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Epibiont molluscs on neogastropod shells from sandy bottoms, Pacific coast of Mexico

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This study quantifies the prevalence, abundance, and spatial distribution of epibiotic molluscs on six common neogastropod species in sandy bottoms, *Hexaplex nigritus*, *Chicoreus regius*, *C. erythrostomus*, *C. brassica*, *Vasum caestus* and *Pleuropoca princeps*. A total of 1478 epibiont specimens belonging to 74 mollusc species were examined. The most of epibiotic species were typical of hard-bottoms, but a few species were typical of soft-bottoms. The results indicate *H. nigritus* is significantly more fouled than the other five species. This can be due to a greater availability of small hollows and a strongly ornamented shell in this species. The spatial distribution of epibionts on the neogastropod shells varied significantly among the different areas into which the shell was subdivided for this study. Fifteen sedentary epibiotic species dominated on all host shells. The costs and benefits of epibiosis are reviewed and the epibiont/host relationship appears to be principally beneficial to epibionts, without a clear benefit for hosts.

INTRODUCTION

Most sessile or sedentary marine animals are highly dependent on physical and morphological characteristics of the substratum to which they adhere. The structure and dynamics of the substratum determine the number of species that can colonize it, and results in a high degree of specialization in epibiotic communities (Sebens, 1991).

Rocky substrata are usually scarce on the bottoms of the continental shelf, and in these sandy and muddy habitats, epibiosis becomes a highly valuable strategy for the survival of sessile and sedentary organisms. Decapod crustaceans and molluscs provide one of the few hard substrata available, and although they may not usually show a high degree of colonization, most of them are hosts to many invertebrates (Conover, 1979; Warner, 1997; Parapar et al., 1997; Silina & Ovsyannikova, 1998; Fernández et al., 1998).

The neogastropods *Hexaplex nigritus* (Philippi, 1845), *Chicoreus regius* (Swainson, 1821), *C. erythrostomus* (Swainson, 1831), *C. brassica* (Lamarck, 1822), *Vasum caestus* (Broderip, 1833) and *Pleuropoca princeps* (Sowerby, 1825) are common inhabitants of sandy bottoms. They can be found from tidal flats to a depth of ~70 m off the Mexican Pacific coasts (Skoglund, 1992). All of them are very active predators. They have a very pronounced ornamentation, with a complex arrangement of spines, especially the four former species, which belong to the family Muricidae. This ornamentation provides a wide variety of refuges for small invertebrates.

The goals of this study are: (1) to describe the composition, abundance and intensity of epibiotic molluscs on six neogastropod species; (2) to describe the spatial distribution of small mollucs on these hosts; and (3) to analyse selection (Ivlev, 1961), overlap (MacArthur & Levins, 1967) and breadth habitat (Levins, 1968) of dominant epibiont species among different biological substrata.

MATERIALS AND METHODS

The study zone is located in the Tropical Pacific, off the Sinaloa coasts, Mexico (Figure 1). In this area sandy bottoms are dominant, although there are occasional rocky patches. Six species of neogastropod molluscs were

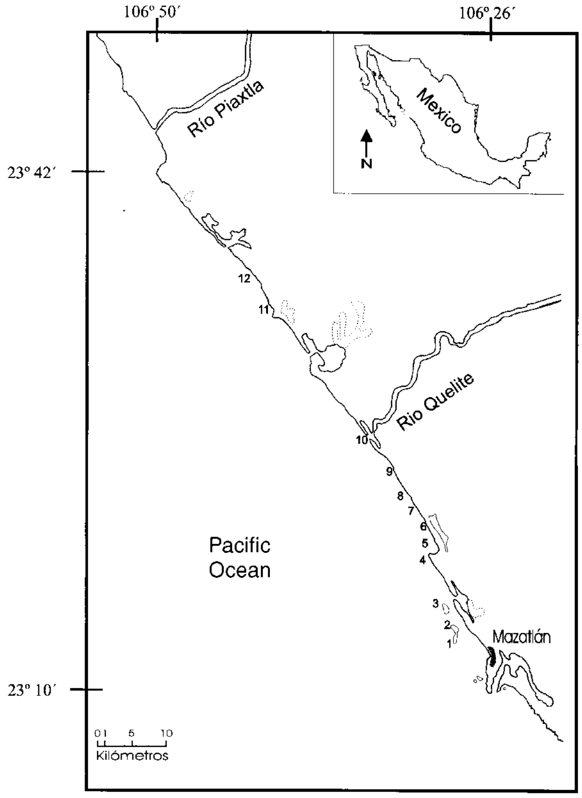

Figure 1. Location of the study area. 1, Isla Lobos; 2, Isla Venados; 3, Isla Pájaros; 4, Ballena; 5, Delfín; 6, Oceánica; 7, Tapahuito; 8, Puentes Cuates; 9, Piedras Negras; 10, A Caballo; 11, Boca Marmol; 12, Los Desechos.

