0	0	0	0	0
Dodecaceria concharum	0.05 (0.22)	0.4 (1.27)	0.45 (1.05)	0.2 (0.42)	0	0	0	0.15 (0.49)	0	3.5 (3.53)
*Capitella minima**	0.4 (0.82)	0.05 (0.22)	0.3 (0.47)	0.5 (0.71)	0	0.3 (0.98)	0.05 (0.22)	0.15 (0.67)	0	0
Polycirrus sp. juv.	0	0	0	0.1 (0.32)	0	0	0	0	0	0
Terebellidae juv.	0	0	0	0	0.2 (0.45)	0	0.05 (0.22)	0	0	0
Fabricia stellaris	0	0.35 (0.81)	0.7 (1.56)	0.5 (0.97)	2.2 (3.03)	0	0.15 (0.49)	0.4 (1.57)	2.0 (3.37)	0
*Fabriciola tonerella****	0	0.7 (1.3)	1.2 (3.66)	3.8 (7.28)	0.6 (1.34)	0	0.25 (0.72)	7.65 (10.81)	8.0 (12.88)	0.5 (0.71)
*Novafabricia infratorquata****	0	0.15 (0.67)	0.1 (0.31)	1.0 (1.94)	0	0	0	0.4 (0.99)	1.75 (2.87)	0
*Amphiglena mediterranea**	0	0	0.05 (0.22)	0	0	0	0	0.65 (1.5)	0.5 (1.0)	2.5 (2.12)
*Oriopsis armandi****	0	0.05 (0.22)	0.2 (0.52)	2.0 (2.62)	0.4 (0.55)	0	0.3 (1.34)	2.55 (4.72)	5.25 (8.54)	0
Sabellidae juv.	0	0	0	0	0	0	0.05 (0.22)	0	0	0
*Filograna implexa**	0	0.3 (1.34)	0	0	0	0	2.05 (4.64)	0.05 (0.22)	1.5 (3.0)	0
Hydroides pseudouncinata	0	0.05 (0.22)	0.05 (0.22)	0.1 (0.32)	0	0	0	0.1 (0.31)	0	0
Protula sp.	0	0.05 (0.22)	0	0	0	0	0	0	0	0
Serpula concharum	0	0.05 (0.22)	0.05 (0.22)	0	0.2 (0.45)	0	0	0.05 (0.22)	0	0
Serpula vermicularis	0	0	0	0	0	0	0	0.05 (0.22)	0	0
*Spirobranchus polytrema***	0.75 (1.68)	2.85 (3.03)	7.15 (6.95)	9.1 (17.82)	1.0 (1.41)	0.1 (0.45)	0.3 (0.47)	3.45 (4.17)	1.5 (1.91)	15.0 (14.14)
*Vermiliopsis striaticeps**	0	0.4 (0.94)	0.65 (0.93)	0	0	0	0.1 (0.31)	0.5 (0.76)	0.5 (1.0)	0
Serpulidae juv.	0	1.0 (2.0)	0.85 (2.16)	2.2 (4.26)	0.6 (1.34)	0	0.3 (0.73)	0	0	0
Janua pagenstecheri	0	1.5 (4.25)	0.3 (1.13)	0	0	0	2.5 (2.28)	0.45 (1.1)	1.0 (2.0)	1.0 (1.41)
*Neodexiospira pseudocorrugata**	0	0.4 (1.39)	0.05 (0.22)	0	0	0	0	0	0	0
*Pileolaria berkeleyana**	0	0.2 (0.52)	0.05 (0.22)	0	0	0	0.55 (2.24)	0	0	0
*Pileolaria militaris**	0	0.05 (0.22)	0	0	0	0	0.2 (0.52)	0	0	0
*Pileolaria heteropoma**	0	0	0.05 (0.22)	0	0	0	0	0	0	0
*Pileolaria striata**	0	0	0.15 (0.67)	0	0	0	0	0	0	0
Spirobidae indet.	0	1.3 (2.6)	0.45 (1.15)	0.4 (0.97)	0	0	11.6 (9.77)	1.1 (3.55)	2.0 (2.83)	4.0 (1.41)
Total	1.25 (1.97)	17.2 (21.35)	19.86 (17.39)	39.4 (73.69)	8.8 (6.5)	1.35 (4.28)	19.05 (13.59)	26.65 (27.76)	26.5 (29.94)	39.0 (32.53)
Number of taxa	4	20	25	22	19	3	15	27	15	19
Diversity H′	0.960	1.920	1.888	1.871	2.620	0.774	1.438	2.065	2.031	2.235
Evenness E_s	0.44	0.64	0.59	0.61	0.89	0.70	0.53	0.63	0.75	0.76

