

Bryozoan facies in the coralligenous community: two assemblages with contrasting features at Port-Cros Archipelago (Port-Cros National Park, France, Mediterranean)

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Abstract. Two bryozoan facies typical of the coralligenous habitat were studied at Port-Cros Archipelago. Both exhibited notable species richness with a small number of quantitatively dominant species (a *Schizomavella* species top-ranked in both cases), but were strikingly different in species composition, size and life-history of colonies, and in the identity and relative part of the higher taxa co-occurring with the bryozoans. The first facies covered rocky and biogenic walls; it was sampled by photo-quadrats at six sites. Bryozoans, sponges and macroalgae were clearly dominant over the other groups, with a hierarchical order depending on site features (rocky walls vs. bioherm edifice). Colonies of the eight most abundant species (1st ranked: *S. mamillata*) in terms of percent cover of walls are long-lived, large and, in most cases, highly calcified and massive. The second bryozoan facies consists in a species-rich assemblage established on leaves of *Flabellia petiolata*, with a particular concentration on the shaded side of leaves and a very low contribution of other higher taxa. All bryozoan species, and especially the five dominant ones (1st ranked: *Schizomavella halimeda*), were short-lived with single-layered, early fertile colonies, thus well adapted to life on a flexible, non-perennial substratum. Thus, these two bryozoan facies illustrate the diversity of the contribution of bryozoans to the coralligenous biodiversity.

Keywords: benthos, hard bottom, sciaphilic assemblage, Bryozoa, photo-quadrat, epiphytes, *Flabellia petiolata*.

Résumé. Faciès à bryozoaires dans la communauté coralligène : deux assemblages avec des traits opposés à Port-Cros (Parc national, France, Méditerranée). Deux faciès à bryozoaires typiques du coralligène ont été étudiés à Port-Cros. Tous deux présentent une richesse spécifique notable, avec un petit nombre d'espèces dominantes quantitativement (une espèce de *Schizomavella* en premier rang dans les deux cas), mais sont très différents par leur composition spécifique, la taille et le cycle de vie des colonies, et par l'identité et la part relative des grands groupes taxonomiques présents avec les bryozoaires. Le premier faciès à bryozoaires occupe les parois rocheuses ou biogéniques ; il a été échantillonné par photo-quadrats. Les bryozoaires, les éponges et les macroalgues étaient nettement dominants par rapport aux autres groupes, avec un ordre hiérarchique variant selon les sites (parois rocheuses vs. bioherme). Les huit espèces dominantes en terme de couverture des parois (1^{er} rang : *S. mamillata*) sont à longue durée de vie et, dans la plupart des cas fortement calcifiées et massives. Le second faciès à bryozoaires consiste en un assemblage riche en espèces établies sur les feuilles de *Flabellia petiolata*, avec une concentration particulière sur les faces

ombragées des feuilles et une très faible contribution des autres groupes. Toutes les espèces de ce faciès, et particulièrement les cinq dominantes (1^{er} rang : *Schizomavella halimeda*), ont des colonies à courte durée de vie, unilaminaires et fertiles très précocement, donc bien adaptées à une vie sur un substrat souple et non pérenne. Ces deux faciès illustrent bien la diversité des contributions des bryozoaires à la biodiversité du coralligène.

Mots-clés : benthos, substrats durs, assemblages sciaphiles, Bryozoa, photo-quadrat, épiphytes, *Flabellia petiolata*.

Introduction

Coralligenous bottoms are exceptional biodiversity hotspots in the Mediterranean coastal zone (e.g. Laubier, 1966; Hong, 1980; Ballesteros, 2006), sheltering high value fisheries resources, attracting most of the diving tourism business because of the outstanding seascapes, but exposed to a wide range of threats. For these reasons, coralligenous bottoms have now become a conservation priority among Mediterranean habitats, together with *Posidonia oceanica* meadows and underwater caves (e.g. UNEP-MAP-RAC/SPA., 2008, 2009; Giakoumi *et al.*, 2013). Therefore, coralligenous bottoms are now a particular focus for studies aiming to assess the status of the coralligenous community (e.g. Peirano *et al.*, 2009; Kipson *et al.*, 2011; Deter *et al.*, 2012a, 2012b; Gatti *et al.*, 2015a, 2015b).

The term ‘coralligène’ was first assigned to a marine habitat by Marion (1883: ‘graviers coralligènes à grands bryozoaires’) for defining aggregations of biota mostly with mineralized parts living free on the surface of coastal detritic sands, i.e. below the deep limit of *Posidonia oceanica* (Linnaeus) Delile seagrass beds. The concept of ‘coralligène’ was considerably broadened by Pérès and Picard (1951, 1964), who defined a coralligenous biocenosis with various “aspects”, “horizons” and “facies”. In reference to studies by Laborel (1961, 1987), Laubier (1966), Sarà (1969) and Hong (1980), the coralligenous community is generally defined as strictly associated with massive bioconstructions (‘bioherm’) built up by coralline red macroalgae¹ (e.g. *Mesophyllum* spp., *Lithophyllum* spp.), and secondarily by invertebrates with mineralized skeletons (Laubier, 1966; Sarà, 1969; Hong, 1980, 1982). I will rather consider here the coralligenous habitat as a complex of sciaphilic assemblages forming a continuum (Boudouresque, 1970) with various intermediate stages, ranging from steeply sloping rocky walls, often shaded by large sea-fans but without well-developed coralline algae at one end, to bioherm constructions forming large bodies of metric size

¹ ‘Algae’ do not correspond to a taxon but to a highly polyphyletic ensemble of organisms. ‘Macroalgae’ correspond to multicellular photosynthetic organisms belonging to Chlorophyta, Rhodophyta (kingdom Archaeplastida) and Phaeophyceae (kingdom Stramenopiles). See Boudouresque (2015) for further information.

on slightly sloping bottoms at the other (Boudouresque *et al.*, 2016; Harmelin, 1994, 2014).