Table 1. *List of species and their abundances found on six neogastropod species.*

Epibiotic species	Biological substrata						C	N	Habitat preferences
	Hexaplex nigritus (190)	*Chicoreus regius* (53)	*Chicoreus erythrostomus* (42)	*Chicoreus brassica* (38)	*Vasum caestus* (22)	*Pleuropoca princeps* (23)			
Radsiella petaloides (Gould, 1846)	1	—	—	—	—	—	16.6	1	hard bottom
Radsiella muscaria (Reeve, 1847)	1	—	—	—	—	—	16.6	1	hard bottom
Lepidozona elenensis (**Sowerby, 1832**)	**21**	—	—	**1**	—	**3**	**50**	**25**	**hard-bottom**
Callistochiton infortunatus Pilsbry, 1893	11	35	—	—	—	—	33	46	hard-bottom
Chaetopleura lurida (**Sowerby, 1832**)	**46**	—	**2**	**13**	—	**1**	**66**	**62**	**hard-bottom**
Lepidochitona beani (Carpenter, 1857)	1	—	—	—	—	1	33	2	hard-bottom
Dendrochiton lirulatus **Berry, 1963**	**8**	**4**	—	—	**4**	—	**50**	**16**	**hard-bottom**
Acanthochitona arragonites (Carpenter, 1857)	1	—	—	—	—	—	16.6	1	hard-bottom
Acanthochitona avicula (Carpenter, 1864)	2	—	—	—	—	—	16.6	2	hard-bottom
Acanthochitona rhodea (Pilsbry, 1893)	4	—	—	—	—	—	16.6	4	hard-bottom
Patelloida semirubida (Dall, 1914)	2	—	—	—	—	—	16.6	2	hard-bottom
Puncturella puntocostata **Berry, 1947**	**34**	**1**	**3**	—	**1**	—	**66.6**	**39**	**hard-bottom**
Diodora alta (C.B. Adams, 1852)	2	2	—	—	—	—	33.3	4	hard-bottom
Lucapinella milleri Berry, 1959	2	—	—	—	—	—	16.6	2	hard-bottom
Tricolia cyclostoma (Carpenter, 1864)	1	—	—	—	—	—	16.6	1	soft-bottom (gravel, coarse sand)
Tricolia perforata (Philippi, 1848)	3	1	—	—	—	—	33.3	4	soft-bottom (sand)
Calliostoma leanum (C.B. Adams, 1852)	1	1	—	—	—	—	33.3	2	hard-bottom and coarse sand
Barleeia alderi (Carpenter, 1857)	4	—	—	—	—	—	16.6	4	soft-bottom
Cyclostremiscus tricarinatus (C.B. Adams, 1852)	1	—	—	—	—	—	16.6	1	soft-bottom
Chonebasis philippii Pilsbry & Olsson, 1945	13	—	1	—	—	—	33.3	14	soft-bottom
Caecum compactum Carpenter, 1857	19	—	1	—	—	—	33.3	20	soft-bottom
Vermetus contortus (Carpenter, 1857)	1	—	—	—	—	—	16.6	1	hard-bottom
Turritella lentiginosa Reeve, 1849	3	1	—	—	—	—	33.3	4	soft-bottom
Hipponix pilosus (**Deshayes, 1832**)	**48**	**1**	**3**	**4**	—	**3**	**83.3**	**59**	**hard-bottom**
Calyptraea mamillaris **Broderip, 1834**	17	**10**	**3**	**1**	—	**9**	**83.3**	**40**	**hard-bottom and coarse sand**
Crepidula aculeata (**Gmelin, 1791**)	**229**	**5**	**12**	—	**1**	**5**	**83.3**	**252**	**hard-bottom**
Crepidula arenata (**Broderip, 1834**)	**79**	**3**	**55**	—	**5**	—	**66.6**	**142**	**hard-bottom**
Crepidula excavata (Broderip, 1834)	4	2	—	—	—	—	33.3	6	hard-bottom
Crepidula striolata Menke, 1851	10	—	—	2	—	—	33.3	12	hard-bottom
Crepipatella ligulata Gould, 1848	4	—	—	—	—	—	16.6	4	hard-bottom
Crucibulum personatum Keen, 1958	5	20	2	—	5	—	**66.6**	**32**	**hard-bottom**
Crucibulum concameratum Reeve, 1859	0	—	2	—	—	—	33.3	2	hard-bottom
Crucibulum monticulus **Berry, 1969**	**4**	**2**	**4**	**2**	—	**3**	**83.3**	**15**	**hard-bottom**
Crucibulum scutellatum (Wood, 1828)	0	—	—	—	3	—	33.3	3	hard-bottom
Crucibulum spinosum (Sowerby, 1824)	4	1	—	—	—	—	33.3	5	hard-bottom
Crucibulum subactum **Berry, 1963**	**4**	—	—	**3**	—	**4**	**50**	**11**	**hard-bottom**
Cerithiopsis pupiformis Carpenter, 1857	7	1	—	—	—	—	33.3	8	hard-bottom