*, recorded for the first time in a hermit crab association, incidental symbiont; **, recorded for the first time in a hermit crab association, facultative symbiont with *Calcinus tubularis* and *Clibanarius erythropus*; ***, recorded for the first time in a hermit crab association, facultative symbiont with *Calcinus tubularis*; †, only found on pebbles.

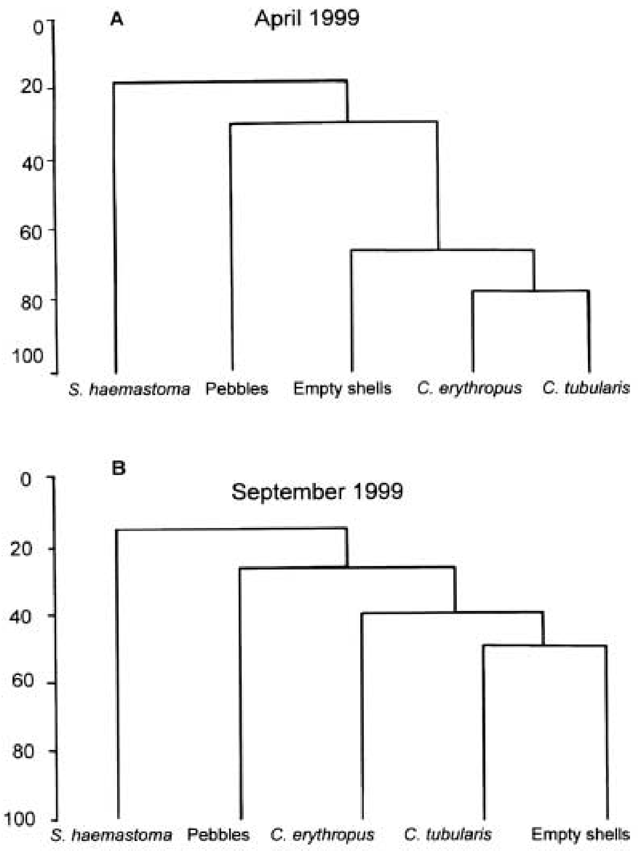

Figure 3. Cluster analysis of polychaetes from live *Stramonita haemastoma*, shells inhabited by the hermit crabs *Calcinus tubularis* and *Clibanarius erythropus*, damaged, empty shells and pebbles from (A) April 1999; and (B) September 1999 using the Bray–Curtis similarity index and double root data transformation.

27.4 ±3.8 mm (N=80); live gastropods: length 41.8 ±7.1 mm, width 27.7 ±4.0 mm (N=40); damaged, empty shells: length 43.2 ±5.7, width 26.2 ±7.9 mm (N=10). All shells were covered with calcareous algae, usually >50% (70.3 ±24.8%) of the surface (Figure 1). The pebbles were slightly larger than the shells: length 48.2 ±9.2 mm, width 34.1 ±3.4 mm, height 25.1 ±5.1 mm (N=4). They were also almost completely covered with calcareous algae.