Bryozoans are repeatedly presented as major contributors to the diversity and the structure of the coralligenous habitat (e.g. Gautier, 1959; Hong, 1980, 1982; Ballesteros, 2006), although relatively few papers have been specifically dedicated to their status in this community (Gautier, 1949, 1959; Harmelin and Hong, 1979; Harmelin and Capo, 2002; Cocito and Lombardi, 2007; Rosso and Sanfilippo, 2009). However, data on the remarkable coralligenous ‘bryodiversity’ can be compiled from more general studies (Tab. I). Bryozoans occupy a variety of microhabitats on the coralligenous bottoms, which can be categorized in 6 types (Fig. 1). These microhabitats present very different features, from very exposed conditions, such as a raised position in the water column for species attached to sea-fans, to a cryptic life within small cavities of walls or interstices of rigid biota, such as sheets of coralline red macroalgae. The great variety of these microhabitats is a major source of the coralligenous bryozoan diversity, including species with very different colony sizes and shapes, life-histories and energy needs. Thus, bryozoans illustrate perfectly Laubier’s view that coralligenous bottoms are a “*carrefour écologique*” (ecological crossroads) (Laubier, 1966). However, in most cases, assessments of the coralligenous community consider exclusively the most visible part of this ‘bryodiversity’, i.e. a few large, erect, easily identified species.

The aim of this study is to describe two bryozoan facies that are typical of coralligenous bottoms but poorly known: (i) facies of bryozoans aggregated on rocky or biogenic walls, and (ii) facies of bryozoans epiphytic on *Flabellia petiolata*.

Table I. Cumulative bryozoan species richness (N Spp) at various geographic scales within coralligenous assemblages from published literature. Harmelin, 1976, part of table I: cumulative number of species listed for ‘PRECOR’ (precoralligenous), ‘COR-GSO’ (coralligenous walls) and ‘Concr. Cor.’ (coralligenous bioherm). Novosel *et al.*, 2004, table II, column ‘CB’ (coralligenous). Ballesteros, 2006: estimated whole species richness. For the categorization of the species richness (= species diversity) according to spatial scale, see Boudouresque (2014).

References	Geographical zones	N Spp
Laubier, 1966	Albères	67
Vidal, 1967	Roussillon	35
Harmelin, 1976	Provence	120
Hong, 1980, 1982	Marseille, Fos	133
Zabala, 1984, 1986	Catalonia, Spain	113
Ballesteros <i>et al.</i> , 1993	Cabrera, Balearic I.	92
Novosel <i>et al.</i> , 2004	Croatia, Adriatic Sea	65
Ballesteros, 2006	Mediterranean	170
Rosso and Sanfilippo, 2009	SE Sicily	60



Figure 1. Coralligenous microhabitats occupied by bryozoans. 1: exposed wall surfaces. 2: interstices, small cavities. 3: epibiotic on sea-fans. 4: epibiotic on other sessile invertebrates. 5: epibiotic on Corallinaceae *Mesophyllum* and *Lithophyllum*. 6: epibiotic on Chlorophyta *Halimeda tuna* and *Flabellia petiolata*. Modified from Harmelin *et al.*, 1985 (part of fig. 9).

Material and methods

Bryozoan facies on coralligenous walls

The composition and structure of the bryozoan facies on coralligenous walls were assessed by underwater photographic sampling at six sites around Port-Cros Archipelago (see below), surveyed in June 2014. The photographic procedure consisted in taking a series of photo-quadrats with the same protocol at each site. Photos were taken with an Olympus Pen EPL2® digital camera with a 9-18 mm zoom lens in an Olympus UW housing equipped with a fixed rectangular frame delimiting a 240 cm² surface area. This photo-quadrat size was chosen for its suitability relative to the structure of the assemblages to be studied. Lighting was supplied by an Inon 240® electronic strobe and a Videolux® torch. Eight photo-quadrats per site were selected on the basis of technical quality and analysed on a large computer screen. Assemblage composition and abundance of components in terms of percent cover in each photo-quadrat were assessed using the classical method of random point sampling (Bohnsack, 1979). Grids with randomly distributed points were used with a minimum of 100 points per quadrat. In some cases, the visual identification of bryozoans at species level was verified by collecting small fragments of colonies for examination with a stereomicroscope. Species richness and abundance (percent cover) of bryozoans and other components were averaged for each site (8 quadrats) and for all sites (48 quadrats).

Bryozoan facies on *Flabellia petiolata*

Sampling of *Flabellia petiolata* (Turra) Nizamuddin (Chlorophyta) was carried out at a site also sampled for the facies on coralligenous walls. This site, VAI-S (see below), was chosen for the occurrence of a dense cover of *F. petiolata* on a well-developed coralligenous bioherm at 36-38 m depth. Analysis of the epiphytic assemblage was performed on both sides of 20 leaves ('fronds') with a stereomicroscope. Leaves were measured for a rough estimate of their average surface area.

