

Article

# Plant Part Age and Size Affect Sessile Macrobenthic Assemblages Associated with a Foliose Red Algae *Phycodrys rubens* in the White Sea

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**Abstract:** Facilitation by foundation species commonly structures terrestrial and marine communities. Intraspecific variation in individual properties of these strong facilitators can affect the whole suite of the dependent taxa. Marine macroalgae often act as ecosystem engineers, providing shelter and substrate for numerous associated organisms. Epibiosis of foliose red algae, however, remains underexplored, especially in the high latitudes. Here we studied sessile macrobenthic assemblages associated with a foliose red algae *Phycodrys rubens* in the White Sea (66° N) shallow subtidal, and the effect of individual plant properties on their structure. The blades of *P. rubens* develop annually, and it is possible to tell the young (usually larger) plant parts from the old ones. We hypothesized that epibenthic community structure depends on plant part age and size. We examined epibiosis on 110 plants at two sites, and the results generally supported our hypotheses. Old plant parts were several times smaller, and had higher total cover than young parts. Sponges strongly dominated the epibiosis on old parts, and young parts were dominated by polychaetes and bryozoans. Plant part surface area negatively correlated with total cover on young parts, while on old parts the relationship was location-specific. On young parts the relative abundance of a polychaete *Circeis armoricana* increased with surface area, and the proportion of sponges decreased. The patterns indicate that epibenthic community structure is linked to the demography of an ecosystem engineer.

**Keywords:** epibiosis; foundation species; facilitation; Arctic; macroalgae; ecosystem engineer

## 1. Introduction

Interspecific biotic interactions are powerful drivers of community structure. Though ecological research has long revolved around competition or predation, in recent decades the interest in positive interactions revealed the crucial role of facilitation [1,2]. Facilitation of multiple dependent species by a strong facilitator ('foundation species', [3]) is common in both terrestrial and aquatic ecosystems, with trees and corals being prominent examples.

Space is one of the most limiting resources in marine benthic communities [4]. Marine macrophytes act as secondary substrate and provide complex habitat architecture, functioning as ecosystem engineers [5]. By hosting numerous epibenthic taxa, they increase abundances and diversity in marine ecosystems (reviewed in reference [6]). Although species composition, spatial structure and functioning of the epibenthic assemblages associated with brown and green algae have been extensively explored (reviewed in reference [7]), macrobenthic epibiosis of red algae has been largely overlooked. The research has been focused on bacterial colonisation and algal anti-fouling activity (e.g., references [8–10]). Epibiotic assemblages has been described mostly for red coralline algae (e.g., [11,12]), whilst the epibiosis

of foliose species is underexplored [13,14] and rarely mentioned in recent reviews (see reference [15]). At the same time rhodophytes are widespread and the most diverse group of multicellular algae [16] utilizing the largest depth range (e.g., Table 4 in reference [17]), and are commonly dominant or subdominant in lower subtidal areas in polar waters [18]. While the effect of biotic interactions on community structure is supposed to weaken with latitude, the evidence for this relationship is mostly based on comparisons of tropical and temperate ecosystems [19,20]. This knowledge gap makes the research on communities from polar regions structured by facilitation especially important.

Research on variation of the effects of foundation species on the associated organisms has mostly focused on interspecific differences between facilitators: e.g., different species of macroalgae [21,22], trees [23,24] or benthic invertebrates [25,26] hosting different dependent assemblages. However, intraspecific individual variation in foundation species has also been recently recognized as an important structuring agent. Individual properties of a facilitator which affect the dependent taxa include its genetic diversity [27], variation in behavioral patterns [28], morphological traits [29] and ontogenetic variation [30,31]. Also, an individual ecosystem engineer can provide a set of functionally different microhabitats, such as tree crowns and hollows or kelp blades and stipes, which develop different associated assemblages of dependent species [29,30,32].

Here we explored sessile macrobenthic assemblages associated with a foliose red algae *Phycodryas rubens* in the White Sea (66° N) shallow subtidal, and the effect of individual plant properties on their structure. *P. rubens* is a red foliose seaweed that is frequently found all around the North Atlantic [18], and is common in the White Sea subtidal. Though individual specimens can be found in the upper subtidal kelp forests, deeper *P. rubens* form a so-called «red algae belt» along with several other red algae. Life history, growth and reproduction of *P. rubens* were studied in various parts of its geographical range [33–37], including a single example of research conducted specifically in the White Sea [38]. Here, *P. rubens* lives for up to four years. The size of an individual plant is highly variable (length varies from 10 to 250 mm, weight—from 0.005 to 12 g [38]). New blades emerge mainly in late winter and early spring. *P. rubens* grows mostly in spring and autumn, and its blades are largest in November. Later under the ice cover (which lasts from November to early May [39]) most blades disintegrate, leaving only midribs which turn into side branches. The following spring these branches develop young blades that are easily distinguishable from older ones throughout the year [38]. Consequently, in summer and autumn an individual plant consists of relatively large, soft and intact young blades, and (for the plants which survived at least one winter) an old part formed by branches and rigid partly disintegrated blades from previous years. We hypothesized that due to the seasonal growth and disintegration patterns of *P. rubens*, epibiotic assemblages may differ on young and old parts of its thallus. We also hypothesized that plant size may affect epibiosis in terms of species composition and abundance, linking the community structure to the demography of an ecosystem engineer.

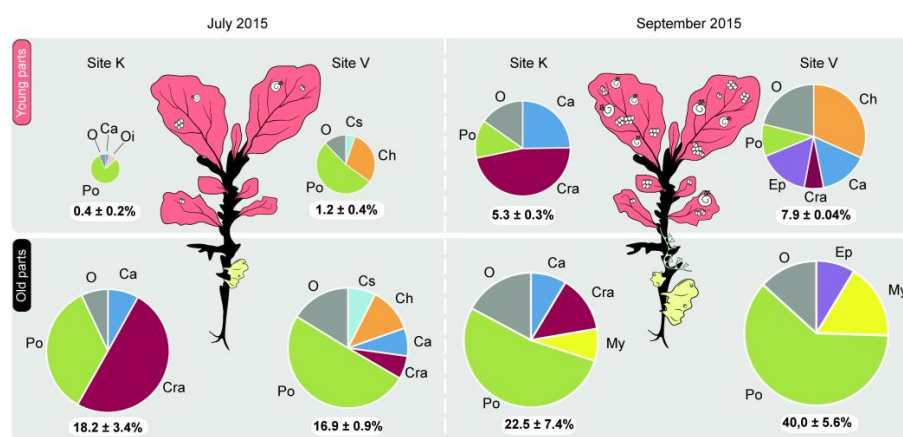
## 2. Materials and Methods

To determine patterns of abundance of sessile organisms associated with *Phycodryas rubens*, SCUBA divers sampled two subtidal sites with contrasting hydrological regimes in the Velikaya Salma Strait between the Karelian shore and Velikii Island in the western part of Kandalaksha Bay (the White Sea): ‘Site K’ (near Kamenukha island, 11 m deep, 66°33.028’ N 33°9.295’ E) and ‘Site V’ (near Velikii island, 12 m deep, 66°33.437’ N 33°6.877’ E). Strong currents in Velikaya Salma Strait are determined by semi-diurnal tides [39]. Site V was located in the narrowest part of the Strait (opposite the White Sea Biological Station of the Moscow State University). Site K was 1.7 km east from Site V in a wider part of the strait closer to the open sea. As a result, the surface current velocity during a flood tide was much higher at Site V, peaking at 1.33 m·s<sup>-1</sup> compared to 0.75 m·s<sup>-1</sup> at Site K (measured in July 2018 at 1 and 5 m depth with a Valeport 106 current meter). Both sites had a rocky bottom with cobble and gravel. Ice cover here typically lasts from December to May. Waters of Velikaya Salma show no thermal stratification because of tidal-mixing with water temperatures not exceeding 6–7 °C until July

and raising up to 17–20 °C in August, while salinity stays closely around 25‰ throughout summer and fall [39,40].