Shells currently and formerly (now damaged and empty) inhabited by hermit crabs were covered with epibiotic growth (Figure 2). A total of 45 polychaete taxa belonging to 13 families were identified (35 taxa in April and 36 in September). The dominant families were the Syllidae (11 taxa; 24% of all taxa), Serpulidae (7; 16%), Spirorbidae (6; 13%) and Sabellidae (5; 11%) (Table 1). Of the 35 taxa associated with hermit crabs, 21 species have not been previously recorded in association with any hermit crab species (described in Table 1). Of these 21 species, the sabellids *Fabriciola tonerella* Banse, 1959, *Novafabricia infratorquata* (Fitzhugh, 1983), *Oriopsis armandi* (Claparède, 1864) and the serpulid *Spirobranchus polytrema* (Philipp, 1844) can be considered as facultative, the others as incidental symbionts. Obligate symbionts were not recorded. Thirty-six taxa were found on shells inhabited by *Calcinus tubularis*, 22 taxa on shells of *Clibanarius erythropus* and 29 taxa on empty, damaged shells. Considering only hermit crabs, *Brania pusilla* (Dujardin, 1839) and *Amphiglena mediterranea* (Leydig, 1851) were found only on shells inhabited by *Calcinus tubularis*, whereas *Pileolaria militaris* (Claparède, 1869) associated only with *Clibanarius erythropus*. Although polychaetes were found on all shells inhabited by hermit crabs, on all damaged, empty shells and on all pebbles they were associated with only 45% (April) and 20% (September) of live *Stramonita haemastoma*. Only four taxa occurred on this shell type.

Based on abundance, the polychaete communities consisted mainly of Sabellida and *Dipolydora armata* (Langerhans, 1880). Mobile epifauna forms were less evident. The highest total abundances were found on a damaged, empty shell in April (246 ind), followed by a shell inhabited by *Calcinus tubularis* in September (96 ind) and by *Clibanarius erythropus* in April (86 ind). The mean abundances on shells inhabited by hermit crabs and on damaged, empty shells were between 17.2 (±21.4) ind shell^{-1} and 39.4 (±73.7) ind shell^{-1}, respectively. In contrast, only about 1.3 (±4.3) ind shell^{-1} (maximum 19 ind shell^{-1}) were found on *S. haemastoma* (Table 1).

The highest mean abundance (16.9 ±42.6 ind shell^{-1} (N=10) and maximum 137 ind) of any species (*D. armata*) was found in April on damaged, empty shells. This species was found on all types of shells but never on pebbles. Only one species, the serpulid *Spirobranchus polytrema*, occurred on all investigated substrates, but in different frequencies: sporadic on *Stramonita haemastoma* (5–20% of investigated shells and maximum 6 ind shell^{-1}), up to 80% on damaged, empty shells in April (maximum 59 ind shell^{-1}) and up to 90% on shells inhabited by *Calcinus tubularis* in April (maximum 27 ind shell^{-1}).

Twenty-eight taxa were recorded on pebbles, and the following eight errant taxa occurred only on this substrate, but in low abundances: *Harmothoe* sp., *Chrysopetalum debile* (Grube, 1855), *Eusyllis* sp., *Haplosyllis spongicola* (Grube, 1855), *Typosyllis cornuta* (Rathke, 1843), *Websterinereis glauca* (Claparède, 1870), *Nematonereis unicornis* (Grube, 1840) and *Lysidice ninetta* Audouin & Milne-Edwards, 1834. The highest diversity and evenness were recorded on pebbles in April and September (Table 1).

The following eight trophic functional groups were identified: discretely motile filter feeders (e.g. Fabriciinae), sessile filter feeders (Serpulidae, Spirorbidae), discretely motile filter- and surface-deposit-feeders (e.g. *D. armata*), sessile surface-deposit-feeders (e.g. Sabellinae), discretely motile surface-deposit-feeders (e.g. Terebellidae), motile carnivores (e.g. Phyllodocidae, Polynoidae), motile herbivores (e.g. Eunicidae, Syllidae) and motile omnivores (e.g. Nereididae, Syllidae). Both qualitatively (number of species) and quantitatively (number of individuals), the discretely motile filter feeders and the sessile filter feeders were the dominant groups. The discretely motile filter- and surface-deposit-feeders were important only quantitatively, and were represented by only two species, of which *D. armata* was by far the most abundant.