Sampling sites

Six sites presenting different aspects of the coralligenous community were selected around Port-Cros Archipelago (Fig. 2). Features of these sites are given in Table II. The different sub-habitat types sampled at these sites are: (i) vertical or slightly overhanging wall shaded by large sea-fans [*Paramuricea clavata* (Risso, 1826)] (GAB-S), (ii) well-developed coralligenous bioherm (GAB-N, VAI-S), (iii) rocky walls mixed with bioherm (GAL, MON) and (iv) overhanging walls of large boulders (VAI-E).

Table II. Features of the six sites sampled around Port-Cros Archipelago (names of sites: see caption of figure 2). Sampling type: photo-quadrat (PhQ), sample of *Flabellia petiolata* (Fp). Substratum: vertical rocky wall (VRW), coralligenous bioherm (CBH), boulder overhang (BO).

Sites	Coordinates N	Coordinates E	Depth (m)	Substratum	Sampling
GAB-S	42°59'10.80"	6°23'41.6"	28-29	VRW	PhQ
GAB-N	42°59'16.05"	6°23'34.80"	38-39	CBH	PhQ
VAI-S	42°59'43.80"	6°24'25.00"	38-40	CBH	PhQ, Fp
VAI-E	42°59'47.53"	6°24'26.04"	16	BO	PhQ
GAL	43°01'13.60"	6°24'33.27"	26-30	VRW-CBH	PhQ
MON	43°01'09.00"	6°21'45.75"	27-29	VRW-CBH	PhQ

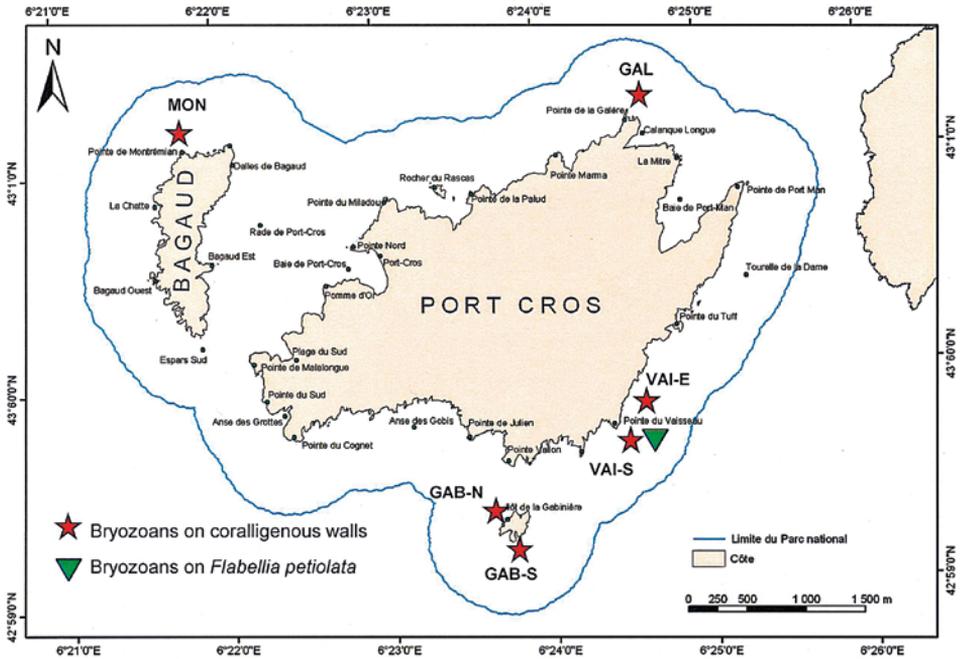


Figure 2. Location of the six coralligenous sites sampled around Port-Cros Archipelago. GAB-S: Gabinière Islet, south side; GAB-N: Gabinière Islet, north side; VAI-S: Vaisseau headland; VAI-E: Vaisseau east side; GAL: Galère headland ridge; MON: Montrémian headland ridge. Peripheral line: historical boundary of the Port-Cros National Park.

Results

Bryozoan facies on coralligenous walls

Composition of the whole assemblage

The abundance of seven higher taxonomic categories was quantified in terms of percent cover of walls (Tab. III). Bryozoans and sponges were

the major occupiers of space, clearly dominant over the other groups when considering the whole set of photos (Tab. III). The cover of these two categories was notably less variable than that of the other groups, as indicated by lower values of the coefficient of variation (CV = 54-56) and narrower ranges of average values calculated within each site (range 2, Tab. III). The relative abundance of bryozoans, sponges and macroalgae at each of the six sites was highly variable (Fig. 3). Bryozoans attained the first rank of abundance at only one site (GAB-S), while sponges were dominant at three sites (VAI-E, Galère, Montrémian) and macroalgae at two sites (GAB-N, VAI-S). The particular abundance of both categories of macroalgae (i.e. coralline and other macroalgae: Fig. 4) was related to the local presence of a well-developed coralligenous bioherm. In contrast, macroalgae were much less abundant at more shaded sites (GAB-S, VAI-E). About 17 species of sponges were visually identified with some confidence, among which *Crella pulvinar* (Schmidt, 1868), *Stylotella incisa* (Schmidt, 1880), *Hemimycale columella* (Bowerbank, 1874), *Pleraplysilla spinifera* (Schulze, 1879) and *Petrosia ficiformis* (Poiret, 1789) were particularly frequent. If non-identified sponges are taken into account, the number of species per photo-quadrat ranged from 2 to 15 and was 6.1 ± 2.8 SD on average. The most variable group was the tunicates, essentially represented by *Aplidium undulatum* Monniot F. & Gaill, 1978, a Polyclinidae typical of this environment. Cnidarians included scleractinians [*Leptopsammia pruvoti* Lacaze-Duthiers, 1897, *Caryophyllia inornata* (Duncan, 1878), *Hoplanguia durotrix* Gosse, 1860], the zoantharian *Parazoanthus axinellae* (Schmidt, 1862) and two gorgonians [*P. clavata*, *Eunicella cavolini* (Koch, 1887)].

