

Spatial niche partitioning in the *Cellaria* meadow epibiont association, northern Adriatic Sea

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Abstract: A diverse assemblage of foraminiferans, rhodophytes, sponges, hydroids, bryozoans, polychaete annelids, and ascidians lives within the dense mat formed by branches of the erect bryozoan *Cellaria salicornioides* that carpets a 35 m deep "meadow" west of Banjole Island offshore of Rovinj, Croatia. A variety of modular growth habits predominates among the epibionts, but almost all the most common species grow laterally by runner-like extensions. Although the depth distribution of each species within the mat has high variance, spatial niche partitioning is indicated because depth distributions of species can be discriminated statistically one from the other. Higher-level clade distribution within the mat generates three statistically defined zones: a shallow zone characterized by foraminiferans, rhodophytes and sponges; an intermediate zone characterized by hydroids, ctenostome bryozoans, annelids and ascidians; and a deep zone characterized by cheilostome and cyclostome bryozoans. The calcified bryozoans also show a pattern in the distribution of growth habits, with erect flexible colonies being on average shallowest, encrusting colonies being intermediate, and erect rigid colonies deepest.

Résumé : Répartition spatiale de l'association d'épibiontes sur une prairie de *Cellaria*, dans l'Adriatique nord. Un assemblage varié de Foraminifères, Rhodophytes, Eponges, Hydraires, Bryozoaires, Polychètes et Ascidies habite la mat dense créée par les ramifications étendues des colonies du Bryzoaire *Cellaria salicornioides* qui forme une prairie, à 35 m de profondeur, située à l'ouest de l'île de Banjole au large de Rovinj, Croatie. Le développement des épibiontes est essentiellement caractérisé par une diversité de modes de croissance, mais presque toutes les espèces les plus communes poussent latéralement au moyen d'expansions comparables à des stolons. Bien que la distribution de chaque espèce dans la mat varie, leur distribution spatiale peut être définie car elle est statistiquement différente d'une espèce à l'autre. La distribution des taxons d'un niveau supérieur dans la mat permet de reconnaître trois zones bien définies: une zone superficielle caractérisée par les Foraminifères, les Rhodophytes et les Eponges; une zone intermédiaire caractérisée par les Hydraires, les Bryozoaires Ctenostomes, les Polychètes, les Ascidies et les Eponges; une zone profonde caractérisée par les Bryozoaires Cheilostomes et Cyclostomes. Les Bryozoaires calcifiés ont aussi une répartition précise, les colonies érigées flexibles étant en moyenne les moins profondes, les colonies encroûtantes étant intermédiaires et les colonies dressées et rigides les plus profondes.

Keywords : Bryozoa, epibionts, growth habit, modular organisms, niche partitioning

Introduction

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Shallow-water sand to mud substrates commonly are covered locally by dense growths of marine grasses. Where

such seagrass stands occur, sediments are less well sorted and biomass and species richness are substantially higher than in nearby bare areas (Stoner, 1980; Castel et al., 1989). Dense stands of other erect-growing modular organisms covering soft-sediment substrates are less well studied, although they are known to occur locally in contemporary marine habitats (Nikolić, 1959; Castel et al., 1989; Henrich et al., 1995) and have been noted in the fossil record back to the Paleozoic (Radenbaugh & McKinney, 1998). The term “modular” is used in this paper in the usual sense of botanists and zoologists to refer to an organism that grows by iterative proliferation of similar functional units (e.g. Jackson et al., 1985; Hughes, 1989) and therefore encompasses colonial organisms such as hydroids and bryozoans and some others such as sponges and rhodophytes that are not colonial but that have life cycles that consist of proliferation of similar units.

The small limestone island of Banjole, offshore from Rovinj, Croatia (Fig. 1), is surrounded by a sand plain that isolates it from other nearby carbonate islands and underwater hills. On the west side of Banjole, the sand plain is 35 meters deep and is barren of epifauna for approximately 7 meters adjacent to the steep-sided limestone mass that rises from the plain to form the island. West of the barren apron, the flat plain is 80-90% covered by a dense meadow of intergrown colonies of the articulated cheilostome bryozoan *Cellaria salicornioides* Lamouroux, 1816 with minor *Cellaria fistulosa* (Linnaeus, 1758). The

meadow extends for an unknown distance westward. The mat of intergrown *Cellaria* colonies locally is so dense and continuous that it can be peeled as large, unbroken sheets of turf from the sand substrate (Fig. 2). Diverse benthic organisms live within the tangle of *Cellaria* branches, most encrusting directly on them.

Vertical gradients in environmental attributes are well known to produce horizontally extended microenvironments that are the basis for vertically stacked tiers of associations of organisms. Such organic tiering is seen within virtually all environments, from forests and soils to the pelagic realm, arborescent marine epibenthic associations and sediment-burrowing and rock-boring marine endobenthos. The *Cellaria* meadow west of Banjole generates a horizontally extended, approximately 5-6 cm thick tangle of branches between the open Adriatic water above and firmly packed sediment below. Within the mat that constitutes the meadow, there are at minimum three microenvironments: - an upper thin zone at outer branch tips that experience reversing tidal flow and storm wave oscillation, - the quiet water region due to baffling by branches within the *Cellaria* mat, - and the sediment-water interface that forms the base of the mat. The middle microenvironment, constituted by the tangle of *Cellaria* branches, could hardly be uniform, but must be a transitional zone in which a complex of physical, chemical, and biological attributes gradually changes from top to bottom.

The purpose of this paper is to document the diverse association of sessile organisms that grow as epibionts within the *Cellaria* meadow west of Banjole (Fig. 1), to assess patterns of distribution of the epibionts within the dense meadow, and to consider some possible causes of their vertical zonation.

Materials and methods

The meadow was sampled by scuba diving in June and November 1997 and again in July 1998. Samples approximately 25 cm x 25 cm were cut by one of us (AJ) on 3 June 1997, 18 November 1997, and 3 July 1998 (Fig. 2). On 3 July 1998, two 25 cm x 25 cm samples were cut, one from densely grown *Cellaria* colonies resembling samples from June 1997 and one from less dense conditions resembling the November 1997 conditions. Individual bushy colonies of *Cellaria* were collected by hand by Masimo Devescovi on 15 July 1998.

The four 25 x 25 cm samples were partially dissected, branch system by branch system. For 10 of the branch systems in each of these samples, all encrusting foraminiferans and multicellular

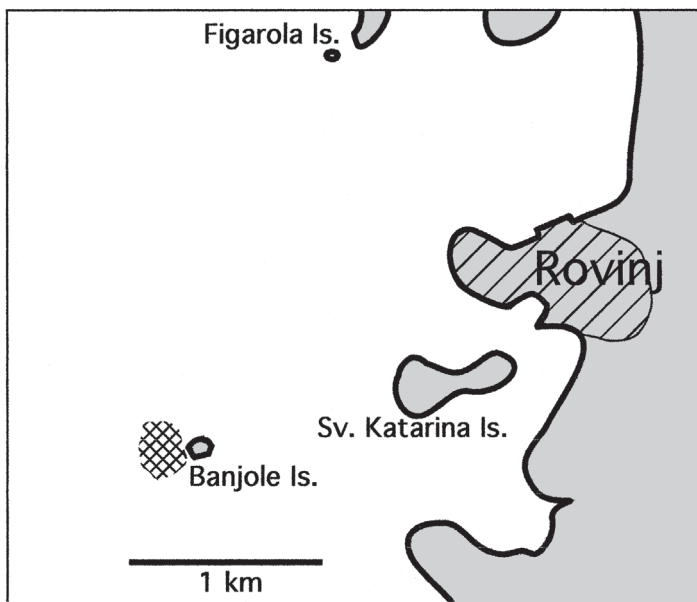


Figure 1. Location of *Cellaria* meadow (cross-hatch pattern), west of Banjole, offshore from Rovinj, Croatia.

Figure 1. Situation de la “prairie” à *Cellaria* (trame croisée), à l’ouest de Banjole, au large de Rovinj, Croatie.



Figure 2. *Cellaria* meadow, 35 m depth, west of Banjole, July 1998. "Normal" dense mat is seen on the lower right, and the reduced density, typical of November 1997, is apparent along the top of the photograph. Width of foreground is approximately 0.3 m.

Figure 2. Prairie de *Cellaria* in situ, à 35 m de profondeur, juillet 1998. Une matte dense normale est visible en bas à droite, tandis que la densité réduite, typique de novembre 1997, est visible en haut de la figure. La largeur au premier plan de la figure est d'environ 0,3 m.

organisms seen at X50 magnification were identified and the branch segment noted to which each was attached.