Bray–Curtis cluster analyses clearly separated the samples from different substrates (Figure 3). A clear differentiation of the shells inhabited by hermit crabs and damaged, empty shells on the one hand from the pebbles and live *S. haemastoma* on the other points to groupings

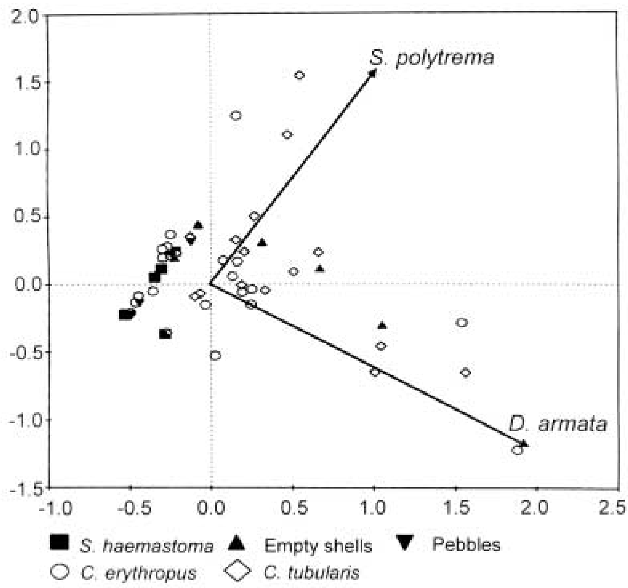

Figure 4. First two principal component analysis (PCA) axes, with the most dominant species (*Spirobranchus polytrema* and *Dipolydora armata*) and projected centroids of polychaetes associated with *Stramonita haemastoma* (N=20), with shells inhabited by *Calcinus tubularis* (N=20) and *Clibanarius erythropus* (N=20), damaged, empty shells (N=10) and pebbles (N=5) from April 1999.

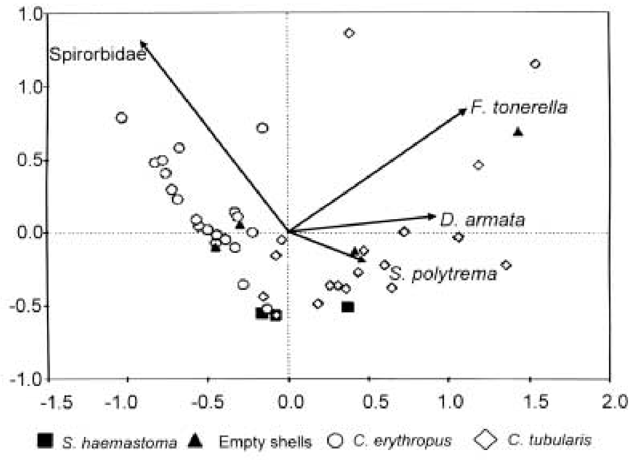

Figure 5. First two principal component analysis (PCA) axes, with the most dominant taxa (Spirorbidae, *Fabriciola tonerella*, *Spirobranchus polytrema* and *Dipolydora armata*) and projected centroids of polychaetes associated with *Stramonita haemastoma* (N=20), with shells inhabited by *Calcinus tubularis* (N=20) and *Clibanarius erythropus* (N=20) and damaged, empty shells (N=4) from September 1999.

within the samples. Accordingly, the polychaetes associated with hermit crab-occupied shells and formerly occupied shells (now damaged and empty) represent distinct communities. These communities were most similar to the fauna associated with pebbles as a component of the surrounding hard bottom. The fauna associated with *S. haemastoma* is most different from all others. In both April and September, these shells exhibited by far the lowest abundance, number of taxa, and diversity (Table 1).