Table III. Structure of coralligenous assemblages on shaded walls harbouring bryozoan facies at six sites around Port-Cros Archipelago. Average percent cover of higher taxa (X), standard deviation (SD), coefficient of variation (CV), range 1: within the global set of 48 photo-quadrats; range 2: within the average values obtained at each of the six sites.

Groups	X ± SD	CV	Range 1	Range 2
Bryozoans	27.6 ± 15.0	54.2	6.1-66.1	18.4-40.8
Sponges	34.3 ± 19.1	55.6	5.0-74.3	26.3-44.5
Cnidarians	5.0 ± 7.7	155.5	0-31.1	0.6-19.7
Serpulids	0.8 ± 1.2	151.2	0-4.1	0.1-2.1
Tunicates	3.7 ± 6.7	184.2	0-29.5	0-13.8
Coralline macroalgae	7.2 ± 10.1	139.8	0-46.0	0.4-16.2
Other macroalgae	16.8 ± 19.1	113.7	0-48.8	0-38.3

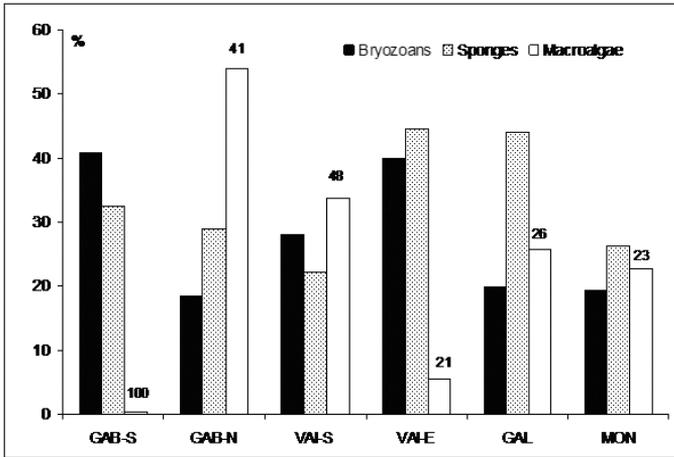


Figure 3. Average percent cover of bryozoans, sponges and macroalgae in the sessile assemblages on shaded walls at six sites at Port-Cros. Numbers above the macroalgae bars are the relative part (%) of coralline algae. Abbreviations of site names: see caption of figure 2.

Features of the bryozoan assemblage

Species richness identified from the photo-quadrats amounted to 25 species (4 cyclostomes + 21 cheilostomes, Tab. VI) when considering all sites, ranged from 7 to 14 species within each site and from 2 to 9 within each photo-quadrat. Eight species quantitatively dominated the bryozoan assemblage. Their hierarchy in cover was determined from the whole set of photo-quadrats and from their top-three ranking at each of the six sites (Tab. IV). The variability of cover (CV: Tab. IV) of these eight species was always high and increased inversely with the species rank. *Schizomavella mamillata* was clearly the most abundant and frequent species, ranking in the top three in 5 out of 6 sites (Tab. IV). All these dominant species are cheilostomes with large colonies (Fig. 4). Two of them, *Reteporella grimaldii* and *Myriapora truncata*, are erect, rigid and robust, although fairly different in their growth-form (convoluted fenestrate blades *versus* arborescent with dichotomous cylindrical ramifications). The six other species develop extensive encrusting colonies with different thickness. *Beania magellanica* is the least calcified species with net-like colonies overgrowing sponges and macroalgae. Conversely, *Dentiporella sardonica*, *S. mamillata* and *S. cornuta* develop massive colonies by active frontal budding – irregular mounds with acute prominences for *D. sardonica*, and domed, mamillate, multilaminar colonies when fully developed for the two *Schizomavella* species. Colonies of *Parasmittina rouvillei* and *S. linearis* are relatively thin multilaminar sheets with an irregular surface that can reach a large size, particularly on overhangs

of boulders. Wall areas harbouring bryozoan facies are prone to intense competition for space between and within higher taxonomic grades (e.g. Archaeplastida, Stramenopiles, Porifera, Bryozoa). Interactions between phyla that are commonly observable on photos involve sponges and encrusting bryozoans with variable overgrowth outcomes, and spatial competition between bryozoan species is also intense. However, if the photographic data attest to the diversity and complexity of the confrontation events between species, they cannot provide substantial information regarding the dynamics of these interactions.