We collected all red macroalgae from 0.25 m<sup>2</sup> square frames randomly placed on the bottom 2–3 m from each other. Three frames per site were obtained on July 6–7, 2015, and two on September 24, 2015. The frames from the same site and month were sampled simultaneously. Two additional frames per site obtained on October 1, 2016 were only used to determine the proportion of *Phycodrys rubens* compared to other macroalgal species (see Figure S1 and Tables S1–S3). All plants collected were identified to the species level (and individually wet weighed in September 2015 and October 2016), but only the thalli of the dominant *P. rubens* from 2015 were used for further examination of epibenthic fauna. Individual *P. rubens* stipe with its blades and rhizoids was regarded as a separate sample. In July, when the covers of epibenthic organisms on *P. rubens* were exceedingly low, epibiosis was examined on 5 random individual *P. rubens* from each frame (30 plants in total). In September 2015 (when the covers were much higher) we examined epibiosis on 15 random individual *P. rubens* plus 5 largest of the remaining arrays from each frame (80 plants in total). These additional largest plants were added to compensate for their disproportionately high contribution in total substrate area and to explore the relationship between the structure of epibiosis and plant size. Per frame, the 5 largest plants together provided 569 ± 157 cm<sup>2</sup> of the total surface area and 56 ± 11 cm<sup>2</sup> of the area covered by epibionts compared to 245 ± 61 and 32 ± 10 cm<sup>2</sup> (correspondingly) contributed by 15 random plants (sites pooled). All the plants were preserved in 10% buffered formalin on sea water prior to examination.

The blades of *P. rubens* develop annually so that the current year's young blades, which constitute the major part of the thallus, are visually distinguishable from the older part remaining from the previous 1–3 years [38]. We examined the epibiosis separately on these two parts (hereafter 'young' and 'old', see Figure 1 for the scheme). Importantly, many plants examined had no old part, especially in September samples. For each young or old plant part we documented its surface area (accurate to 1 mm<sup>2</sup>), and identified to species level (except for sponges) and counted all sessile organisms attached. We determined the area of each sponge found (accurate to 0.1 mm<sup>2</sup>), calculated the number of units (zooids/polyps) in each hydrozoan or bryozoan colony, and individually measured the opercular diameter in serpulid polychaetes (accurate to 0.05 mm<sup>2</sup>) to estimate areas covered and percent covers according to the size-area allometric relationships established from subsamples (Supplementary File 1). Undetermined bryozoan ancestrulae with individual areas less than 0.15 mm<sup>2</sup> were excluded from further analyses.



**Figure 1.** Dominant species composition (on piecharts) and average total cover (in white boxes) of epibiosis on young and old plant parts of *Phycodrys rubens* in July and September 2015. Piechart diameter denotes log total percent covers (frames pooled). Po—Porifera, My—juvenile Mytilidae (*Musculus discors* and *Modiolus modiolus*) (Bivalvia). Ch—*Celleporella hyalina* (Bryozoa), Cra—*Cribrilina annulata* (Bryozoa), Ep—*Electra pilosa* (Bryozoa). Ca—*Circeis armoricana* (Polychaeta). Cs—*Calycella syringa* (Hydrozoa), Oi—*Orthopyxis integra* (Hydrozoa), O—all other species.

To assess the distribution of *P. rubens* by surface area and roughly estimate its contribution to substrate pool for epibenthic organisms, we approximated the surface area of the plants not preserved for examination from their wet weight (in grams) based on linear relationships established from measurements of the plants examined in September 2015. Sessile epibiota was not removed prior to weighing because of logistical constraints. A single outlier extremely heavily fouled by sponges (having, in contrast to all other plants, a sponge weighing more than a plant itself) was excluded. We used separate relationships for young ( $S_{young}$ , cm<sup>2</sup>) and old ( $S_{old}$ , cm<sup>2</sup>) parts of the plant:  $S_{young} = 27.189638 \cdot \text{Weight} + 5.944277$ ,  $R^2 = 0.68$ ,  $n = 79$ , and  $S_{old} = 6.942554 \cdot \text{Weight} + 0.463375$ ,  $R^2 = 0.72$ ,  $n = 79$ .

For the plants with both young and old parts, we analyzed the relationship between the total cover of epibenthic organisms and plant part age (young or old), sampling month (July or September), and site (K or V) with beta-regression (see below), using individual plant ID as a random blocking factor nested in site  $\times$  month interaction. Total cover of epibiosis on the plants with only a young part was analyzed with a reduced model with only month and site as predictors. To assess the relationships between multivariate community structure and plant part age, sampling month and location, we applied permutational analyses of variance (PERMANOVA, see reference [41]) with the same factor sets. We used Bray-Curtis similarities calculated on fourth root transformed percent covers as a distance measure for PERMANOVAs, and visualized multivariate differences between the assemblages associated with plant parts of different ages in September (when both young and old parts were sufficiently covered) with principal coordinates ordination (PCO). We also compared average total cover and the covers of top abundant species between young and old parts of the plants with both young and old parts using the Wilcoxon matched pairs test, and between July and September—with the Mann-Whitney U-test (separately for young and old parts). The covers of top abundant species could not be analyzed in a similar fashion to total cover, since they had zero values, and the only available software implementation of zero-inflated beta-regression mixed models (i.e., supporting random effects) did not converge. Consequently, the covers of top abundant species were only compared between young and old plant parts by using pairwise tests as described above.

To assess the effects of location and individual size variation in the ecosystem engineer on the suite of dependent species, we examined the effects of site, *P. rubens* surface area and their interaction on total percent cover separately for young and old parts of *P. rubens* collected in September 2015 with beta-regression (see below). The effects of the same predictors on Shannon-Wiener species diversity and the number of species were analyzed with type III sum of squares ANCOVAs. We visualized multivariate differences between the assemblages associated with plants of different size and location with PCO based on the Bray-Curtis similarity matrix calculated on fourth root transformed percent covers. The effects of site, plant part surface area and their interaction on multivariate community structure were tested with PERMANOVA analyses [41] separately for young and old plant parts. The relationships between plant part surface area, sampling site and covers of 5 top abundant species were also analyzed with beta-regression. Since the two sites were intentionally selected to have contrasting hydrological regimes, the corresponding effect with two levels was treated as fixed in all the analyses. We did not combine assessing the effects of plant part surface area and age in a single model since many plants in September did not have an old part, and these were, on average, much smaller than the plants having both parts, which would lead to biased estimates.