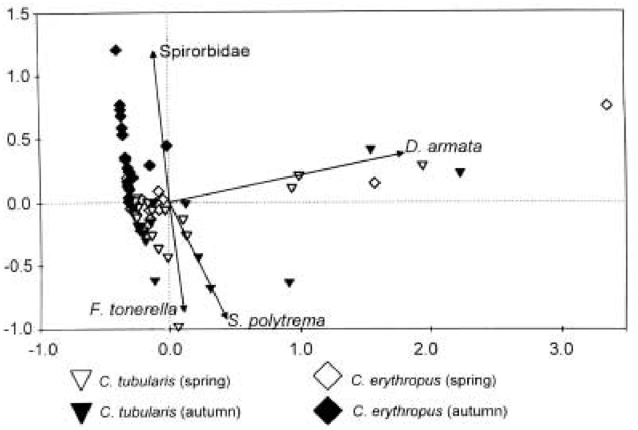

Figure 6. First two principal component analysis (PCA) axes, with the most dominant taxa (Spirorbidae, *Fabriciola tonerella*, *Spirobranchus polytrema* and *Dipolydora armata*) and projected centroids of polychaetes associated with shells inhabited by *Calcinus tubularis* and *Clibanarius erythropus* from April and September 1999 (N=20 each).

The PCAs yielded a more detailed picture of the distribution of polychaete species on different substrates (Figures 4 & 5). The eigenvalues of the first two ordination axes are 0.49 and 0.16 (Figure 4) and 0.38 and 0.21 (Figure 5). Most samples grouped around the intersection of axes in April (Figure 4). However, three shells inhabited by *Clibanarius erytropus*, five inhabited by *Calcinus tubularis* and one damaged, empty shell lie outside this group. In this analysis the variance of the samples is mainly explained by the abundance of two species, *D. armata* and *Spirobranchus polytrema*. Based on these abundance data, *D. armata* dominated the samples (about 70 to 96%), followed by *S. polytrema* (about 48 to 60%). Two different groups of shells exist in September: shells inhabited by *Clibanarius erythropus* and shells inhabited by *Calcinus tubularis* (Figure 5). A Monte Carlo permutation test revealed significant differences between these samples ($P<0.01$). Each two damaged, empty shells were also grouped within these samples respectively, suggesting that *C. tubularis* and *Clibanarius erythropus* had once inhabited these shells. Four taxa explained most of the variance of the September samples. The variance of shells inhabited by *Calcinus tubularis* is explained solely by Spirorbidae (dominance up to 96%), whereas the variance in *C. tubularis* can be attributed to abundance of three species: *Fabriciola tonerella* (dominance up to 40%), *D. armata* (up to 95%) and *S. polytrema* (up to 50%).

A PCA considering only samples of *C. tubularis* and *Clibinarius erythropus* from April and September shows no clear seasonal trend (the eigenvalues of the first two ordination axes are 0.70 and 0.09) (Figure 6). This is quite evident in *Calcinus tubularis*, where April and September samples are mixed. Two shells inhabited by *Clibanarius erythropus* from April were positioned far from all others of this substrate type. These shells were characterized by high abundances and dominances of *D. armata* (81 and 39 ind shell^{-1}; 94% and 71%). The Spirorbidae, *D. armata*, *F. tonerella* and *S. polytrema* explain the variance of these 80 samples.

The PCA of the September data set (Figure 5) shows a clear temporal gradient related to the succession of the shell-associated communities (considered as artificial time series). Accordingly, the development of the true shell-associated fauna started with the occupation of the shells by hermit crabs. Community composition was apparently affected by the particular hermit crab species. On shells inhabited by *C. erythropus*, a spirorbid-dominated (70–90%) community has developed, whereas on shells inhabited by *Calcinus tubularis*, a sabellid-dominated (65–79%) community is present. The samples furthest from *Stramonita haemastoma* can be considered to be most developed with respect to a specific hermit crab association (Figure 5).

DISCUSSION

Of the 48 taxa recorded in this study, only *Novafabricia infratorquata* had not been previously recorded from the Mediterranean Sea. It was previously found in the Caribbean Sea (Mexico and Belize) (Fitzhugh, in litt.). In the present study, *N. infratorquata* occurred only on shells recently or previously inhabited by hermit crabs. All other taxa have been found during investigations of hard substrates and photophilic algal polychaete assemblages in the Mediterranean Sea (e.g. Sardá, 1991; Giangrande et al., 2003). The pebbles are an additional element of this habitat, and the polychaete community associated with this substrate is very similar to hard bottom or photophilic algae communities, especially those found in the 'trottoir' or *Lithophyllum lichenoides* community (Sardá, 1991). This community has been considered as an impoverished assemblage of a photophilic algae community. The data from the pebble samples—24 taxa and diversity values (H′) between 2.2 and 2.6—are similar to those found earlier in a comparable community (15 species, H′=2.6) (Sardá, 1991). The high evenness values determined for the pebble samples (Table 1) are expected for communities where species are randomly distributed and where a complex community organization is absent.