continued

Table 1. *(Continued.)*

	Biological substrata								
Epibiotic species	*Hexaplex nigritus* (190)	*Chicoreus regius* (53)	*Chicoreus erythrostomus* (42)	*Chicoreus brassica* (38)	*Vasum caestus* (22)	*Pleuropoca princeps* (23)	C	N	Habitat preferences
Cerithiopsis subgloriosa Baker et al., 1938	1	—	—	—	—	—	16.6	1	hard-bottom
Seila assimilata (C.B. Adams, 1852)	18	5	—	—	—	—	33.3	23	hard-bottom
Epitonium thylax Dall, 1917	1	—	—	—	—	—	16.6	1	soft-bottom
Melanella dalli (Bartsch, 1917)	3	—	—	—	—	—	16.6	3	on host
Hypermastus cookeanus (Bartsch, 1917)	2	—	—	—	—	—	16.6	2	on host
Aspella myrakeenae Emerson & D'Attilio, 1970	2	—	—	—	—	—	16.6	2	?
Vitularia salebrosa (King & Broderip, 1832)	1	—	—	—	—	—	16.6	1	?
Nassarius bailyii (Pilsbry & Lowe, 1932b)	8	—	—	1	—	—	33.3	9	soft-bottoms (fine and coarse sand)
Nassarius fontainei **(Orbigny, 1841)**	**17**	—	**1**	—	**2**	—	**50**	**20**	soft-bottoms (fine and coarse sand)
Nassarius gemmulosus (C.B. Adams, 1852)	1	—	—	—	—	—	16.6	1	soft-bottoms (fine and coarse sand)
Nassarius limacinus (Dall, 1971)	0	3	—	—	—	—	33.3	3	soft-bottoms (fine and coarse sand)
Anachis nigricans (Sowerby, 1844)	8	—	—	—	—	—	16.6	8	hard-bottom
Anachis pygmaea (Sowerby, 1832)	1	—	—	—	—	—	16.6	1	hard-bottom
Anachis sanfelipensis Lowe, 1935	0	2	—	—	—	—	33.3	2	hard-bottom
Mitrella dorma Baker et al., 1938	2	—	—	—	—	—	16.6	2	hard-bottom
Nassarina helenae Keen, 1971	15	—	—	—	6	—	33.3	21	soft-bottom (coarse sand)
Granulina margaritula (Carpenter, 1857)	1	—	—	—	—	—	16.6	1	soft-bottom (coarse sand)
Bellaspira acclivicosta McLean & Poorman, 1970	0	1	—	—	—	—	33.3	1	soft-bottom (coarse and fine sand)
Pilsbryspira collaris (Sowerby, 1834)	0	—	—	—	2	—	33.3	2	soft-bottom (coarse and fine sand)
Microdaphne trichodes (Dall, 1919)	1	—	—	—	—	—	16.6	1	soft-bottom (coarse and fine sand)
Odostomia scalariformis Carpenter, 1857	1	—	—	—	—	—	16.6	1	on host
Chrysallida vizcainoana **(Baker et al., 1926)**	**45**	**8**	**3**	—	—	—	**50**	**56**	**on host**
Turbonilla azteca Baker et al., 1928	13	—	—	—	—	—	16.6	13	on host
Iselica maculosa (Carpenter, 1857)	0	1	—	—	—	—	33.3	1	on host
Jorunna pardus Behrens & Henderson, 1981	1	—	—	—	—	—	16.6	1	hard-bottom
Arca pacifica (Sowerby, 1833)	1	—	—	—	—	—	16.6	1	hard-bottom
Barbatia gradata (Broderip & Sowerby, 1829)	5	—	—	—	—	—	16.6	5	hard-bottom
Barbatia rostae Berry, 1954	10	—	2	—	—	—	33.3	12	hard-bottom
Anadara mazatlanica **(Hertleing & Strong, 1943)**	**293**	**1**	**12**	**1**	**13**	—	**66.6**	**320**	**hard-bottom**
Modiolus pseudotulipus Olsson, 1961	3	1	—		—	—	33.3	4	hard-bottom
Pteria sterna (Gould, 1851)	1	—	—	—	—	—	16.6	1	hard-bottom
Argopecten circularis (Sowerby, 1835)	1	—	—	—	1	—	33.3	2	hard-bottom
Crassinella ecuadoriana Olsson, 1961	0	—	—	—	1	—	33.3	1	soft-bottom
Crassinella pacifica (C.B. Adams, 1852)	5	—	2	—	—	—	33.3	7	soft-bottom
Cardita laticostata Sowerby, 1833	**38**	**2**	—	**1**	—	—	**50**	**41**	**soft-bottom**
Chione subimbricata (Sowerby, 1835)	1	—	—	—	—	—	16.6	1	soft-bottom
Hiatella arctica (Linnaeus, 1767)	10	1	—	—	—	—	33.3	11	hard-bottom

C, Dajoz's (1971) constancy index, constant and very common species appear in bold; N, total number of individuals of each species; H, habitat preferences. Number of each host neogastropod collected in this study appears in brackets.

collected from October 1997 to October 1998: *Hexaplex nigritus*, *Chicoreus regius*, *C. erythrostomus*, *C. brassica*, *Vasum caestus* and *Pleuropoca princeps*. Samples were collected using the equipment used by fishermen to fish lobster (silken or nylon gill net, with a length between 75 and 200 m, fold of 2.60 m, mesh size between 8.75 and 15 cm).