For all the proportional data (total cover and relative covers of dominant species) where we fitted beta-regression models, we used zero-inflated distributions if zero observations occurred. We addressed heteroscedasticity by modeling the variances where this improved models' quality based on the generalized Akaike Information Criterion (AIC). In one case (relative covers of a bryozoan *Electra pilosa* on old blades) a zero-inflated model could not converge, since all the zero observations were concentrated at one site. Separate models for the two sites were fitted in this case. We checked distributions of residuals using a detrended quantile plot ('worm plot', [42]). Analyses were conducted using the 'gamlss' package [43] for R [44]. To assess the effect of location and plant surface area on average individual size of epibenthic organisms we used type III sum of squares ANCOVAs with



site, area and their interaction as predictors. Replicate 0.25 m<sup>2</sup> frames were pooled by site in all the analyses since (i) their number (2–3 per sample) was too small to be used as a random blocking factor in the models (at least 5–6 levels required), and (ii) plant areas, the proportion of young/old plant parts' surface areas, and total cover of epibenthic organisms showed no significant differences between the simultaneously sampled frames from the same site (Tables S4 and S5). In addition, we supplemented all the analyses supporting our main conclusions with alternative models where we included Frame as a fixed effect (see Tables S6–S10), which had no principal effect on the results. Means are reported  $\pm$  standard error (SE). All the raw data needed to reproduce the analyses are available as supplementary data (Supplementary File 1).

### 3. Results

*P. rubens* was a dominant red algae in all the samples (Table S1). Smallest plants were most abundant, while largest ones contributed most substrate surface for epibionts (Table S2, Figure S1), in total approximately 0.6–1.7 m<sup>2</sup> per 1 m<sup>2</sup> of the bottom in September 2015 and 2.4–3.3 m<sup>2</sup> in September 2016 (Table S3). In terms of surface area young parts of *P. rubens* in September were 2–3 times larger than old ones (Table S3). Also, in September 2015, 57% of individual plants had only a young part and no old part compared to 17% in July. In July 2015 we found, in total, 24 species of sessile epibionts on 30 *P. rubens* individuals examined. There were 11 bryozoans, 9 hydroids, 3 bivalves, 1 ascidian, 1 spirorbid polychaete and unidentified sponges. In September 2015 there were 41 species of sessile epibionts: 20 bryozoans, 11 hydroids, 3 bivalves, 3 ascidians, 2 epiphytic red algae, 1 barnacle, 1 spirorbid polychaete and unidentified sponges on 80 *P. rubens* individuals examined. Total cover (sites and frames pooled) was several times higher in September ( $10.7 \pm 0.9\%$ ) vs. July ( $2.6 \pm 0.4\%$ ).

Effects of plant part age and month on total cover of epibenthic organisms were both significant (Table 1, Table S6). Regardless of location and season total cover was much higher on old than young parts. The difference was significantly higher in July (15–20-fold) compared to September (3–5-fold) (Tables 1 and 2). Total cover on young plant parts in September was dramatically higher than in July (Mann-Whitney U-test,  $Z = -7.374$ ,  $p = 1.66 \cdot 10^{-13}$ , sites pooled). In July, in fact, young parts were almost clear of epibionts. The covers on old parts were also higher in September than in July (Mann-Whitney U-test,  $Z = -2.214$ ,  $p = 0.0241$ , sites pooled). As a result, given the difference in size between young and old plant parts, in terms of substrate area covered in July,  $25 \pm 6\%$  and  $75 \pm 6\%$  of *P. rubens* epibionts occupied young and old parts, correspondingly ( $n = 6$  frames, sites pooled). In September the proportion was  $53 \pm 9\%$  and  $47 \pm 9\%$  on young and old plant parts, correspondingly ( $n = 4$  frames, sites pooled).

In July total and average numbers of species were lower on young plant parts than on old ones at both sites. In September, however, the number of species (being generally higher than in July) was lower on young parts only at Site K. While in July the Shannon-Wiener species diversity index was higher in the epibiosis on old parts compared to young ones, in September in contrast it became higher on young parts compared to old ones regardless of the location (Table 2).

The effects of plant part age, month and location on multivariate community structure were all significant (Table 3, Table S7). Young plant parts in July were nearly empty, in September being co-dominated by bryozoans *Cribrilina annulata*, *Celleporella hyalina* and *Electra pilosa*, a serpulid polychaete *Circeis armoricana*, and sponges. Old parts, in contrast, were strongly dominated by sponges (especially in September) with *C. annulata*, *E. pilosa*, *C. armoricana* and juvenile mytilid bivalves as subdominants (Table 4, Figure 1). In July percent covers of sponges and *C. armoricana* were significantly higher on old parts regardless of the location. *C. annulata*, *C. hyalina* and juvenile mytilids either had equally low covers on old and young plant parts, or were significantly more abundant on old ones, depending on the location. *E. pilosa* was nearly absent (Table 4). In September sponges and juvenile mytilids were significantly more abundant on old parts than on young ones. *E. pilosa* displayed a similar distribution, but only at Site V where it was relatively abundant. In contrast, *C. armoricana* and *C. hyalina* were either equally abundant on young and old parts or more abundant on young parts,

depending on the location (Table 4). In September *C. armoricana* and juvenile mytilid bivalves were subdominant on old parts at both sites, while the subdominant bryozoans were *C. annulata* at Site K and *E. pilosa* at Site V. At the same time on young parts bryozoans comprised more than a half of total cover, with *C. annulata* dominating at Site K, and *E. pilosa* and *C. hyalina* at Site V. Sponges and *C. armoricana* were equally abundant here at both sites (Figure 1). Average size of an individual or colony was either larger on old parts or was not affected by substrate age depending on the species and location (Table 4). On a PCO plot plant parts sampled in September were grouped by age and site, while the old and young parts from same plants were generally shifted from each other along the vector of the sponges abundance (Figure 2).

**Table 1.** Effects of plant part age (fixed, young or old), month (fixed, July or September), and location (fixed, sites K or V) on total cover of *Phycodrys rubens* epibiosis in 2015: beta-regression, mean (logit link) and variance (log link) modeled, frames pooled. Auxiliary non-randomly sampled (in September only) five largest plants per frame not included (see Materials and Methods). Significant terms in a mean model highlighted in bold.