More interesting in the context of this study are the four other substrates. The shell- associated polychaetes, particularly those inhabited by hermit crabs, can be regarded as a unique, discrete community. Thus, about 40 taxa were found associated with shells inhabited by hermit crabs: evenness values are comparatively low and the similarity among these shells, including shells which may have been previously inhabited by hermit crabs (but now damaged and empty) is highest (Figure 3).

No true polychaete community was found associated with *Stramonita haemastoma*, the starting point of the development of a shell-associated fauna, although the surface area of the live shells covered with encrusting algae was the same as that of hermit crab-occupied shells. Only 30% of investigated live gastropods harboured polychaetes. The number of taxa, the abundance as well as the diversity here were lowest (Table 1). Stachowitsch (1980) also reported that live gastropods did not contain endolithic polychaetes and that epibiotic polychaetes were rare. Wahl et al. (1998) assumed mutual grazing and bulldozing to be effective protection against epibiosis in *Littorina littorea* (Linnaeus, 1767). Chemical defence by means of exuded secondary metabolites (toxins or basic/acid mucus) also appears to be a common phenomenon among molluscs (Wahl et al., 1998). Both may also be in effect in *S. haemastoma*.

Because empty shells are considered to be the limiting resource in most hermit crab populations (e.g. Kellog, 1976), hermit crabs enter shells shortly after the death of the gastropods. Both *Clibanarius erythropus* and *Calcinus tubularis* prefer gastropod shells (Busato et al., 1998). Such fresh shells have been termed 'mobile multi-species clumps' (Stachowitsch, 1983) and are in effect 'mobile islands'; anti-fouling mechanisms no longer exist and, importantly, they are hard bottom components with encrusting calcified algal communities amidst photophilic algal assemblages characterized by erect and fleshy species. As mentioned above, the surface area coverage of calcareous algae on the shell surface was about the same in *S. haemastoma*, in shells inhabited by hermit crabs and in empty, damaged shells. Not only the two-dimensional, but also the three-dimensional extension is probably crucial for the settlement of endolithic species. The calcareous algae continue to generate a ramified cavity system which increases the habitat for boring and endolithic species after the hermit crabs enter the shells (Figure 1). Once a boring species has broken the apical cell wall of a calcareous alga (cell wall about 1–2 μm thick), it is already located in this cavity system. Thus, boring species (e.g. *Cliona* spp., *Dipolydora armata* and *Dodecaceria concharum* Ørsted, 1843) prepare the habitat for sessile endolithic, but non-boring species such as small Sabellidae. The thickness of the calcareous algae on live and occupied *S. haemastoma* will be considered in future investigations.

Certain epifaunal species are often associated with specific hermit crab species (Samuelsen, 1970). Thus, the biology and ecology of the crab species may significantly determine the shell fauna. Some hermit crab species may also favour shells inhabited by conspecifics over those inhabited by non-conspecifics. Gherardi & Tiedemann (2004) showed that hermit crabs can even recognize familiar and unfamiliar conspecifics through individual odours. Against this background, the results of the PCA—which revealed significant differences between the polychaete communities associated with *Clibanarius erythropus* and *Calcinus tubularis* in September—are not surprising, even though both species were collected in the same habitat and both are grazers. Moreover, these results show that shells, once occupied by a particular hermit crab species, usually remain in that species: shell exchanges between hermit crab species do not occur or are rare. Thus, the associated fauna on damaged, empty shells should be similar—for a certain time—to those of shells previously inhabited by a particular hermit crab species.