The *Cellaria* mat consisted of a dense tangle of interdigitated branches, and interpenetration of branch systems was most thorough in the dense mats of June 1997 and July 1998. Branch systems could seldom be traced to their point of origin but were usually broken because of manipulation. Branch systems were broken at shallower depths in June 1997 than at subsequent times. Consequently, fewer branch segments were seen in the 10 branch systems examined in June 1997.

Cellaria branches increase by dichotomous bifurcation. Colonies consist of rigidly calcified branch segments connected by narrow, secondarily decalcified flexible nodes that occur at regularly-spaced bifurcation points. Occasionally a flexible node gives rise to only one descendant branch rather than two branches. Position of encrusters on the *Cellaria* branches was recorded following the Horton Analysis protocol, a system of branch order designation used for designation of segment hierarchies in other branching systems (Leopold & Langbein, 1962; Stevens, 1974). All terminal branches were designated by a 1, and each more proximal branch segment was designated by a progressively higher number (Fig. 3). Any terminal segment was designated by a 1, whether or not its companion branch had descendant branches and therefore

had a higher number designation. However, most terminal numbered segments are at far outer ends of branch systems and constitute the upper surface of the mat.

Additional branch segments were disentangled and dissected from the mat samples in order to see larger numbers of the less prolific encrusters and to determine their location by segment. Positions of 667 encrusting organisms were recorded for the June 1997 sample, 1594 for the November 1997 sample, 2231 for the dense *Cellaria* growth July 1998 (including a few records from the hand-collected July 1998 *Cellaria* specimens), and 1259 for the less dense *Cellaria* growth July 1998.

Results

Abundance of *Cellaria*

The *Cellaria* mat on 3 June 1997 covered 80-90% of the sediment surface, which corresponds with the condition seen in the meadow from July to late September for at least the previous ten years. *Cellaria* colonies constituted

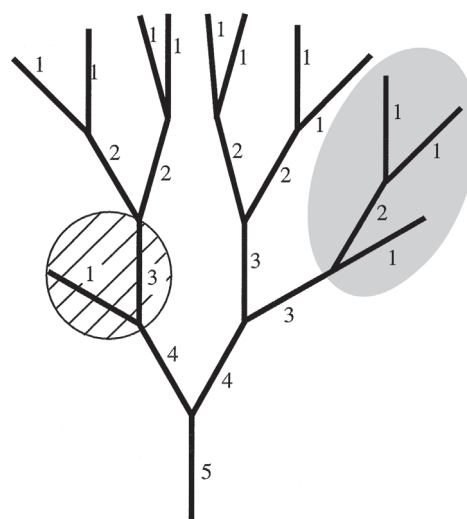


Figure 3. Stylized dichotomously divided branch system, with segments sequentially numbered from distal tips according to protocol of Horton analysis. Shaded area demonstrates junction of a terminal segment (1) with a sister segment (2) that has produced two additional segments at its distal end; the lined area marks the junction of a terminal segment (1) with a sister segment (3) that has multiple generations of descendant segments.

Figure 3. Schéma des ramifications dichotomiques numérotées à partir des branches distales selon le protocole d'analyse de Horton. La partie grise indique la jonction d'un segment distal (1) avec un segment frère (2) qui a produit deux segments à son extrémité distale; l'aire délimitée indique la jonction d'un segment terminal (1) avec un segment frère (3) qui a de multiples générations de descendants.

119 grams (56.6%) of the total 210 grams wet biomass and 52.1 grams (52.3%) of the total 99.6 grams dry skeletal mass within the 25 cm x 25 cm sample area of 3 June 1997. Therefore, among the sedentary epibenthic organisms, *Cellaria* constituted the greatest biomass and dry skeletal mass.

On 18 November 1997 only 50-60% of the sediment surface was covered by *Cellaria*, and colonies were on average shorter than in the previous June, estimated at about 3-4 cm average rather than the 5-6 cm average that characterized the mat in June. *Cellaria* colonies constituted 10.0 grams (17.5%) of the total 57.1 grams wet biomass and 3.7 grams (17.4%) of the total 21.3 grams dry skeletal mass within the 25 cm x 25 cm sample area of 18 November 1997. Even though less than 50% of the totals, *Cellaria* constituted a greater proportion of the biomass and dry skeletal mass among the sedentary organisms and their epibionts than any other species.

The *Cellaria* meadow in July 1998 was characterized by a mosaic of 80-90% and 40-50% cover by *Cellaria* colonies, so that part of the area resembled the June 1997 conditions and part resembled the November 1997 conditions. Biomass and skeletal mass of measured areas were not determined in July 1998.

The contrast in summer and late autumn 1997 conditions, with partial recovery by July 1998 suggests annual growth and die-back of the meadow. This apparently occurs by portions of *Cellaria* colonies breaking off during autumn and winter, with regeneration from the bases of pre-existing colonies during the following summer, similar to the pattern seen in *Cellaria* colonies in the English Channel (Bader, in press). Although recruitment of sexually-produced larvae undoubtedly occurs, its rate is unknown. Larval recruitment and establishment of new colonies appear to account for a relatively small proportion of the annual change in biomass. This is because no known examples of colonies originating from an ancestrula were encountered in the dissected mats, whereas a large number of laterally-budded branches deep within colonies could be seen as the basis for extensive regenerative growth.

Fully dissected branch systems

The majority of the terminal branch segments of *Cellaria* constituted the upper surface of the mat (Fig. 3) and usually originated as dichotomous pairs. However, in the fully dissected and recorded branch systems, 117 of the 1206 terminal branches (i.e., 9%) did not join other terminal branches but instead joined "sister" branches that had a single pair of descendant branches (shadowed area, Fig. 3). This "mismatch" of terminal and subterminal branches was in most cases the result of slightly more vigorous growth of one of the pair so that it had reached its full length and

subsequently had divided into two incompletely developed descendants. Only 46 terminal branches (i.e., 4%) joined "sister" branches with more than one descendant pair of branches (patterned area, Fig. 3); in such instances the mismatched terminal branches were within, rather than at, the surface of the mat. These results were consistent across all four sets of fully dissected branch systems (Table 1).

Table 1. Patterns of junction of terminal branches in fully dissected branch systems. For examples of types of junctions, see Figure 3.

Tableau 1. Distribution des connexions des branches terminales avec les autres branches sur des échantillons entièrement dissociés. Pour les junctions entre segments, voir Figure 3.

Joined to:	June 1997	Nov. 1997	Low density July 1998	High density July 1998	Total
Segment 1	117	298	262	366	1043
Segment 2	12 (9%)	31 (9%)	28 (9%)	46 (11%)	117 (10%)
Segments >2	5 (4%)	23 (7%)	8 (3%)	10 (2%)	46 (4%)
SUM >1*	17 (13%)	54 (15%)	36 (12%)	56 (13%)	163 (14%)

*This is the total number of terminal branch segments that were twinned with branch segments that were not themselves terminal.

Slightly fewer than half (48.2%) of the segments in the four sets of fully dissected branch systems were encrusted by diverse multicellular taxa visible at X50 magnification, but the proportion changed rapidly from outer branch segments to deeper within the colonies. Outer branch segments made up almost half of the total segments (1206/2728) in the fully dissected branch systems, and only a small proportion of these most recently formed outer branch segments were occupied by encrusters (Fig. 4). But beginning with the penultimately formed segments, the majority were encrusted and the proportion increased inwardly within the mat to a point at which encrusting organisms were present on all branch segments. The branch systems examined in November 1997 (open circles in Fig. 4) were the least abundantly encrusted. They deviated from the general pattern of constant inward increase in proportion of branches occupied, having a slight decrease below the sixth level.

The mean number of encrusting taxa per branch segment also increased inwardly from the distal ends of the branch systems (Fig. 5). There were on average 0.13 species per distal branch segment, with an increase to about three species per segment at the eighth level, and a slight decrease below that level. The systems examined in November 1997 generally had the lowest values for diversity per segment, which parallels results for proportion of branch segments occupied.

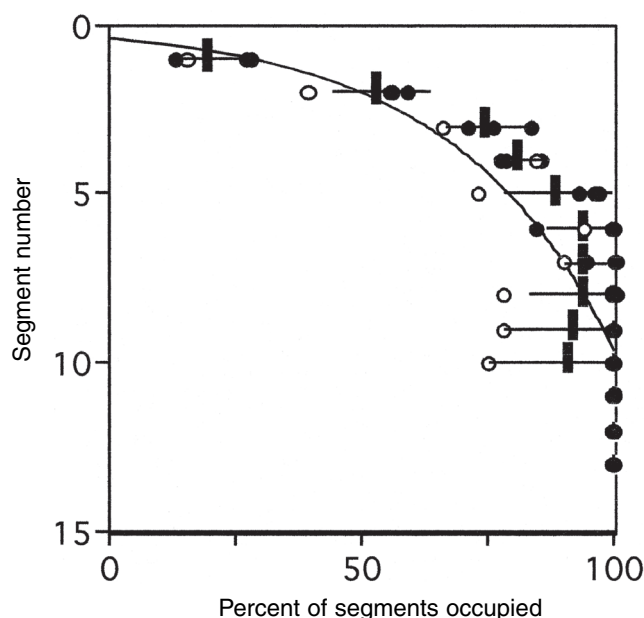


Figure 4. Percent of branch segments occupied by epibionts. June 1997 and July 1998 data are represented by filled circles; November 1997 data are represented by open circles. The curve is based on all four data sets and follows the formula $Y = 0.416 \cdot 10^{0.014X}$. Vertical strokes represent the mean of the mean values, and horizontal lines indicate 1.96 standard error.