Plant Age	Model	Source of Variation	Estimate	SE	t-Value	p
Plants having both old and young parts (with Plant ID as a random blocking factor nested in Site × Month; n = 51 plants)	Mean (Mu)	Intercept	−4.2818	0.2837	−15.091	<0.001
		Site [level ‘K’]	<b>−1.0815</b>	<b>0.5188</b>	<b>−2.085</b>	<b>0.040</b>
		Age [level ‘Old’]	<b>2.5756</b>	<b>0.3670</b>	<b>7.018</b>	<b>&lt;0.001</b>
		<b>Month [level ‘September’]</b>	<b>1.9248</b>	<b>0.3053</b>	<b>6.305</b>	<b>&lt;0.001</b>
		Site × Age	1.1447	0.6280	1.823	0.072
		Site × Month	0.9185	0.5436	1.690	0.095
		<b>Age × Month</b>	<b>−1.3377</b>	<b>0.4900</b>	<b>−2.730</b>	<b>0.008</b>
		Site × Age × Month	0.3832	0.7951	0.482	0.631
	Variance (Sigma)	Intercept	−2.0056	0.2469	−8.121	<0.001
		Site [level ‘K’]	−0.1687	0.3894	−0.433	0.666
		Age [level ‘Old’]	1.1752	0.3558	3.303	0.001
		Month [level ‘September’]	−0.1365	0.3419	−0.399	0.691
		Site × Age	0.3449	0.5409	0.638	0.525
		Site × Month	0.3068	0.4999	0.614	0.541
Age × Month		0.7307	0.5178	1.411	0.162	
	Site × Age × Month	0.9098	0.7330	1.241	0.218	
Plants having only young parts (n = 39 plants)	Mean (Mu)	Intercept	−4.4794	0.2277	−19.674	<0.001
		Site [level ‘K’]	0.5679	0.8158	0.696	0.492
		<b>Month [level ‘September’]</b>	<b>2.4466</b>	<b>0.2839</b>	<b>8.618</b>	<b>&lt;0.001</b>
		Site × Month	−1.1746	0.8399	−1.398	0.172
	Variance (Sigma)	Intercept	−3.3497	0.5212	−6.427	<0.001
		Site [level ‘K’]	1.8791	0.8005	2.347	0.025
		Month [level ‘September’]	2.1793	0.5594	3.896	<0.001
Site × Month		−2.8802	0.8503	−3.387	0.002	

**Table 2.** Average total cover, number of species and Shannon-Wiener diversity index (*H'*) of epibiosis on *Phycodrys rubens* by month, site and plant part age in 2015 (frames pooled).

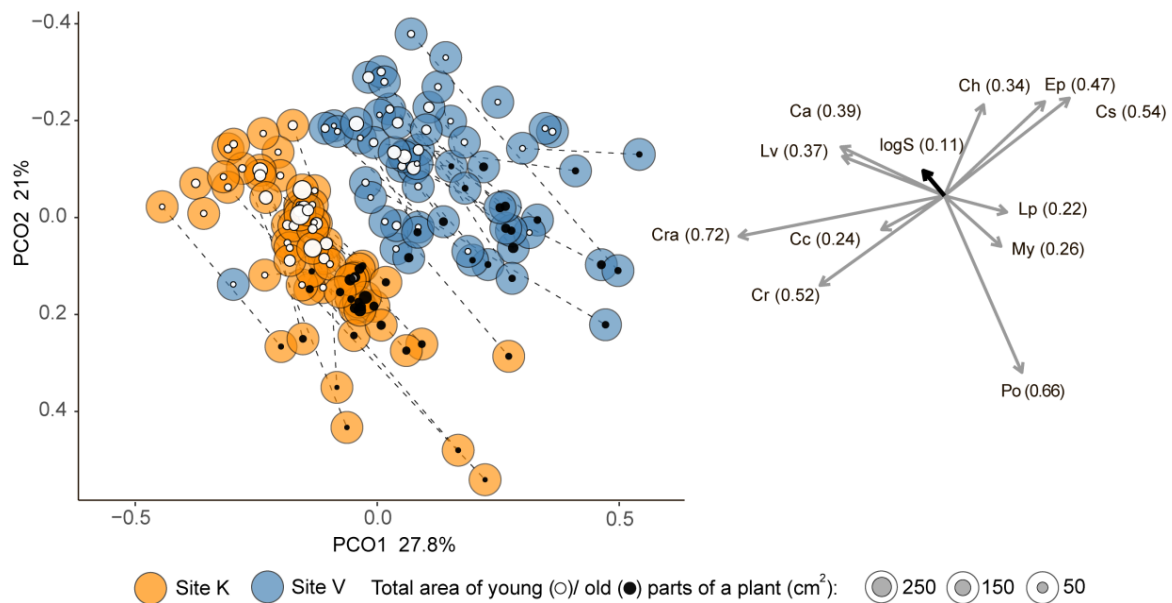
Parameter	Month	Site K		Site V	
		Young	Old	Young	Old
Average total cover, %	July	0.8 ± 0.4	16.2 ± 4.0	1.3 ± 0.4	15.4 ± 3.3
	September	7.1 ± 0.6	35.9 ± 8.7	10.4 ± 1.4	23.8 ± 6.8
Total number of species (average number of species per plant)	July	10	15	16	23
		(3.9 ± 0.5)	(4.8 ± 0.6)	(6.7 ± 0.4)	(7.1 ± 0.8)
	September	26	35	27	27
		(9.8 ± 0.5)	(11.3 ± 1.7)	(8.5 ± 0.5)	(8.8 ± 1.2)
Total <i>H'</i> (average <i>H'</i> per plant)	July	0.83	1.20	1.34	1.67
		(0.67 ± 0.12)	(0.73 ± 0.14)	(0.86 ± 0.09)	(1.16 ± 0.12)
	September	1.63	1.47	2.09	1.39
		(1.33 ± 0.04)	(1.08 ± 0.17)	(1.36 ± 0.07)	(1.29 ± 0.08)

**Table 3.** Effects of plant part age (young or old), month (July or September), and location (sites K or V) on multivariate community structure of epibiosis on *Phycodryis rubens*: type III sum of squares PERMANOVA for 9999 permutations on fourth root transformed covers of sessile epibionts, Bray-Curtis similarity, frames pooled. Significant terms highlighted in bold. [f]—fixed effect, [r]—random effect.

Plant Age	Source of Variation	df	SS	MS	Pseudo-F	p	Unique Permutations
Plants having both old and young parts	Site [f]	1	27,411	27,411	18.56	0.0001	9941
	Month [f]	1	31,635	31,635	21.42	0.0001	9945
	Age [f]	1	24,172	24,172	25.84	0.0001	9930
	S × M [f]	1	7183	7183	4.87	0.0001	9945
	S × A [f]	1	2921	2921	3.12	0.0076	9940
	M × A [f]	1	16,015	16,015	17.12	0.0001	9955
	S × M × A [f]	1	1416	1416	1.51	0.1850	9944
Plant ID (S × M) [r]	47	69,389	1476	1.58	0.0002	9733	
Error	47	43,960	935				
Plants having only young parts	Site [f]	1	2779	2779	2.41	0.0361	9952
	Month [f]	1	11,990	11,990	10.40	0.0001	9949
	S × M [f]	1	3906	3906	3.39	0.0055	9954
	Error	35	40,338	1153			

**Table 4.** Mean percent covers and mean individual sizes (approximated area occupied) of top abundant species on young and old parts of the same *Phycodryis rubens* pairwise compared (Wilcoxon matched pairs test, P). K—Site K, V—Site V. n.v.—no variance or sample size too small. n.c.—no co-occurrence on old and young parts of a single plant. N—sample size. Significantly higher mean in a pair highlighted in bold.