The polychaete community associated with *Clibanarius erythropus* is characterized by spirorbids. Spirorbid-dominated epifaunas are believed to be pioneer communities (e.g. Chalmer, 1982). In general, most spirorbids are considered to be r-strategists with high reproductive rates, and they may therefore dominate in physically controlled habitats. No development of a diverse community, as recorded for shells inhabited by *Calcinus tubularis*, takes place in the shells of *Clibanarius erythropus*. On the other hand, the nature of the recurrent disturbances that might control the development and persistence of pioneer communities on only one of the two hermit crab species remains unclear.

The polychaete fauna associated with *Calcinus tubularis* is dominated by *D. armata*, small species of Sabellidae and *Spirobranchus polytrema*. Within the Sabellidae, *Fabriciola tonerella* shows the highest abundances. This species was first described from submarine caves but has also been found in infralittoral polychaete assemblages associated with *Cystoseira amentacea* and from Demospongiae. It has been categorized as a discretely motile suspension feeder but more details of its ecology are not known. *Fabriciola tonerella* was found in all those parts of the shells that were covered with calcareous algae. Their tubes were almost completely inside the calcareous algae; only the most distal tube part composed of detritus, extended above the algal surface.

Dipolydora armata and *S. polytrema* are regular inhabitants of hard substrate and photophilic algal polychaete assemblages in the Mediterranean Sea (e.g. Sardá, 1991). The former is principally a borer of calcareous algae or hydrozoans (Radashevsky & Nogueira, 2003). It was also found in 1–24% of the shells inhabited by different hermit crab species in the Philippines (Williams, 2001). When present, this species was often abundant, with 35–40 ind cm^{-2} and hundreds of ind shell^{-1} (Williams, 2001). In the present investigation, *D. armata* was found only on shells but never on pebbles. This species is therefore apparently well adapted for living in calcareous substrates, especially on shells covered with calcareous algae and inhabited by hermit crabs: it is therefore considered to be a facultative symbiont of hermit crab associates (Williams & McDermott, 2004).

Spirobranchus polytrema is one of the most dominant species in polychaete communities associated with natural and artificial hard substrates, with concretions of calcareous algae, with the coral *Cladocora caespitosa* (Linnaeus, 1758) and with the sponge *Sarcotragus muscarum* (Schmidt, 1868) at shallow sites in the Mediterranean Sea (e.g. Arvanitidis & Koukouras, 1994; Cinar & Ergen, 1998). Its dominance on such different substrates and its reproduction period throughout the year (Bianchi, 1981) indicate that it is a generalistic species capable of rapidly colonizing a wide range of habitats. *Spirobranchus polytrema* was found in all parts of the shells but was particularly numerous on the aperture.

Reproductive mode is no doubt a potential adaptation for existence on such small-sized habitats—like gastropod shells—where competition for space is very important. For some of the most abundant species—*D. armata*, *Dodecaceria concharum* and *Filograna implexa* Berkeley, 1827—asexual reproduction (architomy, schizometamery and paratomy) has been reported (Bianchi, 1981; Petersen, 1999; Radashevsky & Nogueira, 2003). This strategy ensures that once a shell is colonized, populations can be expanded and maintained asexually. The preferred distribution of species on the shell may also help to avoid or minimize competition, but this remains to be studied in detail.

The results presented here show that the polychaetes associated with shells inhabited by hermit crabs (and covered by encrusting calcareous algae) form a special community different from those of the surrounding habitat (hard bottom with erect, bush-like algae and sponges). The former is dominated by sessile or discretely motile suspension feeders (this paper), whereas the second is dominated by motile syllids (e.g. Cinar & Ergen, 1998; Giangrande et al., 2003). The differences in the abundance and dominance of species on shells inhabited by a given hermit crab species could be explained by different factors. Examples include different succession stages of the associated fauna or different starting-points of the development of a shell-associated fauna due to a different time/season in which a hermit crab first entered an empty shell. Moreover, the life history of hermit crab species certainly helps determine the structure of the community. It has already been shown for four species of Paguridae from Norway (Samuelsen, 1970), but the mechanisms for this determination are still far from clear.

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