Figure 4. Pourcentage des segments portant des épibiontes. Les données de juin 1997 et de juillet 1998 sont représentées en noir ; les données de novembre 1997 sont en blanc. La courbe est basée sur l'ensemble des données. Equation de la courbe : $Y = 0,416 \cdot 10^{0.014X}$. Les barres verticales représentent la moyenne des valeurs moyennes ; les lignes horizontales correspondent à 1,96 fois l'erreur standard.

The most abundant encrusting multicellular taxa, from their points of appearance on the fully dissected branch segments, all increased inwardly in the proportion of branch segments that they occupied (Fig. 6). Distal segments were occupied most commonly by the filamentous red alga *Aglaothamnion* sp. and the stoloniferous ctenostome bryozoan *Walkeria tuberosa* (Heller), which is characterized by local clusters of zooids located along the stolons.

Notably all of the most abundant species are clonal, and all but the ascidian *Polycitor* spp.? extended by creeping stolons. Therefore each clone usually occupied more than one branch segment. The six species reached their greatest proportional cover at varying depths (Fig. 6), reflected also in their depth distribution statistics (Table 2). *Nolella stipata* Gosse occurred on average much deeper than the other abundant species, and its depth distribution was significantly different ($p < 0.05$) from each of the others (Table 3). The next deepest species, a green perophorid

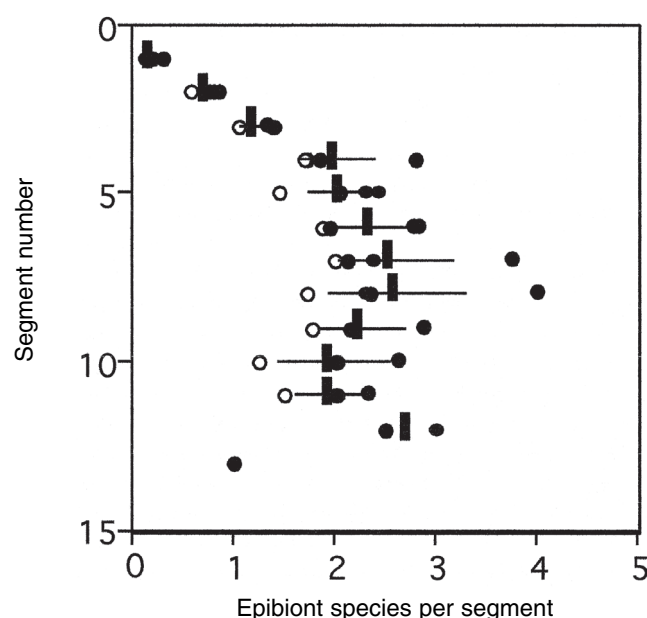


Figure 5. Number of taxa per branch segment. Each point represents the average for one of the four sets of branch systems examined. Vertical strokes and horizontal lines as in Figure 4.

Figure 5. Nombre de taxons sur les différentes branches de *Cellaria*. Chaque point représente la moyenne de quatre groupes de branches examinés. Barres verticales et lignes horizontales comme dans la Figure 4.

ascidian, also had a significantly different distribution from each of the other species except *Campanularia hincksi* Alder.

The attached foraminiferan *Ammonia tepida* (Cushman) was excluded from the descriptions given above, which are based exclusively on multicellular organisms attached to the *Cellaria* branch systems. Population density of *A. tepida* was so high in July 1998 that its inclusion would have masked the patterns of distribution that can otherwise be seen within the mat. A summary of the distribution pattern of *A. tepida* is given in the following section.

Distribution of attached taxa

The most common groups of organisms attached to branches of *Cellaria* are Bryozoa, followed in sequence by Rhodophyta, Sarcodina, Urochordata, Annelida, Porifera, and Cnidaria. Differences in depth distribution within the *Cellaria* mat could be seen among these groups (Fig. 7, Table 4). The bryozoan clade Cyclostomata was on average the deepest-occurring taxon, and its distribution differed significantly from distributions of all other groups. Given the large number of individual records for each group, depth distribution of almost all groups differs from each other group. The only exceptions are the shallow-occurring

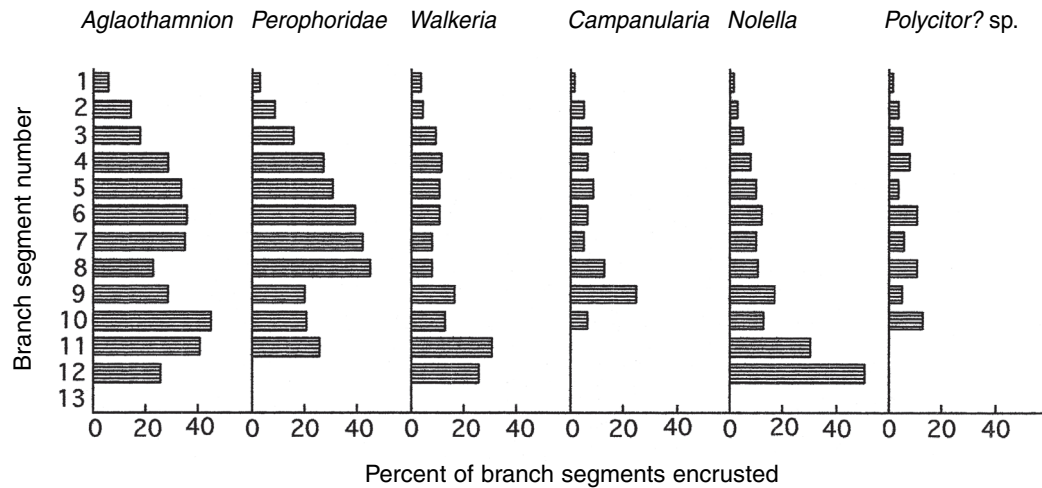


Figure 6. Percent of branch segments occupied by the six most common species in the fully dissected branch systems.

Figure 6. Pourcentage des segments occupés par les six taxons les plus communs trouvés dans les échantillons entièrement dissociés.

Table 2. Supplementary descriptive statistics of distribution of the six most abundant multicellular attached species within the *Cellaria* mat, listed in order of decreasing abundance.

Tableau 2. Localisation statistique des six espèces les plus abondantes sur les ramifications de *Cellaria*, donnée par ordre d'abondance décroissante.

Species	Mean*	Depth of attachment (branch segment number)				Skewness	Kurtosis
		Median	Mode	Std Dev.			
<i>Aglaothamnion</i> sp.	3.53	3	2	2.17		1.087	1.014
<i>Perophoridae</i> , gen. et sp. indet.	3.97	4	3, 4	2.27		0.816	0.194
<i>Walkeria tuberosa</i>	3.76	3	3	2.19		1.170	1.615
<i>Campanularia hincksi</i>	3.60	3	3	2.21		1.067	0.570
<i>Nolella stipata</i>	4.66	4	4	2.48		0.828	0.462
<i>Polycitor?</i> sp. 1	3.49	3	2	1.95		0.956	0.663

*Mean = (\sum branch segment number)/number of segments; Median = the middle segment number when encrusted segments are listed in increasing numerical sequence; Mode = most commonly occurring encrusted segment number

Table 3. Mann-Whitney U test comparisons (p values) of depth distributions of the six most abundant attached multicellular species in the fully dissected branch systems of *Cellaria*.

Tableau 3. Comparaison (valeur-p), basée sur le test de Mann-Whitney U, des profondeurs où vivent les six espèces de métazoaires fixés les plus fréquentes sur les différentes branches de *Cellaria* entièrement dissociées.

	A. sp.	Pero.	W. t.	C. h.	N. s.
<i>Perophoridae</i> gen et sp. indet.	.001				
<i>Walkeria tuberosa</i>	.513	.016			
<i>Campanularia hincksi</i>	.701	.080	.917		
<i>Nolella stipata</i>	<<.001	.003	<<.001	<.001	
<i>Polycitor?</i> sp. 1	.760	.027	.822	.921	<<.001

A. sp. = *Aglaothamnion* sp.; Pero. = *Perophoridae*, gen et sp. indet.; W. t. = *Walkeria tuberosa*; C. h. = *Campanularia hincksi*; N. s. = *Nolella stipata*

Rhodophyta and Porifera, and some pairings between the intermediate-depth groups Hydroidea, Ctenostomata, Annelida, and Ascidia.