Species	Site	Mean Percent Cover, %				Individual Mean Area, mm <sup>2</sup>					
		Young parts		Old parts		P	N	Young parts		Old parts	
<i>Circeis armoricana</i>	K	0.02 ± 0.01	<b>1.01 ± 0.28</b>	<b>0.002</b>	12	0.044 ± 0.005	<b>0.534 ± 0.042</b>	<b>0.003</b>	11		
	V	0.03 ± 0.01	<b>1.06 ± 0.28</b>	<b>0.006</b>	13	0.039 ± 0.001	<b>0.512 ± 0.038</b>	<b>0.005</b>	10		
<i>Cribrilina annulata</i>	K	0.00 ± 0.00	<b>5.33 ± 2.17</b>	<b>0.004</b>	12	0.127 ± 0.000	<b>2.793 ± 0.420</b>	<b>0.018</b>	7		
	V	0.01 ± 0.00	0.67 ± 0.52	0.508	13	0.140 ± 0.010	2.593 ± 0.313	0.068	4		
<i>Electra pilosa</i>	K	0.00 ± 0.00	0.00 ± 0.00	n.v.	12		n.c.		0		
	V	0.00 ± 0.00	0.17 ± 0.13	0.686	13		n.c.		0		
<i>Celleporella hyalina</i>	K	0.00 ± 0.00	0.01 ± 0.01	0.686	12		n.c.		0		
	V	0.39 ± 0.07	<b>1.83 ± 0.58</b>	<b>0.013</b>	13	0.625 ± 0.055	<b>2.133 ± 0.265</b>	<b>0.004</b>	11		
Porifera	K	0.37 ± 0.35	<b>8.72 ± 4.37</b>	<b>0.028</b>	12	11.369 ± 8.069	20.981 ± 17.081	n.v.	2		
	V	0.61 ± 0.48	<b>8.20 ± 3.27</b>	<b>0.017</b>	13	41.056 ± 21.573	24.138 ± 7.306	0.465	4		
Juvenile mytilids	K	0.00 ± 0.00	0.28 ± 0.23	0.345	12	1.732	14.628	n.v.	1		
	V	0.02 ± 0.01	<b>0.68 ± 0.24</b>	<b>0.002</b>	13	0.629 ± 0.118	1.086 ± 0.655	0.463	6		
<i>Circeis armoricana</i>	K	1.38 ± 0.09	1.79 ± 0.28	0.326	25	0.250 ± 0.014	<b>0.578 ± 0.020</b>	<b>0.000</b>	21		
	V	<b>1.31 ± 0.14</b>	0.55 ± 0.16	<b>0.003</b>	21	0.325 ± 0.011	<b>0.451 ± 0.044</b>	<b>0.010</b>	16		
<i>Cribrilina annulata</i>	K	2.78 ± 0.33	3.38 ± 0.62	0.300	25	1.005 ± 0.069	<b>1.510 ± 0.152</b>	<b>0.002</b>	22		
	V	0.38 ± 0.07	0.22 ± 0.09	0.099	21	1.229 ± 0.238	1.463 ± 0.196	0.208	8		
<i>Electra pilosa</i>	K	0.05 ± 0.02	0.06 ± 0.02	0.664	25	0.639 ± 0.173	0.722 ± 0.147	0.508	11		
	V	1.50 ± 0.33	<b>3.61 ± 0.91</b>	<b>0.016</b>	21	1.923 ± 0.287	2.755 ± 0.651	0.063	21		
<i>Celleporella hyalina</i>	K	0.17 ± 0.05	0.27 ± 0.07	0.092	25	0.697 ± 0.066	<b>1.620 ± 0.289</b>	<b>0.015</b>	17		
	V	<b>2.92 ± 0.40</b>	0.82 ± 0.14	<b>0.000</b>	21	1.408 ± 0.152	1.599 ± 0.144	0.287	17		
Porifera	K	1.34 ± 0.42	<b>19.14 ± 5.68</b>	<b>0.000</b>	25	8.216 ± 1.309	18.355 ± 6.490	0.147	19		
	V	0.72 ± 0.33	<b>15.92 ± 4.33</b>	<b>0.000</b>	21	8.683 ± 1.842	53.231 ± 36.658	0.279	13		
Juvenile mytilids	K	0.19 ± 0.11	<b>2.23 ± 0.69</b>	<b>0.000</b>	25	1.955 ± 0.548	<b>7.417 ± 1.472</b>	<b>0.002</b>	16		
	V	0.12 ± 0.05	<b>5.43 ± 1.53</b>	<b>0.001</b>	21	2.170 ± 0.873	5.808 ± 1.277	0.060	12		



**Figure 2.** Principal coordinates ordination (PCO) of sessile species percent covers on young and old parts of *Phycodryus rubens* in September 2015. Bray–Curtis similarity on fourth root transformed data. Dashed lines connect young and old parts of a single plant in those having both. Species with  $R^2$  (in brackets)  $> 0.2$ : Po—Porifera; My—juvenile Mytilidae (*Musculus discors* and *Modiolus modiolus*) (Bivalvia); Cc—*Callopora craticula* (Bryozoa), Ch—*Celleporella hyalina* (Bryozoa), Cr—Crisiidae (*Crisia eburnea* and *Crisiella producta*) (Bryozoa), Cra—*Cribrilina annulata* (Bryozoa), Ep—*Electra pilosa* (Bryozoa), Lv—*Lichenopora verrucaria* (Bryozoa); Cs—*Calycella syringa* (Hydrozoa), Lp—*Lafaea pocillum* (Hydrozoa); Ca—*Circeis armoricana* (Polychaeta); logS—log-transformed total surface area of the corresponding plant part (young or old).

Since in July we did not sample largest plants, which contribute the most substrate surface, the connection between the epibiosis structure and plant surface area was studied based on September samples. Total cover of epibionts on young and old plant parts had different relationships with their surface area (Table 5 and Table S8, Figure 3). The relationship was negative for the total cover on young plant parts at both sites. The smallest plants with the total area of the young part being less than 10 cm<sup>2</sup> had young parts that were 3.1%–38.8% ( $9.7 \pm 1.1\%$  on average) covered, while the total cover of young parts in the largest plants (young part  $>50$  cm<sup>2</sup>) never exceeded 8.6%. Total cover on young parts at Site K was generally lower than at Site V. In contrast, the effect of surface area on total cover of old plant parts was site-specific, strongly positive on Site V and almost absent at Site K (Table 5 and Table S8, Figure 3). The total cover on old plant parts at Site K was higher than at Site V.

On young plant parts, the Shannon–Wiener diversity index ( $H'$ , calculated from percent covers) and the number of species both significantly increased with surface area with a slope that was different between the sites (there was a significant Site  $\times$  Area interaction). On old parts only the number of species was positively affected by the plant part surface area, while  $H'$  was not affected neither by area nor by location (Table 6, Table S9). Plant surface area and location significantly affected the multivariate community structure both on old and young plant parts (Table 7, Table S10). On the PCO plots plant parts of both age grouped by sampling site (along the primary axis of variation) and along the surface area gradient (secondary axis of variation) (Figure 4, Figure 5).



**Table 5.** Effects of plant part size (surface Area of the corresponding part, cm<sup>2</sup>) and location (Sites K or V) on total cover of epibiosis on young and old parts of *Phycodryas rubens* in September 2015: beta-regression, mean (logit link) and variance (log link) modeled, frames pooled. Significant terms in a mean model highlighted in bold.