A total of 711 neogastropod specimens was collected, of which 401 possessed epibiotic molluscs. Other epibiotic organisms like polychaetes, hydrozoans, ascidians appeared, but the most of epibionts were molluscs. The differential distribution of each epibiont species on the host shell was determined. Four shell areas were studied: spire (I), body whorl (II), base of siphonal fasciole (III) and peristome (IV). The number and position of epibionts in each area were noted, and the specimens were then stored in 70% ethanol.

The similarity among different biological substrata was analysed on the basis of specific composition of epibionts by using the Bray–Curtis dissimilariy index (Bray & Curtis, 1957), previous standardization of data, using the UPGMA (unweighted pair-group method using arithmetic averages) aggregation algorithm. The Shannon–Weaver diversity, Margalef's richness and Pielou's evenness indices were calculated within different habitats. The non parametric Kruskal–Wallis test was used to compare the distribution of epibionts among different parts of the shell.

To determine the most common epibionts, Dajoz's (1971) constancy index was used, which is defined by the following equation:

$$\mathrm{C_{A1}} = \frac{\mathrm{N_{A1}}}{\mathrm{N_1}} \times 100 \qquad (1)$$

constancy of one species A ($\mathrm{C_{A1}}$) within a community 1, is the ratio between the number of samples where the species exists ($\mathrm{N_{A1}}$) and the total number of samples within that community ($\mathrm{N_1}$).

According to this index, the following categories were used: Rare, <12%; not very common, 13–24%; common, 25–49%; very common, 50–74%; constant, 75–100%.

Three indices were applied for constant and very common species (Table 1).

(a) Habitat breadth (Levins, 1968). B is maximum when the same number of individuals occur in each habitat, so that the species does not discriminate among the different habitats and has the broadest possible niche. B is ranged from 1 to n, where n is the total number of habitats.

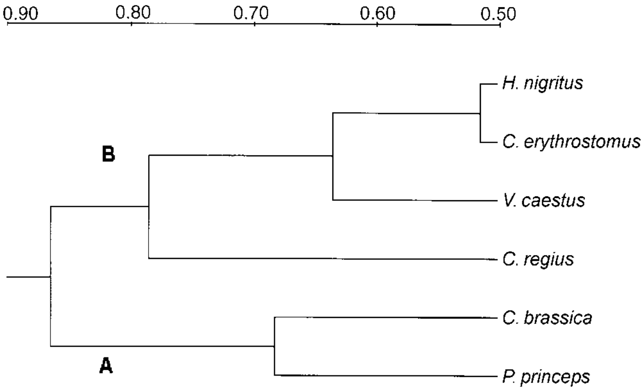

Figure 2. Cluster analyis based on the epibiont species of six biological substrates, using the Bray–Curtis (1957) dissimilarity index.

$$B = \frac{1}{\sum pj^2} \qquad (2)$$

p_j=proportion of individuals found in or using habitat j (estimated by $\mathrm{N_{jj}}$/Y), Nj=number of individuals found in or using habitat j, Y=S $\mathrm{N_j}$=total number of individuals sampled. It is sometimes useful to standardize the Levins' measure by dividing B by the total number of available habitats.

$$BA = \frac{B-1}{n-1} \qquad (3)$$

(b) Electivity index (Ivlev, 1961). It can be used in habitat preference studies (Krebs, 1989). This index varies from 1.0 to +1.0, with values between 0 and +1 indicating preference and values between 0 and 1 indicating avoidance.

$$E_i = \frac{r_1 - n_i}{r_i + n_i} \qquad (4)$$

r_i=percentage of species i in the habitat, n_i=availability or frequency of the habitat in environment.

(c) Niche overlap index (MacArthur & Levins, 1967). This index estimates the extent to which the niche space of species k overlaps that of species j. The MacArthur–Levins measure has been largely replaced by a very similar but symmetrical measure. This measure of overlap ranges from 0 (no habitats used in common) to 1.0 (complete overlap).