Table IV. Dominant bryozoan species (rank 1-8 in brackets) in terms of percent cover of walls at six coralligenous sites around Port-Cros Archipelago. Average value, standard deviation ($X \pm SD$), coefficient of variation (CV) and percentage of occurrence (% Oc.) in 48 photo-quadrats. Ranking of these eight species at each of the six sites: top three (1-2-3), -: presence with lower ranking, -: absent. See caption to Figure 3 for the names of the sites.

Dominant species (walls)	$X \pm SD$	CV	% Oc.	GAB-S	GAB-N	VAI-E	VAI-S	GAL	MON
<i>Schizomavella mamillata</i> (1)	5.2 ± 7.6	146	52.1	-	2	2	1	1	3
<i>Parasmittina rouvillei</i> (2)	4.7 ± 8.7	185	31.3	2	-	1	-	-	-
<i>Schizomavella linearis</i> (3)	4.1 ± 7.8	190	43.8	1	-	-	-	-	2
<i>Dentiporella sardonica</i> (4)	3.3 ± 7.2	218	56.3	3	1	-	-	2	-
<i>Beania magellanica</i> (5)	2.8 ± 5.4	193	41.7	-	-	-	2	-	1
<i>Reteporella grimaldii</i> (6)	1.8 ± 4.4	244	27.1	-	3	-	-	3	-
<i>Schizomavella cornuta</i> (7)	1.8 ± 4.5	250	29.2	-	-	-	3	-	-
<i>Myriapora truncata</i> (8)	1.5 ± 4.2	280	29.2	-	-	3	-	-	-

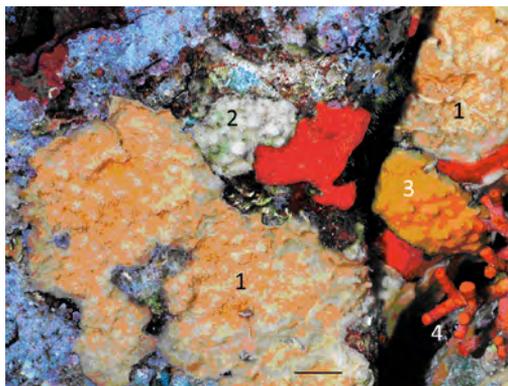


Figure 4. Four cheilostome bryozoans coexisting on the same area of coralligenous wall (Montrémian, 27 m). 1: *Parasmittina rouvillei*, 2: *Dentiporella sardonica*, 3: *Schizomavella mamillata*, 4: *Myriapora truncata*. Bar scale: 2 cm.

Bryozoan facies on *Flabellia petiolata*

Composition of the whole assemblage

The epiphytic assemblage on leaves of *Flabellia petiolata* was largely dominated by bryozoans (Fig. 5A) and comprised, in addition to them, tiny individuals of encrusting corallines, some patches of algal turf, small (juvenile?) spirorbid annelids and some few foraminifers. This assemblage presented side-related variations in taxonomic structure indicating that, in most cases, one side was more exposed to light than the other. Coralline seaweeds and spirorbids were present on both sides but more abundant on exposed sides while the two other components were not observed on the shaded sides.

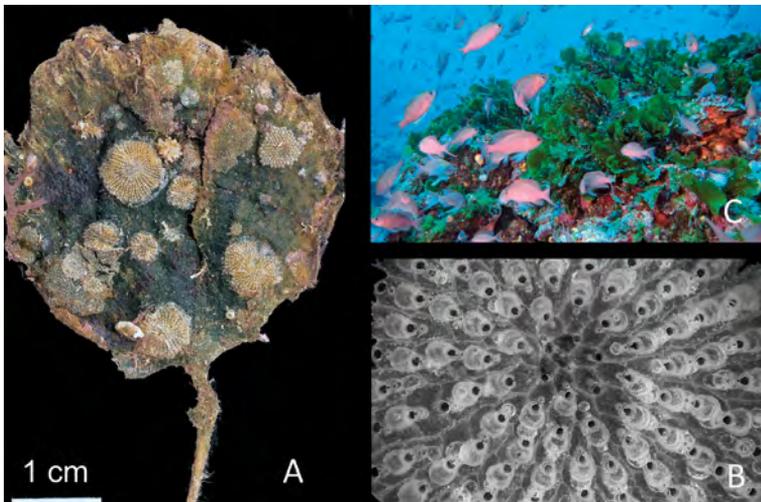


Figure 5. *Flabellia petiolata*. A: leaf heavily colonized by bryozoans, particularly *Schizomavella halimeda*. B: central part of a colony of *S. halimeda* showing the early production of ovicells around the ancestrula. C: coralligenous bioherm with a dense cover of *F. petiolata* and a shoal of the teleost *Anthias anthias*.