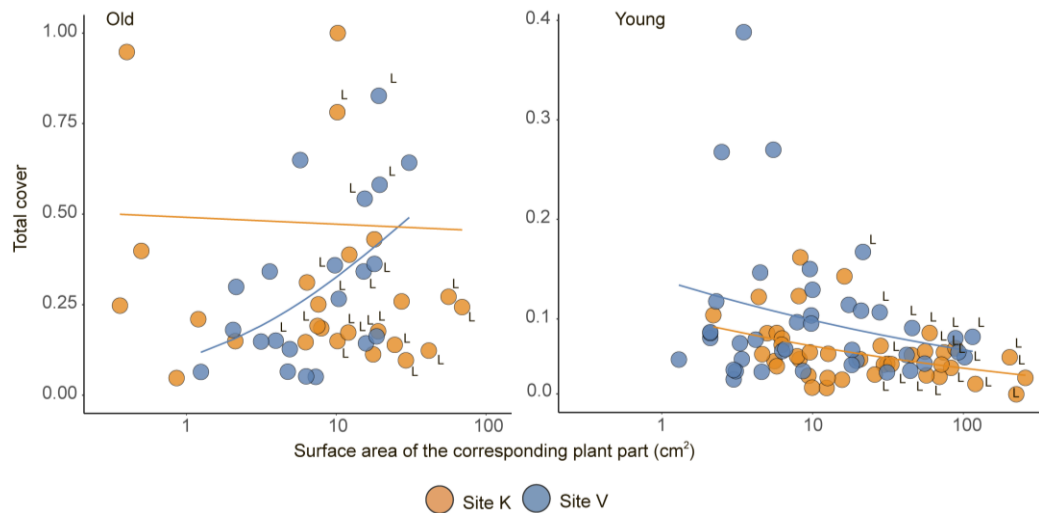
Age	Model	Source of Variation	Estimate	SE	t-Value	p
Young parts (n = 80)	Mean (Mu)	Intercept	-2.1837	0.1084	-20.15	<0.001
		<b>Site [level 'K']</b>	<b>-0.3542</b>	<b>0.1330</b>	<b>-2.66</b>	<b>0.009</b>
		<b>Area</b>	<b>-0.0035</b>	<b>0.0014</b>	<b>-2.59</b>	<b>0.012</b>
		Site × Area	0.0005	0.0016	0.36	0.718
	Variance (Sigma)	Intercept	-1.2891	0.1561	-8.26	<0.001
		Site [level 'K']	-0.7823	0.2157	-3.63	0.001
		Area	-0.0182	0.0040	-4.52	<0.001
		Site × Area	0.0150	0.0045	3.40	0.001
Old parts (n = 46)	Mean (Mu)	Intercept	-1.6614	0.3020	-5.50	<0.001
		<b>Site [level 'K']</b>	<b>1.5420</b>	<b>0.4281</b>	<b>3.60</b>	<b>0.001</b>
		<b>Area</b>	<b>0.0754</b>	<b>0.0236</b>	<b>3.20</b>	<b>0.003</b>
		<b>Site × Area</b>	<b>-0.0908</b>	<b>0.0241</b>	<b>-3.76</b>	<b>0.001</b>
	Variance (Sigma)	Intercept	-0.6186	0.3181	-1.95	0.059
		Site [level 'K']	2.0841	0.4057	5.14	<0.001
		Area	0.0118	0.0252	0.47	0.642
		Site × Area	-0.0710	0.0269	-2.63	0.012

**Table 6.** Effects of plant part size (surface Area of the corresponding part, cm<sup>2</sup>) and location (Sites K or V) on the number of species and diversity (H') on young and old plant parts of *Phycodryas rubens* in September 2015: type III sum of squares ANCOVAs, frames pooled. Arrows show the sign of the relationship where covariate effect or interaction is significant. Significant terms are highlighted in bold.

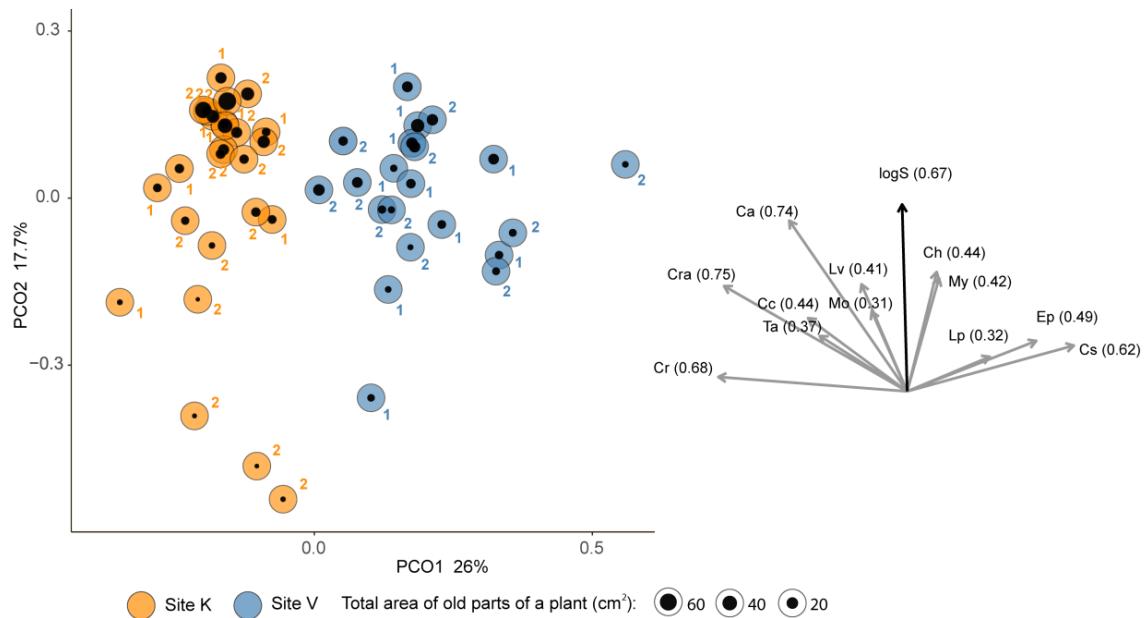
Age	Parameter	Source of Variation	df	Sum of Squares	F-Value	p	Sign
Young parts	H' (based on % cover)	Site	1	0.0022	0.024	0.877	
		<b>Area</b>	<b>1</b>	<b>1.7838</b>	<b>19.375</b>	<b>&lt;0.001</b>	↑
		<b>Site × Area</b>	<b>1</b>	<b>1.1779</b>	<b>12.794</b>	<b>0.001</b>	K↑ V↑
		Error	76	6.9969			
	Number of species	Site	1	19.2	2.9658	0.089	
		<b>Area</b>	<b>1</b>	<b>671.4</b>	<b>103.8066</b>	<b>&lt;0.001</b>	↑
		<b>Site × Area</b>	<b>1</b>	<b>71.3</b>	<b>11.0285</b>	<b>0.001</b>	K↑ V↑
		Error	76	491.5			
Old parts	H' (based on % cover)	Site	1	0.4989	1.9486	0.170	
		Area	1	0.2183	0.8526	0.361	
		Site × Area	1	0.6183	2.4152	0.128	
		Error	42	10.752			
	Number of species	Site	1	36.1	2.8909	0.096	
		<b>Area</b>	<b>1</b>	<b>551.8</b>	<b>44.1654</b>	<b>&lt;0.001</b>	↑
		Site × Area	1	8.9	0.7151	0.403	
		Error	42	524.7			

**Table 7.** Effects of plant part size (surface Area of the corresponding part, cm<sup>2</sup>) and location (Sites K or V) on the multivariate community structure of epibiosis on young and old plant parts of *Phycodryas rubens* in September 2015: type III sum of squares PERMANOVA for 9999 permutations on fourth root transformed covers of sessile epibionts, Bray-Curtis similarity, frames pooled. Significant terms are highlighted in bold.