Fifty-eight species-level taxa attached to branches of *Cellaria* were recognized within the sections of the mat examined, and additional species were represented in the sponges, cnidarians, bryozoans, and polychaetes that could not be resolved (Appendix). Some species were relatively constant in relative abundance and in depth of attachment, while others varied either temporally or spatially among the four samples studied in detail (Table 5). Most species (65%) had mean depths of attachment between branch segments 3 and 5 (Fig. 8)

Among the six most common multicellular species, the green compound perophorid ascidian was most variable in relative abundance: it was not encountered in the June 1997 sample, and it was dominant in the November 1997 sample,

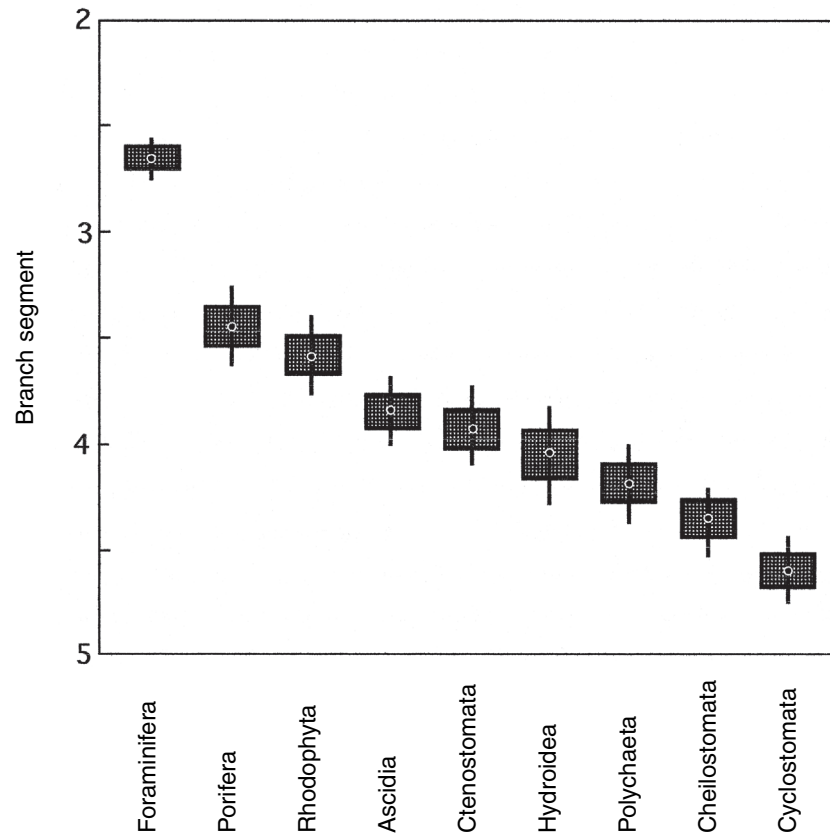


Figure 7. Depth distributions of the major attached taxa within the *Cellaria* mat. Dots mark mean values, shaded boxes indicate standard error, and bars indicate 1.96 standard error.

Figure 7. Distribution, selon la profondeur, des taxons d'ordre supérieur dans la matte de *Cellaria*. Les points indiquent les valeurs moyennes ; les rectangles ombrés indiquent l'erreur standard ; les barres correspondent à 1,96 fois l'erreur standard.

Table 4. Mann-Whitney U tests for differences in depth distributions of the major attached taxa within the *Cellaria* mat.

Tableau 4. Tests de Mann-Whitney U pour les différences dans la localisation des principaux taxons, fixés selon la profondeur, dans la colonie de *Cellaria*.

	Rho	Sar	Por	Hyd	Cyc	Cte	Che	Ann
Sarcodina	<<.001							
Porifera	.630	<<.001						
Hydroidea	.001	<<.001	.001					
Cyclostomata	<<.001	<<.001	<<.001	<<.001				
Ctenostomata	.004	<<.001	.002	.664	<<.001			
Cheilostomata	<<.001	<<.001	<<.001	.001	.023	<<.001		
Annelida	<<.001	<<.001	<<.001	.183	<<.001	.035	.017	
Ascidia	.013	<<.001	.007	.252	<<.001	.578	<<.001	.005

Rho = Rhodophyta; Sar = Sarcodina; Por = Porifera; Hyd = Hydroidea; Cyc = Cyclostomata; Cte = Ctenostomata; Che = Cheilostomata; Ann = Annelida

with pronounced differences in abundance between the low- and high-density samples taken in July 1998. Some of the

variation between the latter three samples may be due to patchiness of distribution, but the species was not

Table 5. Average depth of occurrence (scored by branch segment number) and number of observations for the most abundant epibionts on *Cellaria* in each of the four samples. Averages are given as both mean and median, followed by number of observations.

Tableau 5. Indication de la profondeur et du nombre d'observations des épibiontes les plus abondants sur les *Cellaria* dans chacun des quatre prélèvements. Les indications sont données à la fois par la moyenne et la médiane, suivies du nombre des observations.

Taxon	Mean/Median/Number of observations			
	June 97	Nov. 97	Low-d. 98	High-d. 98
<i>Ammonia tepida</i>	---	3.22/3/77	2.48/2/620	2.22/2/648
<i>Aglaothamnion</i> sp.	3.42/3/81	3.68/3/249	4.00/3/116	2.67/2/99
Perophoridae, gen et sp. indet.	---	4.13/4/208	5.20/5/20	3.60/3/156
<i>Walkeria tuberosa</i>	3.76/3/86	3.30/3/105	4.78/3/45	3.33/3/139
<i>Polycitor?</i> sp. 1	3.88/4/26	3.09/3/56	3.81/3/32	3.51/3/60
<i>Nolella stipata</i>	4.20/3/5	4.28/4/29	5.19/4/63	4.22/4/45
<i>Campanularia hincksi</i>	2.62/3/24	3.98/3/46	3.71/3/41	3.77/3/13

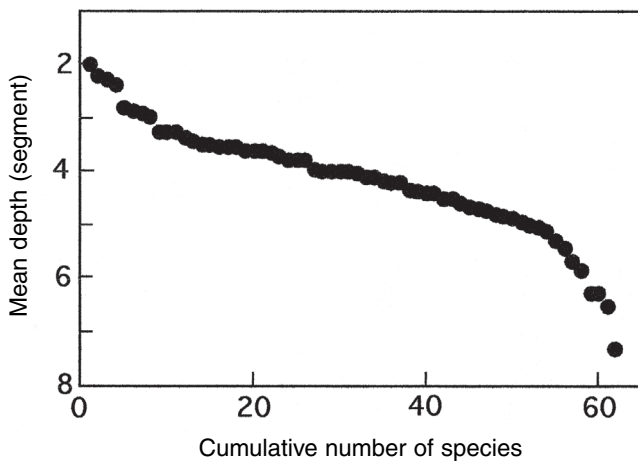


Figure 8. Mean depth of attachment of each species.

Figure 8. Profondeur moyenne de fixation des épibiontes.

encountered at all in several additional samples of the *Cellaria* mat seen in June 1997 nor in any of the samples of the *Cellaria* mat examined during the previous ten years. Its abundance in the November 1997 and July 1998 samples apparently represents a population bloom. The green perophorid ascidian was significantly shallower in the high-density 1998 section than in the other two sections in which it occurred (Mann-Whitney U test, $p < 0.01$ for both comparisons).

Aglaothamnion sp. was common in all sections of the *Cellaria* mat, but like the green perophorid ascidian, it also was significantly shallower in the high-density 1998 section in comparison with its other occurrences (Mann-Whitney U test, $p < 0.001$ for each). Depth distribution of *Aglaothamnion* sp. in the other three sections were indistinguishable from one another at $p = 0.05$.

The greatest temporal variation was seen in *Ammonia tepida*, which was not encountered in the June 1997 section. However, it was moderately abundant in the November 1997 section, and was found in profusion in both July 1998

sections (Table 5) as well as in all other samples of the *Cellaria* mat taken in a random transect on 15 July 1998. This population bloom of *A. tepida* also resulted in the shallowest distribution of all the organisms seen in the various sections of the *Cellaria* mat examined. In both the low-density and the high-density 1998 sections, the modal distribution of *A. tepida* was on the 1st segment, with distribution patterns (Table 5) that are significantly different from each of the other abundant species. *A. tepida* occurred at mid-mat levels in November 1997, with distribution generally similar to many multicellular taxa. However, its distribution in both the low-density and high-density mats 1998 was significantly shallower than its earlier occurrence (Mann-Whitney U, $p < 0.001$) and also shallower than any other abundant taxon within the same samples (Mann-Whitney U, $p < 0.01$) except for *Aglaothamnion* sp. in the high-density mat, where both species were unusually shallow in occurrence.