Table 2. *(H′) Shannon–Weaver diversity index, (J) Pielou's evenness index and (D) Margalef's specific richness index, for each biological substrate.*

	Biological substrata					
	Hexaplex nigritus	*Chicoreus regius*	*Chicoreus erythrostomus*	*Chicoreus brassica*	*Vasum caestus*	*Pleuropoca princeps*
Shannon–Weaver diversity (H′)	4.03	3.59	2.67	2.62	3.10	2.70
Specific richness (D)	21.38	11.64	7.37	6.15	26.16	4.78
Evenness (J)	0.66	0.77	0.66	0.78	0.86	0.90

$$o_{jk} = \frac{\sum^{2} P_{ij} P_{ik}}{\sqrt{P_{ij}^{2} P_{ik}^{2}}} \qquad (5)$$

O_{jk}=Pianka's measure of niche overlap between species j and species k, p_{ij}=proportion of habitat i of the total habitats used by species j, p_{jk}=proportion of habitat i of the total habitats used by species k, n=total number of habitats.

RESULTS

Specific composition of the different biological substrata

The percentage of epibiosis varied among the different neogastropod species. *Hexaplex nigritus* presented the highest value (65.81%) followed by *Chicoreus brassica* (62.22%), *C. erythrostomus* (55%), *C. regius* (49.42%), *Vasum caestus* (52%) and *Pleurocopa princeps* (43.33%).

A total of 1478 epibionts belonging to 74 species was examined (Table 1). Gastropods were specifically better represented (69.74%), followed by bivalves (15.78%) and chitons (14.48%). With respect to the number of individuals, gastropods were the dominant group (69.96%), followed by bivalves (21.98%) and chitons (8.06%).

Hexaplex nigritus presented the highest number of epibiotic species of chitons, gastropods and bivalves, while *P. princeps* was the poorest substratum, on which only chitons and gastropods appeared. On the other hand, *H. nigritus* presented the highest Shannon diversity value and *C. brassica* presented the lowest (Table 2). *Vasum caestus* had the highest specific richness while *P. princeps* presented the lowest.

The dendrogram analysis showed the differences among different habitats. This classification technique separated the habitats into two major groups (Figure 2). The habitats which made up group A (*C. brassica* and *P. princeps*) showed the lowest levels of specific richness. The habitats which made up group B (*H. nigritus*, *C. regius*, *C. erythrostomus* and *V. caestus*) were very heterogeneous.

Pleuropoca princeps and *C. brassica* substrata were principally colonized by mollusc species with low locomotive capacity, which adhered to the substratum like a sucker or searched for small hollows to take refuge. On the rest of the biological substrata additional juvenile phases of species with greater locomotive capacity were observed.

Fifteen species which represented 79.57% of the total epibionts were very common and constant (Table 1) due to their appearance frequencies in the six habitats.

Habitat breadth, habitat selection and niche overlap

Species which presented a greater habitat breadth (Table 3) were *Cardita laticostata*, *Anadara mazatlanica*, *Crepidula aculeata* and *Puncturella punctocostata*. That is, they were less selective than *Crucibulum monticulus*, *Calyptraea mamillaris*, *C. subactum*, *Dendrochiton lirulatus* and *C. personatum*, which showed a greater specialization for the type of substratum. More stenotypical species chose *Hexaplex nigritus*, except for *C. mamillaris* and *C. personatum* which preferred *Chicoreus regius*.

Puncturella punctocostata and *Crepidula aculeata* had a greater selectivity for *H. nigritus* than *Cardita laticostata* and *A. mazatlanica*. *Crepidula arenata* preferred *Chicoreus erythrostomus*, avoiding *Vasum caestus* and *C. regius*, and to a lesser degree, *H.nigritus* (Table 3). *Nassarius fontainei* and *Chrysallida vizcainoana* preferred *H. nigritus*, strongly avoiding *Chicoreus erythrostomus*.

The highest overlap indices occurred between *A. mazatlanica/Cardita laticostata* (0.845), *C. laticostata/P. punctocostata* (0.830) and *C. laticostata/Crepidula aculeata* (0.839) (Table 4). These values were over the critical value of 0.5–0.6 (MacArthur & Levins, 1967), and they were higher than those found among limpet species (Black, 1979) and rats (Schroder & Rosenzweig, 1975) and they are considered critical values. The lowest overlapping occurred between *Crucibulum subactum/Calyptraea personatum* (0.008) and

Table 3. *Levins' measure standardized (B_A) and Ivlev's selection index for constant and very common species.*

	Ivlev's selection index Biological substrata						Levins' index B_A
Epibiotic species	*Hexaplex nigritus*	*Chicoreus regius*	*Chicoreus erythrostomus*	*Chicoreus brassica*	*Vasum caestus*	*Pleuropoca princeps*	
Lepidozona elenensis	0.486	—	—	−0.882	—	−0.310	0.076
Chaetopleura lurida	0.384	—	−0.786	−0.580	—	−0.868	0.134
Dendrochiton lirulatus	0.282	0.041	—	—	−0.534	—	0.332
Puncturella punctocostata	0.226	−0.799	−0.733	—	−0.940	—	0.060
Hipponix pilosus	0.363	−0.764	0.061	−0.787	—	−0.800	0.096
Calyptraea mamillaris	0.081	0.342	−0.739	−0.925	—	−0.261	0.466
Crepidula aculeata	0.212	−0.892	−0.826	—	−0.990	−0.949	0.041
Crepidula arenata	−0.265	−0.913	0.422	—	−0.918	—	0.232
Crucibulum personatum	0.425	0.928	−0.185	—	−0.684	—	0.250
Crucibulum monticulus	0.597	−0.164	−0.304	−0.656	—	−0.071	0.718
Crucibulum subactum	0.572	—	—	−0.404	—	−0.257	0.391
Nassarius fontainei	0.257	—	−0.818	—	−0.785	—	0.072
Chrysallida vizcainoana	0.251	−0.592	−0.671	—	—	—	0.098
Anadara mazatlanica	0.051	−0.973	−0.916	−0.990	−0.907	—	0.036
Cardita laticostata	0.147	−0.311	—	−0.926	—	—	0.032