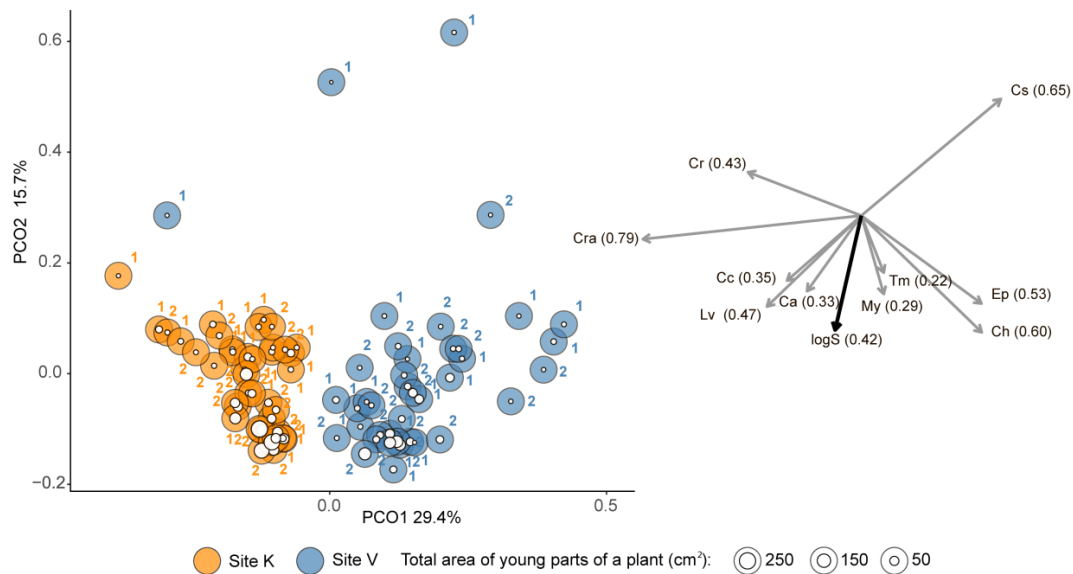
Age	Source of Variation	df	SS	MS	Pseudo-F	p	Unique Permutations
Young parts	<b>Area</b>	<b>1</b>	<b>5498</b>	<b>5498</b>	<b>6.62</b>	<b>0.0001</b>	9952
	<b>Site</b>	<b>1</b>	<b>13,841</b>	<b>13,841</b>	<b>16.69</b>	<b>0.0001</b>	9936
	Site × Area	1	1593	1593	1.92	0.0651	9937
	Error	76	63,026	829			
Old parts	<b>Area</b>	<b>1</b>	<b>4709</b>	<b>4708</b>	<b>3.97</b>	<b>0.0001</b>	9948
	<b>Site</b>	<b>1</b>	<b>9780</b>	<b>9780</b>	<b>8.25</b>	<b>0.0001</b>	9936
	Site × Area	1	2043	2043	1.72	0.0782	9946
	Error	42	49,782	1185			



**Figure 3.** Total percent cover of epibiosis on young and old parts of *Phycodryis rubens* in September 2015 by surface area of these parts. ‘L’ marks auxiliary non-randomly sampled 5 largest plants per frame. Fit lines plotted according to significant relationships (see Table 5 for details on beta-regression models).



**Figure 4.** Principal coordinates ordination (PCO) of sessile species percent covers on old parts of *Phycodryis rubens* in September 2015. Bray-Curtis similarity on fourth root transformed data. Labels (1 or 2) indicate the replicate frame number. Species with  $R^2$  (in brackets)  $> 0.2$ : Mo—*Molgula* sp. (Ascidiacea); My—juvenile Mytilidae (*Musculus discors* and *Modiolus modiolus*) (Bivalvia); Cc—*Callopora craticula* (Bryozoa), Ch—*Celleporella hyalina* (Bryozoa), Cr—Crisiidae f. gen. spp. (Bryozoa), Cra—*Cribrilina annulata* (Bryozoa), Ep—*Electra pilosa* (Bryozoa), Lv—*Lichenopora verrucaria* (Bryozoa), Ta—*Tegella armifera* (Bryozoa); Cs—*Calycella syringa* (Hydrozoa), Lp—*Lafaea pocillum* (Hydrozoa); Ca—*Circeis armoricana*; logS—log-transformed surface area of an old plant part.



**Figure 5.** Principal coordinates ordination (PCO) of sessile species percent covers on young parts of *Phycodryus rubens* in September 2015. Bray-Curtis similarity on fourth root transformed data. Labels (1 or 2) indicate the replicate frame number. Species with  $R^2$  (in brackets)  $> 0.2$ : My—juvenile Mytilidae (*Musculus discors* and *Modiolus modiolus*) (Bivalvia); Cc—*Callopora craticula* (Bryozoa), Ch—*Celleporella hyalina* (Bryozoa), Cr—Crisiidae (*Crisia eburnea* and *Crisiella producta*) (Bryozoa), Cra—*Cribrilina annulata* (Bryozoa), Ep—*Electra pilosa* (Bryozoa), Lv—*Lichenopora verrucaria* (Bryozoa); Cs—*Calycella syringa* (Hydrozoa), Tm—*Tiaropsis multicirrata* (Hydrozoa); Ca—*Circeis armoricana* (Polychaeta); logS—log-transformed surface area of a young plant part.

Four of the five top abundant taxa (hereafter ‘dominants’) on old and young plant parts in September 2015 were common: *Circeis armoricana*, *Cribrilina annulata*, *Electra pilosa* and sponges. While *Celleporella hyalina* was the fifth one on young parts, old blades were co-dominated by juvenile mytilids. Together these 5 top abundant taxa contributed  $79.9 \pm 2.7\%$  ( $n = 46$ ) of total cover on old plant parts, and  $79.6 \pm 1.9\%$  ( $n = 80$ ) on young parts (sites and frames pooled). Composition of these dominants strongly changed with the surface area on young parts and much less on old ones. In terms of relative abundances, either plant part surface area or its interaction with Site affected *C. armoricana*, *C. hyalina* and sponges on young parts, and only *C. annulata* on old parts (Table 8, Figure 6). In addition, average colony size in *C. hyalina* on young parts was negatively correlated with area (Table S11). *C. armoricana* relative cover on young parts increased with area at both sites (but faster at Site K) (Table 8). Its individual size also slightly increased with area at Site V (Table S11). Sponges, in contrast, decreased their relative abundance (slightly slower at Site K) on larger young parts at both sites (Table 8). Overall, on young parts only *C. armoricana* of all the dominants showed similar constant increases of area covered with increasing substrate area at both sites (Figure 6).

On old plant parts, *C. annulata* was the only dominant species with relative abundance significantly affected by surface area of *P. rubens*. However, the effect was negative at Site V, where the covers of *C. annulata* were very low, and almost absent at Site K, where this bryozoan was abundant. In addition, while the non-zero values of *C. annulata* relative abundance decreased with increasing area, the frequency of its absence also decreased on larger plants (as indicated by a significant effect in Nu-model, see Table 8), further reducing the net effect.