Modular growth characterizes the Porifera, Hydroidea, Bryozoa, and some Ascidia. Modularity did not in itself significantly affect depth of attachment within the *Cellaria* mat (Mann-Whitney U test, $p = 0.110$, $N = 3679 + 441$). Foraminifera are excluded from this comparison because their extraordinary 1998 abundance overwhelms and masks patterns seen in the multicellular species in which population density fluctuated less.

The modular organisms commonly grew erect and extended into the water column away from the substratum to which they are attached; others were entirely or predominantly recumbent (Appendix), commonly extending in vine-like runners along or across branches, or expanding peripherally as patches. Two different depth-distribution patterns within the *Cellaria* mat emerged, when depth distributions of all erect species were combined together, and all encrusting species were combined together.

The erect and encrusting growth habits occurred at all depths within the *Cellaria* mat. The median and mean depths of attachment for erect modular organisms were 4

and 4.21, and the median and mean for encrusters were 4 and 3.96. The distributions are significantly different (Mann-Whitney U, $p = 0.001$; $N = 529 + 3150$). Even though the median values are identical, differences in their mean values demonstrate that there is a higher proportion of greater depths for erect organisms relative to encrusting organisms.

The most common erect modular organisms are cyclostome and cheilostome bryozoans. Comparisons of depth-distribution of erect versus encrusting colonies within these two groups show different patterns. There is no detectable difference in overall depth distributions of erect and encrusting cyclostomes, both of which had almost identical distributions (median and mean values of 4 and 4.64 for erect, and 4 and 4.59 for encrusting cyclostomes; Mann-Whitney U, $p = 0.854$; $N = 227 + 331$). In contrast, erect cheilostomes were significantly shallower (mean = 4.08, median = 4, $N = 149$) than encrusting cheilostomes (mean = 4.47, median = 4, $N = 447$) (Mann-Whitney U, $p = 0.029$).

Discussion

General distribution of dense growths of *Cellaria*

The cheilostome bryozoan genus *Cellaria* has a broad depth and geographic distribution, commonly occurring as individual arborescent tufts attached by stolons to various skeletal and rock substrata. Live colonies have been reported attached to pebbles, rock walls, and various organic substrates including diverse carbonate skeletons, hydroids, octacorals, and the thecate ascidian *Microcosmus*; on scoured (bare rock) to low-energy (mud and foraminiferal ooze) surfaces; from cold temperate to equatorial localities; and from less than 20 m to over 1000 m deep (Gautier, 1962; Cook, 1985; Gordon, 1986; Henrich et al., 1995). A study of bryozoan fragments in sediments of the Rhône delta recorded abundant *Cellaria* fragments in sediments deposited in water as shallow as 1.5 m, with the implication that the fragments were locally derived (Lagaaij & Gautier, 1965). Most species characteristically occur at shelf depths (generally less than 100 m), although one species appears to be exclusively bathyal (Gordon, 1986).

In the northeastern Adriatic, *Cellaria* occurs commonly on diverse hard substrata, from about 20 m down to the greatest local depth of about 66 m. The cheilostome bryozoan species *Pentapora foliacea* (Solander) formerly dominated the epifauna at 40 meters and deeper, and *Cellaria* was its primary attached epibiont (Nikolić, 1959, Fig. 2). The biocoenosis dominated by *Pentapora*, or locally by *Cellaria* has long been known as the *Hippodiplosia* biocoenosis or *Hippodiplosia* facies (*Hippodiplosia* = *Pentapora*) (Gamulin-Brida et al., 1968; Seneš, 1989). This

association dominates much of the muddy sea floor at about 35 m and deeper off the Istrian coast. Within this general association, however, the boundary between *Pentapora*-dominated and *Cellaria*-dominated assemblages is currently in flux. The *Pentapora foliacea* population in the vicinity of Rovinj was exterminated during anoxic events of 1989-90. *Cellaria* populations at 40 m and deeper recovered before *P. foliacea*, which only began to recover in the late 1990's. The deeper associations currently dominated by *Cellaria* (with increasing proportions of *P. foliacea*) are not included in the current study, because they appear to be a temporary stage in the recovery succession, in contrast with the longer-term stable community seen on the west side of Banjole.

Dense, patch-like thickets of intergrown *Cellaria sinuosa* (Hassall) and *C. fistulosa* have been reported at 80 m depth in the English Channel off Roscoff, France (Henrich et al., 1995). These *Cellaria* thickets were described as occurring on a substrate of gravels to boulders and to be the principal source of nearby storm-generated bryomol sediments that are dominated by *C. sinuosa* and *C. fistulosa* skeletons. Thus the habitat is different for the English Channel thickets off Roscoff and the meadows off Rovinj, the latter of which developed on a silt substratum and from which the skeletal debris accumulated - and most of which eventually corroded - in situ, rather than being swept into *Cellaria*-dominated banks and dunes.

Cellaria fistulosa and *C. salicornioides* fragments are distributed differently from one another in the area centred on the Rhône delta (Lagaaij & Gautier, 1965), but both are most abundant in areas of 'slow' rates of sediment accumulation well away from sediment-laden waters emanating from the mouth of the Rhône River and are absent in areas of 'high' rates of sediment accumulation directly in front of the river's mouth. In an approximately 40-60 m deep area of low sediment accumulation west of the delta, more than 1000 *C. fistulosa* fragments per 100 grams of dry sediment may be found for a distance estimated at about 15 km parallel with the shore and up to 5 km wide perpendicular to the shore. Such high concentrations of *C. fistulosa* fragments in the sediment suggest that it grows in thickets or a meadow across the region. Sediment in this area is marl to sandy marl, in contrast with the gravels to boulders reported by Henrich et al. (1995) for *C. fistulosa* meadows in the English Channel. *C. salicornioides* is found in the vicinity of the Rhône delta only in moderate concentrations, in two small areas at about 10 m depth where it co-occurs with *C. fistulosa*, and across a larger eastern area where depths exceed 110 m. Although the distribution and abundance of *Cellaria* in the vicinity of the Rhône delta are based on skeletal accumulation in superficial sediment, it appears that *C. fistulosa* grows densely there, in an environment intermediate in physical

characteristics between those of the thickets off Roscoff and the meadow off Rovinj.

Temporal variation in density of *Cellaria* meadow

The reason(s) for the decrease in density of cover in the *Cellaria* meadow, from June 1997 to November 1997, is not clear. Previous observations of the meadow (by AJ) gave estimates of 80-90% cover (14 August and 29 September 1987, 7 June 1988, 9 October 1990, 8 June 1995). If winter die-back is usual, one would expect some deterioration or incomplete regrowth to be noticed in the October and June observations prior to 1987, but it was not. The 1997-1998 winter die-back may be an unusual event, a relatively prolonged instance of an annual event, or even normal but previously unnoticed annual variation, given that most previous examinations of the mat occurred in relatively warm months. The temporal and within-colony patterns of loss and regeneration are currently under investigation (Bader, McKinney & Jaklin, in preparation).

Epibionts within the *Cellaria* meadow

The thickets off Roscoff and the meadow off Rovinj are similar in providing a microenvironment for diverse marine invertebrates. The Roscoff *Cellaria* thickets were reported as hosting diverse encrusting bryozoans, small decapods, bivalves, hydrozoans, and foraminiferans (Henrich et al., 1995). Genera for two of the five associated epibionts named by Henrich et al. (1995) also occurred in the Rovinj thickets: *Turbicellepora* and *Buskea*, although both are so uncommon in the Rovinj *Cellaria* meadow that neither was encountered in the dissected and closely examined branch systems.

Mean depth of attachment of individual species within the *Cellaria* mat apparently is due to a complex of microenvironmental factors plus larval behaviour. Some potentially important factors have not been investigated by us. These include vertical gradients within the mat in oxygen concentration, water movement, light intensity, concentration of bacteria, phytoplankton availability, concentration of dissolved organic matter, season of epibiont recruitment, and depth of penetration into the mat of potential predators.

The steady inward increase in percent of *Cellaria* branches that have one or more organisms attached (Fig. 4) is probably due, at least in part, to age of the branches. Terminal branches are the most recently formed and are least commonly encrusted. It is reasonable to attribute the low percentage of epibiont occupation of the light golden terminal branch segments, some of which may not have been fully grown, to their short time of existence during which larvae of potential epibionts could settle. Successively higher branch segment numbers correspond

directly with greater age of the segments as the succession of branches is traced back to the colony origin, because new branch segments are budded terminally. However, the high correlation of branch segment number with percent that are encrusted ($r=0.752$, $p<<0.001$, $N=44$) cannot confidently be attributed solely to increased age and therefore availability for encrustation. Too many other microenvironmental factors may influence settlement of larvae of the epibionts, including the undocumented potential factors listed above.