Features of the bryozoan assemblage

Species richness of bryozoans identified on *F. petiolata* leaves amounted to 33 species (Tab. VI: 15 Cyclostomata, 18 Cheilostomata), with 30 species on the shaded sides and only 21 species on the exposed sides. The mean value of species number per side was notably high and showed the same differential between exposed and shaded sides: it was nearly double on the shaded sides (Tab. V). Cyclostomes presented the highest side-related difference in species richness, with clearly lower scores on exposed sides (Tab. V). Overall, and particularly on shaded

sides, species richness of cyclostomes was remarkably high, only a little lower than that of cheilostomes (Tab. V). Abundance of bryozoans in terms of colony number was unexpectedly high, particularly on shaded sides where the density in colonies was 3 times higher than on exposed sides (Tab. V). Five cheilostomes species were clearly dominant in abundance (Tab. V): *Schizomavella halimeda*, *Haplopoma impressum*, *Chorizopora brongnarti*, *Escharina vulgaris* and *Escharoides coccinea*. These species accounted for 67 % of the total abundance on the two sides, and the percentage of occurrence of each of them was very high (75-100 %: Tab. V). All these dominant species developed small, sheet-like, unilaminar encrusting colonies that are circular in most cases. These five species were also dominant in surface area covered on each leaf and presented the largest colonies. However, the maximum size reached by colonies of the dominant species on each frond is relatively modest. The widest range was observed in *S. halimeda* (2.3-7.2 mm in diameter). Most colonies are juxtaposed without apparent interactions, and very few cases of overgrowth between colonies were observed. Another prominent feature of these dominant species is the early development and great abundance of ovicells despite the relatively small size of colonies. In *S. halimeda*, the first ranked dominant species, 81 % of colonies were fertile and most zooids, except a few around the ancestrula, were ovicellate (Fig. 5B). In the four other dominant species, the frequency of fertile colonies ranged from 52 to 73 % (Tab. V).

Table V. Features of the bryozoan assemblage on leaves of *Flabellia petiolata*. (1) Species richness (N spp.), abundance (N col.) and density of colonies per cm². (2) Dominant bryozoan species (rank 1-5 in brackets) on leaves of *F. petiolata*: relative abundance of colonies (% N Col., total number of colonies: 615), percentage of ovicellate colonies (% Ov. Col.) and percentage of occurrence on both sides of 20 leaves (% Oc.).

Bryozoans on <i>F. petiolata</i>	Exposed sides	Shaded sides	Both sides
Mean N bryozoan spp.	4.7 ± 2.2 SD	8.6 ± 2.3 SD	6.6 ± 3.0 SD
Total N Cyclostomata spp.	8	14	15
Total N Cheilostomata spp.	13	16	18
Mean N bryozoan col.	8.2 ± 4.3 SD	23.1 ± 7.8 SD	15.0 ± 9.4 SD
Total N col. Cyclostomata	29	60	89
Total N col. Cheilostomata	130	396	526
Density col. / cm ²	0.5	1.5	1.0
Dominant species	% N Col.	% Ov. Col.	% Oc.
<i>Schizomavella halimeda</i> (1)	18.5	81	95
<i>Haplopoma impressum</i> (2)	17.6	65	100
<i>Chorizopora brongnarti</i> (3)	11.9	52	85
<i>Escharina vulgaris</i> (4)	9.9	73	85
<i>Escharoides coccinea</i> (5)	9.3	68	75

Table VI. Species identified (i) on the walls of six coralligenous sites from 48 photo-quadrats and (ii) on leaves of *Flabellia petiolata* (both sides of 20 leaves). Growth form categories: uniserial encrusting (UE), pauciserial encrusting (PE), spot encrusting (SE), multiserial encrusting (ME), massive multiserial encrusting (mound: MO), flexible erect (FE), pauciserial rigidly erect (PRE), multiserial rigidly erect (MRE). n.i.: not identified at genus level.

Bryozoan species	Coralligenous walls	<i>Flabellia petiolata</i>	Growth form
Order CYCLOSTOMATA Busk, 1852			
<i>Annectocyma</i> sp.	-	X	PE
<i>Crisia</i> sp.	X	X	FE
<i>C. fistulosa</i> Heller, 1867	-	X	FE
<i>C. pyrula</i> Harmelin, 1990	-	X	FE
<i>C. recurva</i> Heller, 1867	-	X	FE
Diastoporidae n.d.	-	X	ME
<i>Diplosolen obelia</i> (Johnston, 1838)	-	X	ME
<i>Disporella</i> sp.	-	X	SE
<i>D. neapolitana</i> (Waters, 1918)	X	-	ME
<i>Entalophoroecia</i> sp.	-	X	PE
<i>Eurystrotos compacta</i> (Norman, 1866)	-	X	SE
<i>Filicrisia geniculata</i> Milne Edwards, 1838	-	X	FE
<i>Idmidronea atlantica</i> Forbes in Johnston, 1847	X		PRE
<i>Mecynoecia delicatula</i> (Busk, 1875)	-	X	PRE
<i>Patinella radiata</i> (Audouin, 1826)	X	X	SE
<i>Tubuliporina</i> sp.	-	X	PE
<i>T. hemisepta</i> Harmelin, 1976	-	X	SE
Order CHEILOSTOMATA Busk, 1852			
<i>Aetea sica</i> (Couch, 1844)	-	X	UE
<i>Adeonella calveti</i> Canu & Bassler, 1930	X	-	MRE
Ascophora n.i.	X	-	ME
<i>Beania magellanica</i> (Busk, 1852)	X	X	ME
<i>Bugula</i> sp.	-	X	FE
<i>Caberea boryi</i> (Audouin, 1826)	X	X	FE
<i>Cellaria</i> sp.	X	-	FE
<i>Celleporina mangneviliana</i> (Lamouroux, 1816)	X	X	MRE
<i>Chorizopora brongnarti</i> (Audouin, 1826)	-	X	ME
<i>Criblaria hincksi</i> (Friedl, 1917)	-	X	ME
<i>C. radiata</i> (Moll, 1803)	X	-	ME
<i>Dentiporella sardonica</i> (Waters, 1879)	X	-	MO
<i>Escharina vulgaris</i> (Moll, 1803)	-	X	ME
<i>Escharoides coccinea</i> (Abildgaard, 1806)	-	X	ME
<i>Haplopoma impressum</i> (Audouin, 1826)	-	X	ME
<i>Membraniporella nitida</i> (Johnston, 1838)	X	-	ME
<i>Metroperiella lepralioides</i> (Calvet, 1903)	-	X	ME
<i>Microporella cf. ciliata</i> (Pallas, 1766)	-	X	ME-SE
<i>Mollia patellaria</i> (Moll, 1803)	X	-	ME
<i>Myriapora truncata</i> (Pallas, 1766)	X	-	MRE
<i>Parasmittina rouvillei</i> (Calvet, 1902)	X	X	ME
<i>Pentapora fascialis</i> (Pallas, 1766)	X	-	MRE