Table 4. *McArthur & Levins' overlap index for constant and very common species.*

	McArthur & Levins' overlap index													
	Le	Cl	Dl	Pp	Hp	Cma	Cac	Car	Cp	Cmo	Cs	Nf	Cv	Am
Chaetopleura lurida	0.592													
Dendrochiton lirulatus	0.339	0.291												
Puncturella punctocostata	0.720	0.618	0.354											
Hipponix pilosus	0.670	0.576	0.329	0.700										
Crucibulum mamillaris	0.275	0.235	0.146	0.286	0.266									
Crepidula aculeata	0.753	0.646	0.370	0.787	0.732	0.299								
Crepidula arenata	0.378	0.325	0.186	0.396	0.368	0.152	0.413							
Crucibulum personatum	0.030	0.026	0.078	0.032	0.029	0.079	0.033	0.018						
Crucibulum monticulus	0.128	0.111	0.066	0.133	0.124	0.064	0.138	0.103	0.028					
Crucibulum subactum	0.192	0.169	0.092	0.197	0.184	0.096	0.206	0.103	0.008	0.058				
Nassarius fontainei	0.700	0.601	0.345	0.731	0.680	0.277	0.764	0.384	0.031	0.128	0.456			
Chrysallida vizcainoana	0.655	0.563	0.324	0.685	0.637	0.263	0.716	0.360	0.043	0.121	0.179	0.665		
Anadara mazatlanica	0.759	0.651	0.373	0.830	0.737	0.301	0.828	0.416	0.033	0.139	0.207	0.770	0.721	
Cardita laticostata	0.768	0.659	0.377	0.802	0.747	0.305	0.839	0.426	0.035	0.141	0.210	0.779	0.730	0.845

Le, *Lepidopleura elenensis*; Cl, *Chaetopleura lurida*; Dl, *Dendrochiton lirulatus*; Pp, *Puncturella punctocostata*; Hp, *Hipponix pilosus*; Cma, *Calyptraea mammillaris*; Cac, *Crepidula aculeata*; Car, *Crepidula arenata*; Cp, *Crucibulum personatum*; Cmo, *Crucibulum monticulus*; Cs, *Crucibulum subactum*; Nf, *Nassarius fontainei*; Cv, *Chrysallida vizcainoana*, Am, *Anadara mazatlanica*

C. personatum/*Crepidula arenata* (0.018), which indicated that these species shared very different habitats. Species with similar behaviour and habits (*Calyptraea subactum*, *C. personatum*, *Crucibulum monticulus*, *Crepidula aculeata* and *C. arenata*) presented low overlapping values among them.

Distribution and location of epibionts on the various biological substrata

Epibionts occupied different positions on the six substrata. Generally, the most heavily colonized parts were areas II and I. However, differences in distribution of epibionts were observed on the different substrata.

Hexaplex nigritus: area II presented a greater density of individuals (39.02%) followed by I (32.50%), III (21.18%) and IV (7.28%) (Kruskal–Wallis, $P<0.001$) (Figure 3). However, the number of species was higher in area I (53 species) than in area II (46 species). Gastropod species with low locomotive capacity dominated in area I (e.g. *Lepidozona elenensis*, *Chaetopleura lurida*, *Dendrochiton lirulatus*). Juveniles of species with a greater locomotive activity dominated in area II. *Anadara mazatlanica* was found most abundantly (83.56%) in area III, lodging into a small hole created between a varix and the siphonal fasciole. Species which strongly adhered to the substratum appeared in area IV, with high percentages of *P. punctocostata* (54.71%), *Calyptraea mamillaris* (41.17%), *Crepidula arenata* (38.46%) and *Chaetopleura lurida* (30.43%).

Chicoreus regius: area I was the most colonized (39.82%), followed by area II (35.39%), III and IV (12.38%) (Kruskal–Wallis, $P<0.001$). Area I presented the greatest number of species (22 species), while areas II, III and IV did not have as many (13, four and four species, respectively). Within area III, *Anadara mazatlanica* occupied the same position as on *H. nigritus*. Four very abundant species with strong adherence to the substratum appeared in area IV.