From *Cellaria* branch segment one through eight, the increase in number of epibiont species per segment (Fig. 5) corresponds with the pattern of increase in percent of segments that are encrusted. However, there is a contrasting pattern from segment eight inward, with an almost steady decrease in number of epibiont species per segment. This probably is not due to an actual decrease in number of epibiont species on the oldest branch segments in the colonies, but is more likely due to a decrease in the number that are visible. The basal segments commonly are engulfed completely in thick sponge crusts that grow indiscriminately over the substrate and obscure the remains of epibionts that preceded them.

Precision of depth of settlement is not high for most species, as seen in the high variance of segment number on which settlement occurred. This is true for shallow- and deep-occurring species. There is no correlation between mean depth of occurrence of taxa and coefficient of variation either for individual species for which >10 individuals were encountered (Spearman rank order correlation, $r=-0.124$, $p=0.405$, $N=47$) nor for clade (Spearman rank order correlation, $r=-0.317$, $p=0.406$, $N=9$).

Larval behaviour of epibionts must play some role in determining depth of settlement within the *Cellaria* mat, because each species has a characteristic depth of attachment (Fig. 8), which in many cases differs significantly from depth of attachment of at least some other species (e.g. Table 3). Between-species differences in depth of attachment cannot be ascribed solely to behaviours and preferences that are clade-specific, because among the most abundant species, significant differences exist between two species of ascidians and also between two species of ctenostome bryozoans (Table 3). In fact, the two ctenostome species are among the most different in depth of their occurrence, with *Walkeria tuberosa* being among the shallowest species and *Nolella stipata* among the deepest. The importance of larval behaviour can perhaps be seen most clearly between two species of the cyclostome bryozoan genus *Crisia*. *Crisia recurva* Heller and *Crisia ramosa* (Harmer) have distinctly different distributions (Mann-Whitney U test, $p << 0.001$), with *Crisia recurva* occurring on average deep within the mat and *C. ramosa* being one of the shallowest species (Fig. 9).

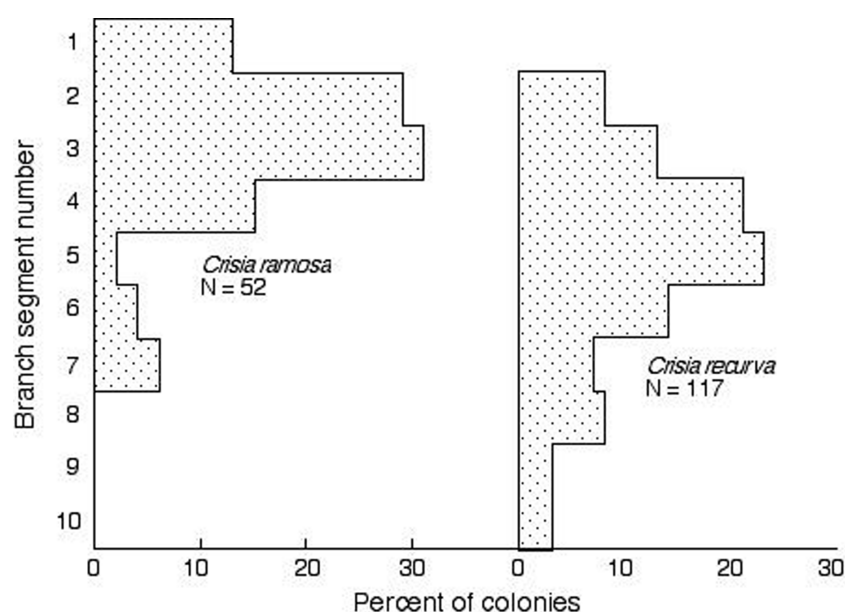


Figure 9. Distribution of *Crisia ramosa* and *Crisia recurva* on branch segments of *Cellaria*. The presence of *C. ramosa* from branch segment 5 to 7 may be due to a misidentification of *C. recurva* as *C. ramosa*, early in the study.

Figure 9. Distribution de *Crisia ramosa* et *Crisia recurva* sur les segments de *Cellaria*. La présence de *Crisia ramosa* sur les segments 5 à 7 est peut-être due à une confusion de cette espèce avec *Crisia recurva*, au début de ce travail.

Aglaothamnion sp., the only photosynthetic organism scored, is among the shallowest-occurring species. Its depth of attachment was greater in November 1997, and in the low-density July 1998 condition, than in the two high-density *Cellaria* mat samples (Table 5). Settling spores apparently attached upon first contact with a substrate. The deeper attachment in the low-density mat conditions was probably due to a less-dense screen of terminal branch segments across the top of *Cellaria* colonies, so that spores penetrated deeper within the mat before encountering a surface to which they could attach.

The shallowest species of all, the foraminiferan *Ammonia tepida*, was absent or in low abundance prior to July 1998, when a population bloom made it by far the most abundant species visible at X50 magnification. Individuals of *A. tepida* were much more abundant on the light-coloured terminal branch segments than on the older branches that were darker brown in colour. Preferential aggregation higher in the mat at some stage in the life history of *A. tepida* is indicated, because it was concentrated at about half the depth of *Aglaothamnion*. Dark colour of *Cellaria* cuticle is assumed to result from abundant bacteria, and the foraminiferans may have settled preferentially on the

surfaces where bacteria were less abundant. Alternatively, since the foraminiferans are capable of slow movement, they may have settled deeper within the mat and gradually moved toward the outer surface of the mat, stimulated by one of the vertical environmental gradients.

If multicellular species are combined into groups (clades, growth forms), some expected patterns of depth distribution are seen and others are counterintuitive.

The shallow average occurrence of sponges is due to several species that have mean depths within the mat that are less than that of *Aglaothamnion* (Appendix). In contrast with the deeper-occurring groups that feed on phytoplankton or zooplankton (Cnidaria, Cyclostomata, Ctenostomata, Cheilostomata, Annelida, Ascidia), Porifera are known to feed on bacteria as well as on phytoplankton (Buss & Jackson, 1981). If non-sedentary bacteria are more abundant in ambient water deeper within the mat than at its surface, we would expect epibiotic sponges to occur more deeply in the *Cellaria* mat than did bryozoans, given that bryozoans feed almost exclusively on phytoplankton that can be

depleted by sponges (Buss & Jackson, 1981). Part of the reason for the shallow distribution of sponges may be that they commonly grew from one segment onto another, either by growing along branches or by bridging across from one branch system to another. Shallow sponges that grew onto several branch segments were scored as present on each of the segments where they were present. Therefore a shallow, well developed encrusting sponge could generate several near-terminal segment scores, whereas an organism confined to a single branch segment was scored only once. This discrepancy may have influenced the mean of the scored depths of sponges relative to cyclostomes, cheilostomes, and annelids. However, common stoloniferous growth of cnidarians, ctenostomes and ascidians produced similar potential for a single clone to extend across and be scored as present on several branch segments, yet they occurred significantly deeper within the mats than did sponges (Table 4).

The ascidians, ctenostomes, cnidarians, and annelids form an intermediate-depth group (Fig. 7), each of which is not significantly different in mean depth from at least one another in the group but which all are significantly different from mean depths of the shallower-occurring sponges and

Appendix. Depth of attachment of organisms encrusting *Cellaria* within the dense mat. Erect modular taxa are indicated by (E), and radially spreading encrusting modular taxa are indicated by (C); for mode, see table 2. Multiple modes are indicated by m.

Annexe. Profondeur de fixation des organismes encroûtants sur les *Cellaria* dans la matte dense. Les taxons modulaires dressés sont indiqués par (E) ; les taxons modulaires encroûtants sont indiqués par (C) ; pour les modes voir tableau 2. Les modes multiples sont indiqués par m.