Bryozoan species	Coralligenous walls	<i>Flabellia petiolata</i>	Growth form
<i>Prenantia cheilostoma</i> (Manzoni, 1870)	-	X	ME-SE
<i>Puellina gattyae</i> (Landsborough, 1852)	-	X	ME
<i>Reteporella grimaldii</i> (Jullien, 1903)	X	-	MRE
<i>Savignyella lafontii</i> (Audouin, 1826)	-	X	FE
<i>Schizomavella</i> sp.	X	-	ME
<i>S. asymetrica</i> Calvet, 1927	X	-	ME
<i>S. cornuta</i> (Heller, 1867)	X	-	ME
<i>S. halimeda</i> Gautier, 1955	-	X	ME
<i>S. linearis</i> (Hassall, 1841)	X	-	ME
<i>S. mamillata</i> (Hincks, 1880)	X	-	ME-MO
« <i>Scrupocellaria</i> » sp.	X	-	FE
<i>Turbicellepora avicularis</i> (Hincks, 1862)	X	-	MRE
<i>Umbonula ovicellata</i> Hastings, 1944	-	X	ME

Discussion

Bryozoan facies on coralligenous walls

The six coralligenous sites sampled at Port-Cros for the purpose of characterizing the associated bryozoan assemblages presented a variety of features corresponding to different aspects of the coralligenous continuum. Bryozoan facies were present both on shaded walls of a drop-off with large *Paramuricea clavata* and of large boulders, and on sites with variously developed coralligenous bioherm outcrops. This diversity of aspects is reflected in the relative abundance of bryozoans, sponges and macroalgae, particularly corallines, at the six sites (Fig. 3), with a disparity between shaded sites and those more exposed to light, with an extensive bioherm. However, the distribution of the 8 most abundant bryozoan species (Tab. IV) is relatively constant, despite this variety of local features. All these dominant species develop large, perennial colonies which are, except for *Beania magellanica*, highly calcified and, thus, are significant components of the coralligenous bioconstruction (Fig. 4). The large size of massive species with three-dimensional growth, such as *Dentiporella sardonica*, *Schizomavella mamillata* or *S. cornuta*, suggests that these species are many decades old. Because of typical colour and shape features, these dominant species can be easily identified. Their common occurrence in the coralligenous community was confirmed by numerous underwater observations and photographic data from other localities along the Provence coast. The variability of their hierarchical ranking at the different sites sampled around Port-Cros suggests that marked changes are likely to occur in other geographical conditions. It is noticeable that two *Schizomavella* species with the same growth-shape, *S. mamillata* and *S. cornuta*, are both top-ranked

in the coralligenous community of two geographically distant localities, Port-Cros and Leuca (S Italy, Ionian Sea; Cocito and Lombardi, 2007), respectively.

The structure and composition of the bryozoan assemblages analysed here depend to a large extent on the sampling method used, which was focused on species aggregations on small areas of substratum, which are thought to be essential components of the coralligenous community. Another approach at a broader spatial scale would have enabled description of the distribution of more scattered species, such as large erect species associated or not with gorgonians (e.g. *Turbicellepora avicularis*, *Pentapora fascialis*, *Smittina cervicornis* (Pallas, 1766), *Adeonella calveti*), which are the most commonly considered bryozoans in surveys of coralligenous grounds (e.g. Harmelin and Capo, 2002; Gatti *et al.*, 2015).

Assemblage on *Flabellia petiolata*

The sampled leaves of *F. petiolata* were heavily colonized by small biota, among which bryozoans were by far the dominant group. This condition indicates that (i) most of the large leaves were old at the time of sampling (June), (ii) chemical defences in *F. petiolata* are poorly deterrent to bryozoan settlers, and (iii) larvae of bryozoan settlers were locally in abundant supply. The reproduction and life cycle of *F. petiolata* were studied by Meinesz (1980). The pedunculate fan-shaped leaves (gametophyte stage) are budded from a creeping stolon and disintegrate after gamete release (holocarp) in autumn, their lifespan not exceeding one year and probably shorter (Meinesz, pers. comm.). The toxicity of *F. petiolata* may vary according to the community and time of the year: this seaweed was classified as non-toxic in all seasons in a sciaphilic community and occasionally toxic in more photophilic communities in late springtime (Marti *et al.*, 2004). It is strongly avoided by the herbivorous sea urchin *Paracentrotus lividus* (Lamarck, 1816) (Boudouresque and Verlaque, 2013), but this echinid, not observed in the sampled sites, is not a component of the coralligenous community except, occasionally, at juvenile stage (Ballesteros, 2006). Thus, leaves of *F. petiolata* constitute small, discrete, non-rigid, short-lived substrates with poor chemical defences against bryozoans. These features are assumed to be the leading ecological drivers that influence the nature and structure of the epiphytic assemblages on leaves. The abundance and diversity of bryozoans established on the *F. petiolata* leaves were most likely correlated to particular site features. The location of the sampled site at the deepest part (35-38m) of a steep rocky headland suggests that two local features were particularly beneficial to the supply in bryozoan larvae: (i) the hard bottom on which *F. petiolata* was attached was a coralligenous bioherm at 35-45 m depth, i.e. a habitat extremely rich