Chicoreus erythrostomus: most of the epibionts appeared in area IV (43.47%), while fewer individuals were found in area II (30.43%) and area I (26.08%) (Kruskal–Wallis, $P<0.01$). However, the greatest number of species were found in area I (nine species). Epibionts like limpets, with low mobility, dominated in this substratum. There were no differences in specific composition between areas I and II. *Crepidula arenata*, *Hipponix pilosus* and *C. aculeata* occurred most abundantly in area IV (90.90, 66.66 and 58.33%, respectively).

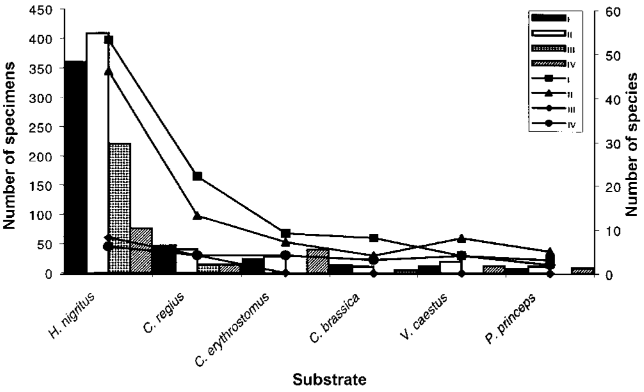

Figure 3. Number of specimens and epibiotic species in each area of the six biological substrates. Bars indicate number of specimens, lines indicate number of species. (I) spire; (II) body whorl; (III) base of shell-siphonal fasciole; (IV) peristome.

Chicoreus brassica: the highest number of epibionts was found in area I (44.82%), followed by area II (37.93%) and IV (17.24%) (Kruskal–Wallis, $P<0.01$). The greatest number of species appeared in area I (eight species). Species from the genera *Hipponix*, *Crucibulum*, *Crepidula*, *Lepidozona* and *Chaetopleura* occurred most abundantly, although they did not show a clear preference for the different parts of the shell.

Vasum caestus: most of the epibionts were found in area II (45.45%), followed by area I (27.27%) and IV (27.27%) (Kruskal–Wallis, $P<0.05$). Specific compositon did not change significantly between area I and II,

Table 5. *Percentages of occurrence for constant and very common epibiont species on each area of shell.*

	Different areas of the shells			
Epibiontic species	Area I	Area II	Area III	Area IV
Lepidozona elenensis	31.14	31.14	25.71	0.00
Chaetopleura lurida	33.87	35.48	3.22	27.41
Dendrochiton lirulatus	62.5	31.15	6.25	0.00
Puncturella punctocostata	50	33.33	0.00	16.66
Hipponix pilosus	38.09	36.50	15.87	9.52
Calyptraea mamillaris	25	25	0.00	50
Crepidula aculeata	42.29	41.89	0.00	15.81
Crepidula arenata	25.35	40.14	0.00	34.50
Crucibulum personatum	43.75	0.00	15.62	40.62
Crucibulum monticulus	43.75	50	0.00	6.25
Crucibulum subactum	36.36	63.63	0.00	0.00
Nassarius fontainei	65	35	0.00	0.00
Chrysallida vizcainoana	66.66	11.11	22.22	0.00
Anadara mazatlanica	8.11	28.57	63.31	0.00
Cardita laticostata	51.61	48.38	0.00	0.00

although area II (eight species) had more species than areas I and IV (four species in both). Moreover, *Crucibulum personatum*, *C. scutellatum*, *Crepidula aculeata* and *C. arenata* were almost the only species found in area IV.

Pleurocopa princeps: area II (41.37%) was the most colonized, followed by area IV (31.03%) and I (27.58%) (Kruskal–Wallis, $P<0.05$). The number of species did not change significantly between areas II, I and IV (five, three and two species, respectively). Sedentary species pertaining to the genera *Lepidozona*, *Chaetopleura*, *Lepidochitona*, *Hipponix*, *Calyptraea*, *Crepidula* and *Crucibulum* colonized this substrate. *Hipponix pilosus* and *Calyptraea mamillaris* dominated in area IV (100 and 66.6%, respectively).

Significant differences could be observed in the distribution of constant and very common species on the different areas of the shell (Kruskal–Wallis, $P<0.001$). Each epibiont species showed a clear tendency to occur on different specific areas of the shell. Most of these species occurred mainly in areas I and II (Table 5), except for *Calyptraea mamillaris* (area IV, 59.80%) and *Anadara mazatlanica* (area III, 66.78%). *Lepidochitona elenensis*, *Dendrochiton lirulatus*, *Puncturella punctocostata*, *Hipponix pilosus*, *Crepidula aculeata*, *Crucibulum personatum*, *Nassarius fontainei*, *Chrysallida vizcainoana* and *Cardita laticostata* occurred most abundantly in area I (>54.63%), while *Chaetopleua lurida*, *Crucibulum monticulus* and *Calyptraea subactum* dominated in area II (>58.33%).