Taxon	Number observed	Depth of attachment (branch segment number)			
		Range	Mean	Median	Mode
Rhodophyta	(554)	1-12	3.54	3	2)
<i>Aglaothamnion</i> sp.	545	1-12	3.53	3	2
<i>Halymenia</i> sp.	9	2-6	4.11	4	m
Sarcodina	(1563)	1-12	2.41	2	1)
<i>Ammonia tepida</i>	1551	1-12	2.37	2	1
Astrorhizidae, Gen. et sp. indet.	12	3-8	5.42	5	m
Ciliata	(24)	1-5	2.88	3	2)
Folliculinid	24	1-5	2.88	3	2
Porifera	(385)	1-9	3.41	3	1)
<i>Anchinoe tenacior</i> (C)	101	1-9	3.50	3	3
<i>Halichondria?</i> sp. (E)	24	1-5	2.67	3	4
<i>Haliclona</i> sp. (C)	9	3-7	4.78	5	—
<i>Hymedesmia?</i> sp. (C)	24	1-8	4.62	5	5
<i>Leuconia</i> sp. (E)	32	1-6	2.19	2	1
<i>Leucosolenia</i> sp. (E)	18	1-9	3.72	3	2
<i>Tedania anhelans</i> (C)	153	1-9	3.48	3	1
Demospongiae, Gen. et spp. indet. (C)	24	1-8	3.35	3	3
Cnidaria	(400)	1-11	3.99	3	3)
<i>Campanularia hincksi</i> (E)	124	1-10	3.60	3	3
<i>Obelia</i> sp.	32	1-9	3.78	4	4
<i>Sertularella</i> sp. (E)	10	2-6	3.60	3.5	—
Hydroidea, Gen. et spp. indet.	234	1-11	4.10	4	3
Annelida	(453)	1-12	4.09	4	3)
<i>Filograna</i> sp.	106	1-9	3.64	3	3
<i>Pomatoceros triqueter</i>	39	1-9	4.33	4	4
<i>Serpula vermicularis</i>	14	3-10	5.86	5	5
<i>Spirorbis</i> sp.	166	1-10	4.21	4	4
Polychaeta (organic tube) Gen. et spp. indet.	42	1-9	3.24	3	2
Polychaeta (agglutinated tube) Gen. et spp. indet.	86	1-12	4.40	4	3
Bryozoa					
Cyclostomata	(558)	1-12	4.61	4	4)
<i>Annectocyma</i> sp. (E)	39	2-12	5.67	5	5
<i>Crisia ramosa</i> (E)	52	1-7	2.98	3	3
<i>Crisia recurva</i> (E)	117	2-10	5.03	5	5
<i>Crisia</i> sp. (E)	27	1-8	3.52	3	2
<i>Diplosolen obelia</i> (C)	1	5	5.00	5	5
<i>Disporella hispida</i> (C)	5	3-5	4.20	4	m
<i>Exidmonea atlantica</i> (E)	19	1-8	4.68	4	4
<i>Patinella radiata</i> (C)	2	4	4.00	4	4
<i>Plagioecia patina</i> (C)	119	1-10	5.12	5	5
<i>Tubulipora liliacea</i> (C)	177	1-9	4.41	4	4
Ctenostomata	(551)	1-12	3.91	3	3)
<i>Amathia pruvoti</i>	2	4-5	4.50	4.50	m
<i>Bowerbankia gracilis</i> (C)	25	1-9	4.36	4	m
<i>Bowerbankia</i> sp. (C)	7	2-6	3.43	3	2

<i>Nolella stipata</i>	142	1-12	4.66	4	4
<i>Walkeria tuberosa</i>	375	1-12	3.59	3	3
Cheilostomata	(523)	1-11	4.37	4	(5)
<i>Aetea truncata</i>	105	1-11	4.71	5	5
<i>Beania hirtissima</i> (C)	6	5-8	6.50	6.50	m
<i>Beania magellanica</i> (C)	36	1-9	4.92	5	3
<i>Caberea boryi</i> (E)	17	1-9	4.00	4	2
<i>Caulibugula</i> sp. (E)	18	1-10	3.78	3.5	4
<i>Celleporina canariensis</i> (C)	42	1-10	5.29	5	5
<i>Celleporina</i> sp. (C)	123	1-9	3.79	3	3
<i>Chartella tenella</i> (E)	23	2-9	4.83	5	2
<i>Microporella ciliata</i> (C)	80	1-9	4.01	4	m
<i>R. septentrionalis</i> (E)	21	2-9	4.86	5	4
<i>Schizomavella linearis</i> (C)	11	3-9	6.27	7	7
<i>Schizomavella rudis</i> (C)	4	5-7	6.25	6.5	7
<i>Schizoporella dunkeri</i> (C)	3	2-10	7.33	10	10
<i>Scrupocellaria delilii</i> (E)	26	1-7	2.81	2	2
<i>S. scruposa</i> (E)	1	8	8.00	8	8
Gen. et spp. indet. (C)	7	2-6	4.00	4	—
Mollusca	(4)	2-4	2.50	2	(2)
Mytilidae, Gen. et sp. ind.	3	2	2	2	2
<i>Crepidula</i> sp.	1	4	4	4	4
Urochordata	(651)	1-11	3.80	3	(2)
Perophoridae (green), Gen. et sp. indet. (C)	384	1-12	3.97	4	m
<i>Polycitor?</i> sp. 1 (white) (C)	174	1-10	3.49	3	2
Styelidae (red), Gen. et sp. indet. (C)	11	1-11	4.18	4	2
<i>Polycitor?</i> sp. 2 (orange) (C)	71	1-9	3.52	3	3
Styelidae (orange), Gen. et sp. indet. (C)	1	6	6.00	6	6
Styelidae (clear), Gen. et sp. indet. (C)	8	1-7	4.00	4	4
Clavelinidae? (clear), Gen. et sp. indet. (C)	2	3-5	4.00	4	m

rhodophytes. Each clade in this group is also significantly different in mean depth from the deeper-occurring cheilostome and cyclostome clades.

The deep, relatively cryptic, average occurrence of cheilostome bryozoans is consistent with the widely documented larval behaviours and commonly cryptic field distributions of many species in this clade (Harmelin, 1977, 1980, 1985, 1997; Jackson & Winston, 1982; Lescinsky, 1993; McKinney, 1996). The behaviour of settling larvae in the majority of cheilostome species studied leads them to quiet, poorly lit, generally cryptic surfaces (Ryland 1974; McKinney & McKinney, 1993), and it is apparently the behaviour of larvae that produced the relatively deep position of most cheilostome colonies within the *Cellaria* mat. Post-settling mortality by predation may also influence the distribution patterns of bryozoan colonies (Keough & Downes 1982; Walters, 1992), but no small-scale durophagous predators were found within the *Cellaria* mat, and all branch segments were examined at sufficient detail that colonies of even two or three zooids were seen. Predation was therefore considered to play a vanishingly

small role in determining the distribution pattern of any of the skeletalized epibionts that grew within the *Cellaria* mat.

Cyclostome bryozoans are on average more cryptic than are cheilostomes. They tend to occur more abundantly on interior and downward-facing surfaces of skeletal debris than on exposed shell surfaces (Eggleston, 1972; Harmelin, 1977; Ward & Thorpe, 1991; Lescinsky, 1993; McKinney, in press). In the deep recesses of caves, however, cyclostomes may be found equally abundantly on lower and upper surfaces (Harmelin, 1980), and in some of the more deeply recessed parts of caves are among the dominant species (Harmelin, 1985).

Ryland (1974) reported that there was no experimental work on swimming and settling behaviours of cyclostome larvae. That is still true. However, previously determined field distributions suggest that during the final stage of swimming and during metamorphosis, cyclostome larvae seek quiet, dark microenvironments. Cyclostomes are on average the deepest-occurring epibionts in the *Cellaria* mat, which is further indirect evidence that larvae of most cyclostome species seek quiet, deep, and/or dark

microenvironments. In the *Cellaria* mat, larval behaviour is almost certainly the sole cause of the cryptic distribution rather than interaction of larval behaviour and post-settlement predation.

Although erect growth was seen in three sponge species and three hydroid species, it was most commonly seen in cheilostome and cyclostome bryozoans. This strong association of erect growth with cheilostome and cyclostome bryozoans, which were the two clades that occurred at the greatest depth within the *Cellaria* mat, is the reason that erect-growing modular organisms were found to occur deeper than encrusting organisms.

Except for *Reteporella septentrionalis* (Harmer) (represented by 21 colonies), erect cheilostomes were either continuously flexible or composed of rigid segments separated by flexible nodes. Flexible, erect bryozoans can withstand highly energetic environments (review in McKinney & Jackson, 1989; McKinney, 1996). The higher tolerance to kinetic stress may be why the erect cheilostomes occur on average higher within the *Cellaria* mat than do encrusting cheilostomes. (Compare these distributional patterns with the even more informative patterns within cyclostomes, discussed below.)

The lack of significant difference in depth of pooled erect and pooled encrusting cyclostomes is due to a higher proportion of rigid colonies among the erect cyclostomes than in erect cheilostomes. If depth of attachment of articulated (flexible) erect cyclostomes (mean=4.28) is compared with depth of attachment of rigid colonies (mean=5.34), there is a highly significant difference (Mann-Whitney U, $p < 0.001$, $N = 196$ articulated and 58 rigid). Comparing each of these with encrusting cyclostomes, depth of the shallower, articulated erect forms is significantly different (Mann-Whitney U, $p = 0.004$) and the rigid erect forms are marginally different (Mann-Whitney U, $p = 0.044$). The sequence of distribution of cyclostome growth habits (articulated erect to encrusting to erect rigid) from the surface of the *Cellaria* mat parallels the sequence seen in cheilostomes and is consistent with the pattern seen at larger scales from energetic to quiet water (McKinney & Jackson, 1989).