in bryozoans (e.g. Hong, 1980) and (ii) the high frequency of bottom currents that are vectors of larvae, attested by the occurrence of large, permanent shoals of the planktivorous fish, *Anthias anthias* (Fig. 5C).

Therefore, the main constraints that candidates for settlement on leaves of *F. petiolata* have to cope with during their development are two intrinsic features of this micro-habitat, i.e. the ephemeral availability of the algal substrate and its flexible nature. Successful bryozoans in this assemblage present growth-forms and life-history traits that are particularly well-suited to these ecological conditions. These species develop moderately calcified, unilaminar, encrusting colonies that are apt to grow rapidly on a flexible substrate and reproduce early with a large number of ovicells. These features, commonly present in *Schizomavella halimeda* (Fig. 5B) and other dominant species, are typically those of fugitive species that can colonize opportunistically, with short life-cycles, ephemeral substrates or early successional stages on new perennial substrates (e.g. Centurión and López Gappa, 2011).

The taxonomic structure of the bryozoan assemblage on shaded sides of *F. petiolata* was characterized by an unusual diversity of cyclostomes, which was close to that of cheilostomes (14 vs. 16 spp., Tab. V). Moreover, if only species of “Ascophora” (= ascophoran neocheilostomes; Gordon, 2014) are considered, the ratio Cyclostomata/Ascophora reaches 1.17, which is a value very close to that found in other ephemeral habitats, such as *Posidonia oceanica* leaves, but also in dark caves (Harmelin, 2000). This paradoxical analogy was attributed by Harmelin (2000) to particular environmental constraints occurring in these habitats that could diminish the suitability of ascophorans, normally dominant over cyclostomes in Quaternary assemblages (McKinney, 1992).

Despite its species name and high dominance on *F. petiolata* highlighted here, *Schizomavella halimeda* is not an exclusive epiphyte of *Halimeda tuna* (J. Ellis & Solander) Lamouroux and *F. petiolata*. It has been described by Gautier (1955, as *Smittina halimeda*) from a small colony encrusting a dead bryozoan colony collected at Castiglione (now Bou Ismaïl, Algeria), but he noted its particular frequency on *H. tuna* at Marseilles and Villefranche. Furthermore, Gautier (1962) erroneously synonymized this species with *Schizomavella discoidea* (Busk, 1859) and confirmed its frequency on *H. tuna*, although also present on other sciaphilic macroalgae, shells and stones. The same distribution was noted by Zabala (1986) and by López de la Cuadra and García Gómez (2001) in their redescription of *S. halimeda* from Mediterranean Iberian coasts.

Conclusion

The two bryozoan facies studied at Port-Cros are established in fundamentally different coralligenous sub-habitats: rocky or biogenic walls vs. *Flabellia petiolata*, a macroalga with an ephemeral development of leaves. Both facies are species-rich, while exhibiting contrasting features: species composing them have strikingly different life-histories, growth-forms and sizes. These differences are well illustrated by the colony traits of the two *Schizomavella* species that are first-ranked in both facies and characteristic of the coralligenous community: large, massive and long-lived for *S. mamillata* (1st rank on walls), small, unilaminar and short-lived for *S. halimeda* (1st rank on *F. petiolata*). These two facies represent a significant part of the species diversity of bryozoans in the coralligenous community, but another facies established in small cavities, particularly in inner interstices of the coralligenous bioherm, includes a large number of highly cryptic species (Harmelin, 1976; Hong, 1980). It is worth noting that the most easily observable components of the bryozoan assemblages on coralligenous walls, i.e. the large erect species, also occur at the surface of flat detritic bottoms, typified by Marion (1883) as “gravieres coralligènes à grands bryozoaires” (“coralligenous gravels with large bryozoans”) when they are not altered. Such aggregations of large species (mainly *Pentapora fascialis*, *Smittina cervicornis*, *Myriapora truncata*, *Cellaria* sp., *Hornera frondiculata*) were observed around Port-Cros: off the Passe des Grottes (Laborel *et al.*, 1976), at 60m depth off Cap Cagnet (unpublished personal observation, July 1987) and west of the Sec de la Gabinière at 70m depth in May 2014 (Holon and Harmelin, 2014). This last observation revealed an extraordinary bryozoan bank made up essentially of a vast aggregation of *P. fascialis* and *S. cervicornis* colonies. Such facies of large erect bryozoans attests to the lack of clear boundaries between part of the coralligenous community and the epifauna of surrounding coastal detritic bottoms.

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