DISCUSSION

The majority of sedentary epibionts, except for chitons, were suspension-feeding organisms which are favoured by the currents generated by the movement of the mollusc host, which guarantees the availability of food. *Calyptraea mamillaris*, *Crepidula arenata* and *C. aculeata* dominated on different parts of the shells, area IV, I and II, respectively. This can be explained by their tendency to be gregarious species, which monopolize the space where they grow, impeding or restricting the settlement of larvae of other species as a side effect of space occupation (McGee & Targett, 1989).

Since most marine communities experience intense competition for substrate space (Paine, 1974; Jackson, 1977; Marcus et al., 1997), colonization of living substrates may be beneficial to epizoans. Epibiosis on molluscs can involve some costs for the host, such as an increase in weight, since the host will be less agile and more vulnerable to predators (Overstreet, 1983). However, many other host species benefit from epibiosis in terms of camouflage (Key et al., 1995). Some authors have postulated competition for nutrients (particulate, dissolved and gaseous) between epibiont and host (Novak, 1984; Bronmark, 1985). When the epibiotic partners exhibit the same trophic requirements, water reaching the host may be already partially depleted after passage through the 'epibiotic filter'. In this study, however, trophic requirements were different, since all hosts were carnivorous, preying on large organisms, principally bivalves, while the greatest part of epibionts occupied a different trophic niche: suspension-feeders (40%), deposit-feeders (9.33%), herbivores (17.33%), small carnivorous predators of sponges, hydrozoans and ascidians (28%), and parasites of small invertebrates (5.33%).

The most of organisms which colonized the different neogastropods were species typical of hard substrata, the shell of the neogastropod constituting a hard substrate for them. In an environment where sandy bottoms dominate, colonization of these living substrates may be beneficial to epizoans which require hard surfaces. On the other hand, epibiotic settlement frequently implies a hydrodynamically favourable position (Linskens, 1963; Keough, 1984, 1986). Other factors could be the free transport offered by mobile hosts which may improve nutrient conditions (site change, currents) and facilitate dispersal and gene-flow among epibiont populations. A few species typical of soft-bottoms like *Nassarius* sp., *Bellaspira acclivicosta*, *Epitonium thylax*, *Caecum* sp. and *Turritella lentiginosa* appeared on neogastropod shells. Their occurrence could be accidental, or maybe they found availability of food on shells (polychaetes, sponges, detritus...).

Another advantage of epibiosis is the camouflage and availability of refuges which host shells provide, principally muricids, among them *Hexaplex nigritus*, contributing with its strong ornamentation to the defence against possible predators. Moreover, the strong ornamentation provides microhabitats of protection for juvenile phases of mobile individuals. Thus, we observed that juvenile mobile individuals dominated on *H. nigritus*, lodging among spines of the shell (areas I and II). In the same way, *Anadara mazatlanica* lodged into a hollow formed by the varix and the siphonal fasciole (area III), staying protected from possible predators. The biggest sedentary species of the genus *Crucibulum* occurred on the parts of the shell where they had a greater surface to which to adhere, that is, in areas I (many times eroded), II and IV. On the other hand, the smaller-size chitons dominated on *H. nigritus*, adhering to the spines of area I. In this zone, which is the most eroded in aged molluscs, filamentous and coralline algae, (which are the food of the small chitons) are settled. The carnivorous species like *Cerithiopsis pupiformis*, *Jorunna pardus*, *Bellaspira acclivicosta*, *Mitrella dorma*, *Granulina margaritula* and the parasites

Odostomia scalariformis, *Aspella myrakeenae* and *Turbonilla azteca* were more abundant in zone I, where potential prey and hosts appeared (sponges, hydrozoans, ascidians and polychaetes).

One benefit for the neogastropod could be camouflage, because the epibiotic cover can play a protective role (Wahl, 1989). However, this is not very clear in this study, due to the limited surface occupied by all epibiotic organisms. On the other hand, the mobile hosts may expose the epibionts to environments where the temperature, salinity, and/or dissolved oxygen are suitable for the neogastropod hosts, but harmful for the colonizers (Marcus et al., 1997). However, the ecological range of the neogastropod hosts and small mollusc epibionts was similar.

The high overlap values observed between some species can show evidences for interspecific competition among species (Black, 1979). However, no evidence for interspecific competition appeared in this study since species belonging to the same genus avoided competition through habitat selection (different hosts or different areas in the shell). On the other hand, the highest overlapping occurred between species which exploited different resources (*Anadara mazatlanica*, *Cardita laticostata* and *Crepidula aculeata*).

In this study, it appears to be a greater benefit to the small epibiont molluscs than to the neogastropod hosts. Therefore, small molluscs used neogastropod shells as an available habitat in sandy bottoms (epibiotic association), in addition to facilitating their transport (phoretic association). Besides, hosts supplied food for small carnivorous and parasitic epibiotic molluscs. On the other hand, neogastropods, due to their strong ornamentation, offered a bigger surface to which to adhere, and better protection, for mollusc epibionts.

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