There is only partial overlap between the epibionts on *Cellaria* within the meadow and the epibionts that encrust shell litter on the nearby sandflats that have less extensive cover by arborescent organisms. No publications are focussed specifically on the diversity and biomass of shell-encrusting epibionts, but the hard substrate-attaching algae, sponges, cnidarians, and ascidians in lists (Vatova, 1949; Zavodnik, 1971) of taxa in biocoenoses that characterize the sandy and muddy inter-island regions of the Istrian coast contain, in general, much more robust epibionts than those that characterize the *Cellaria* mat.

Table 6. Comparison of the most common bryozoans encrusting shell litter on sandflats in the vicinity of Rovinj with the most common cheilostome bryozoans encrusting *Cellaria* branch segments. Each of the two lists for the cheilostomes and for the cyclostomes is given from most abundant to least abundant. Species that characteristically grow into encrusting sheets larger than about 10 mm² are marked by an asterisk. Data on the most abundant shell-encrusting bryozoans are from McKinney (in press).

Tableau 6. Comparaison entre les Bryozoaires encroûtants les plus communs sur les coquilles des ensablements aux environs de Rovinj et les Bryozoaires Cheilostomes encroûtants les plus communs sur les segments ramifiés des *Cellaria*. Les deux listes, celle des Cheilostomes et celle des Cyclostomes, sont données par ordre d'abondance décroissant. Les espèces qui en grandissant, se transforment en couches encroûtantes d'une surface supérieure à 10 mm² sont indiquées par un astérisque. Les données sur les espèces les plus abondantes de Bryozoaires encroûtant les coquilles sont tirées de McKinney (sous presse).

Shell-encrusting	<i>Cellaria</i> -encrusting
Cheilostomata	
* <i>Chorizopora brongniartii</i> (Audouin)	<i>Celleporina</i> sp. nov.
* <i>Schizoporella dunkeri</i> (Reuss)	<i>Microporella ciliata</i> (Pallas)
* <i>Reptadeonella violacea</i> Johnston	<i>Celleporina canariensis</i> (Aristegni)
<i>Callopora dumerilii</i> (Audouin)	* <i>Beania magellanica</i> (Busk)
* <i>Schizoporella magnifica</i> (Hincks)	<i>Schizomavella linearis</i> (Hassall)
<i>Microporella ciliata</i> (Pallas)	<i>Beania hirtissima</i> (Heller)
* <i>Schizomavella discoidea</i> (Busk)	<i>Schizomavella rudis</i> (Manzoni)
<i>Fenestulina malusii</i> (Audouin)	<i>Schizoporella dunkeri</i> (Reuss)
<i>Schizotheca fissa</i> (Busk)	
* <i>Schizomavella marsupifera</i> (Busk)	
Cyclostomata	
<i>Tubulipora liliacea</i> (Pallas)	<i>Tubulipora liliacea</i> (Pallas)
<i>Diplosolen obelia</i> (Johnston)	<i>Plagioecia patina</i> (L.)
<i>Plagioecia patina</i> (L.)	<i>Disporella hispida</i> (Fleming)
<i>Disporella hispida</i> (Fleming)	<i>Lichenopora radiata</i> (Audouin)
<i>Tubulipora plumosa</i> (Harmer)	<i>Diplosolen obelia</i> (Johnston)

The most common shell-encrusting cheilostome bryozoans generate large, indiscriminately spreading sheet-like colonies (Table 6), but among these species found as large colonies on shells, only *Schizoporella dunkeri* (Reuss) was found on *Cellaria* branch segments, where it was both uncommon and small. Only *Microporella ciliata* (Pallas) was abundant on both shell litter and on *Cellaria*. Like all encrusting cheilostomes other than *Beania magellanica*

(Busk) that were abundant on *Cellaria*, *M. ciliata* typically formed small colonies (2.9 mm² on shell litter; even smaller on *Cellaria*). *B. magellanica*, the only species that formed large spreading sheets on *Cellaria*, generates lightly calcified, flexible sheets that bridged across gaps between branches and attached to the branches by basal kenozooids. All of the most common shell-encrusting cheilostomes are rigidly calcified and closely adherent to the shell substratum; the flexibility of *B. magellanica* colonies may have been the feature that allowed it to occur commonly and to grow to relatively large size on the articulated *Cellaria* substratum.

There is no conspicuous difference in size of cyclostome colonies on shell litter and *Cellaria* branch segments: all the common cyclostome species grow into small colonies. The list of species occurring on both substrata also is almost identical (Table 6), but relative abundance of some species is quite different. *Tubulipora liliacea* (Pallas) and *Diplosolen obelia* (Johnston) are the two most common cyclostome species on shell litter (McKinney, in press), but while *T. liliacea* is common on *Cellaria*, only a single colony of *D. obelia* was encountered. *Disporella hispida* (Fleming) is also rare on *Cellaria* but common on shell litter. Growth habits of all the cyclostome species appear to be suitable for growth within the *Cellaria* mat, and it is not clear why *D. obelia* and *D. hispida* are so uncommon there.

Conclusions

A diverse association of epibionts is attached to branches of the densely developed *Cellaria salicornioides* colonies that grow as an extensive meadow on the west side of Banjole, near Rovinj, Croatia. Although each species, and the clades to which the species belong, show high variance in their vertical distributions, niche partitioning is suggested because depth distributions of many species pairs, as well as most clade pairs, differ significantly.

The *Cellaria* mat degraded from the usual 80-90% cover to only 40-50% cover over the substrate between June and November 1997, and it had only partially recovered by July 1998. It is not clear whether this degradation and regrowth is part of an annual cycle or is a less frequent or unusual die-back and recovery. A few epibiont species underwent a population bloom during the study interval (June 1997 to July 1998), but most of the epibionts maintained relatively constant densities on the *Cellaria* branch segments during the entire study interval.

A population bloom of the foraminiferan *Ammonia tepida* occurred prior to the July 1998 sampling of the meadow so that it became by far the most common species encountered in the study. The most common of the species with more stable populations were all modular, and all but

one of the most common species had threadlike, flexible, stoloniferous growth that allowed them to spread beyond a single branch segment. Their abundance may therefore not reflect high larval recruitment rate but rather the ability to extend and break into local, independently functioning units.

Various biotic zones can be discriminated by the vertical distribution of epibionts within the *Cellaria* meadow. Distributions of individual species are centred at shallow mid-depths of the mat, with well over half the species having mean depths at 3.5 to 5 branch segments down from the branch tips at the surface of the mat. Individual species differed significantly in their depth distributions, indicating niche partitioning along horizontal planes. Focussing on the aggregate of individual species indicates that epibionts are concentrated below the most recently formed, outer branch segments and above the most stagnant area within the mat, near the sediment-water interface.

Grouping the species into clades allows the continuum of overlapping species distributions to be resolved into three zones. The outermost zone is the region of concentration of relatively simple eukaryotes: rhodophytes, foraminiferans, and most sponges. The middle zone is the region of concentration of most hydroids, ctenostome bryozoans, annelids, and ascidians. The deepest zone is characterized by a concentration of cheilostome and cyclostome bryozoans.

Cheilostome and cyclostome bryozoans account for most of the erect epibionts. The concentration of colonies of these two clades in the deeper regions of the mat results in average deeper occurrence of erect modular organisms than of encrusting modular organisms (modular organisms are distributed among the sponges, hydroids, bryozoans, and ascidians.) However, within the cheilostomes and cyclostomes, flexible erect colonies have the shallowest average distribution, encrusting colonies are deeper, and rigid erect colonies have the deepest average distributions. This distribution pattern within the cheilostomes and cyclostomes parallels large-scale geographic trends from relatively high energy to low energy environments.

There is no evidence for whole-organism predation or for durophagous predation on the epibionts within the *Cellaria* mat. Known swimming and settling behaviours of cheilostomes and previous field studies of distribution of cyclostomes indicate that both groups tend to prefer relatively protected sites in which to grow, and cyclostomes seek more cryptic sites than do cheilostomes. The apparent absence of whole-colony predation within the *Cellaria* mat, the distribution of cheilostomes and cyclostomes within the mat relative to the other clades, and the known preference of these bryozoans for protected sites in which to settle, all together suggest that the distribution of taxa within the *Cellaria* mat is largely the result of larval settling

behaviours and choices rather than post-settlement predation.

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