**Table 8.** Effects of plant part size (surface Area of the corresponding part, cm<sup>2</sup>) and location (Sites K or V) on relative abundances of 5 top abundant species on young and old plant parts of *Phycodryis rubens* in September 2015: zero-inflated (logit link) beta-regression, mean (logit link) and variance (log link) modeled, frames pooled. I—intercept, Sources of variation: S—Site (K), A—plant part surface area. The model did not converge for *E. pilosa* on old blades since all the zero observations were at Site K, thus two separate models for the two sites were fitted. Significant terms in mean and zero models highlighted in bold.

Species		Mean Model (Mu)		Variance Model (Sigma)		Zeros Model (Nu)	
		Estimate (SE)	p	Estimate (SE)	p	Estimate (SE)	p
<b>Young Parts (n = 80)</b>							
<i>Cribrilina annulata</i>	I	-2.4951 (0.1870)	<0.001	2.0878 (0.2763)	<0.001	-0.1898 (0.7094)	0.790
	S	<b>2.1997</b> <b>(0.2236)</b>	<b>&lt;0.001</b>	-0.0523 (0.3811)	0.892	-21.2419 (5354.2603)	0.997
	A	0.0007 (0.0028)	0.806	0.0238 (0.0075)	0.002	-0.1596 (0.1069)	0.140
	S × A	0.0006 (0.0030)	0.842	-0.0180 (0.0083)	0.033	-0.1596 (71.9445)	0.998
<i>Electra pilosa</i>	I	-1.7665 (0.1845)	<0.001	1.6823 (0.2641)	<0.001	2.0963 (2.0629)	0.313
	S	<b>-1.9029</b> <b>(0.2571)</b>	<b>&lt;0.001</b>	2.0667 (0.3928)	<0.001	-2.3008 (2.1404)	0.286
	A	0.0030 (0.0035)	0.3958	0.0125 (0.0073)	0.089	-1.1162 (0.7365)	0.134
	S × A	-0.0073 (0.0040)	0.0756	-0.0075 (0.0081)	0.359	1.0704 (0.7370)	0.151
<i>Celleporella hyalina</i>	I	-0.8769 (0.1452)	<0.001	1.5891 (0.2785)	<0.001	1.9564 (2.0067)	0.333
	S	<b>-2.3326</b> <b>(0.2234)</b>	<b>&lt;0.001</b>	1.7150 (0.3971)	<0.001	-1.6762 (2.1876)	0.446
	A	0.0019 (0.0017)	0.271	0.0334 (0.0076)	<0.001	-1.0639 (0.7096)	0.138
	S × A	<b>-0.0059</b> <b>(0.0025)</b>	<b>0.019</b>	-0.0264 (0.0084)	0.002	0.9373 (0.7146)	0.194
<i>Circeis armoricana</i>	I	-2.1489 (0.1509)	<0.001	-0.8095 (0.1605)	<0.001		
	S	<b>0.8676</b> <b>(0.1785)</b>	<b>&lt;0.001</b>	-0.4126 (0.2279)	0.074		
	A	<b>0.0063</b> <b>(0.0024)</b>	<b>0.012</b>	-0.0098 (0.0043)	0.025	no zeros	
	S × A	-0.0046 (0.0026)	0.077	0.0065 (0.0048)	0.180		
Porifera	I	-0.8429 (0.2670)	0.002	0.6823 (0.3210)	0.037	-0.1903 (0.4041)	0.639
	S	0.0421 (0.3471)	0.904	0.8275 (0.4501)	0.070	0.4485 (0.6518)	0.494
	A	<b>-0.0221</b> <b>(0.0049)</b>	<b>&lt;0.001</b>	0.0341 (0.0089)	<0.001	-0.0103 (0.0123)	0.405
	S × A	<b>0.0116</b> <b>(0.0056)</b>	<b>0.040</b>	-0.0303 (0.0095)	0.002	-0.0272 (0.0232)	0.244
<b>Old Parts (n = 46)</b>							
<i>Cribrilina annulata</i>	I	-1.5135 (0.7367)	0.046	4.3858 (1.5457)	0.007	6.0933 (2.6097)	0.024
	S	-0.0450 (0.7783)	0.954	-3.0769 (1.5904)	<b>0.060</b>	<b>-6.4730</b> <b>(2.7646)</b>	<b>0.024</b>
	A	<b>-0.1484</b> <b>(0.0434)</b>	<b>0.001</b>	0.0246 (0.0779)	<b>0.754</b>	<b>-0.4881</b> <b>(0.1982)</b>	<b>0.018</b>
	S × A	<b>0.1505</b> <b>(0.0439)</b>	<b>0.001</b>	0.0137 (0.0796)	0.865	0.2536 (0.2567)	0.329
<i>Electra pilosa</i> (separate models for the two sites)	Site V: I	-1.1564 (0.4217)	0.014	0.1092 (0.4254)	0.801	no zeros	
	Site V: A	-0.0509 (0.0290)	0.117	-0.0420 (0.0343)	0.237		
	Site K: I	-4.9332 (0.4195)	<0.001	4.9017 (0.6593)	<0.001	1.5588 (0.8440)	0.080
	Site K: A	-0.0132 (0.0134)	0.339	0.0141 (0.0213)	<b>0.514</b>	<b>-0.1572</b> <b>(0.074)</b>	<b>0.048</b>

Table 8. Cont.

Species		Mean Model (Mu)		Variance Model (Sigma)		Zeros Model (Nu)	
		Estimate (SE)	p	Estimate (SE)	p	Estimate (SE)	p
Juvenile mytilids	I	-1.4250 (0.3840)	<0.001	0.5747 (0.5548)	0.306	2.5499 (1.9499)	0.198
	S	-0.2370 (0.4135)	0.570	-0.5368 (0.6891)	0.440	-0.2620 (2.3573)	0.912
	A	-0.0089 (0.0195)	0.650	0.1132 (0.0412)	0.009	-0.8268 (0.5108)	0.113
	S × A	-0.0006 (0.0196)	0.977	0.0372 (0.0447)	0.410	-0.0138 (0.6892)	0.984
<i>Circeis armoricana</i>	I	-3.2273 (0.3373)	<0.001	3.7427 (0.5848)	<0.001	0.7101 (1.0069)	0.485
	S	<b>1.2267</b> <b>(0.4094)</b>	<b>0.005</b>	-2.1756 (0.7120)	0.004	51.2633 (299.8967)	0.865
	A	-0.0327 (0.0247)	0.192	0.0015 (0.0392)	0.970	-0.2601 (0.1598)	0.111
	S × A	0.0317 (0.0251)	0.214	0.0577 (0.0428)	0.185	-50.1948 (286.5729)	0.862
Porifera	I	-0.7947 (0.3675)	0.036	1.3691 (0.4779)	0.007	1.0340 (2.8280)	0.716
	S	0.7172 (0.4500)	0.119	-1.2206 (0.5771)	0.040	-15.466 (225.1950)	0.946
	A	0.0426 (0.0294)	0.155	-0.0216 (0.0355)	0.546	-1.1330 (1.1680)	0.338
	S × A	-0.0469 (0.0298)	0.123	0.0883 (0.0387)	0.028	1.1330 (9.672)	0.907

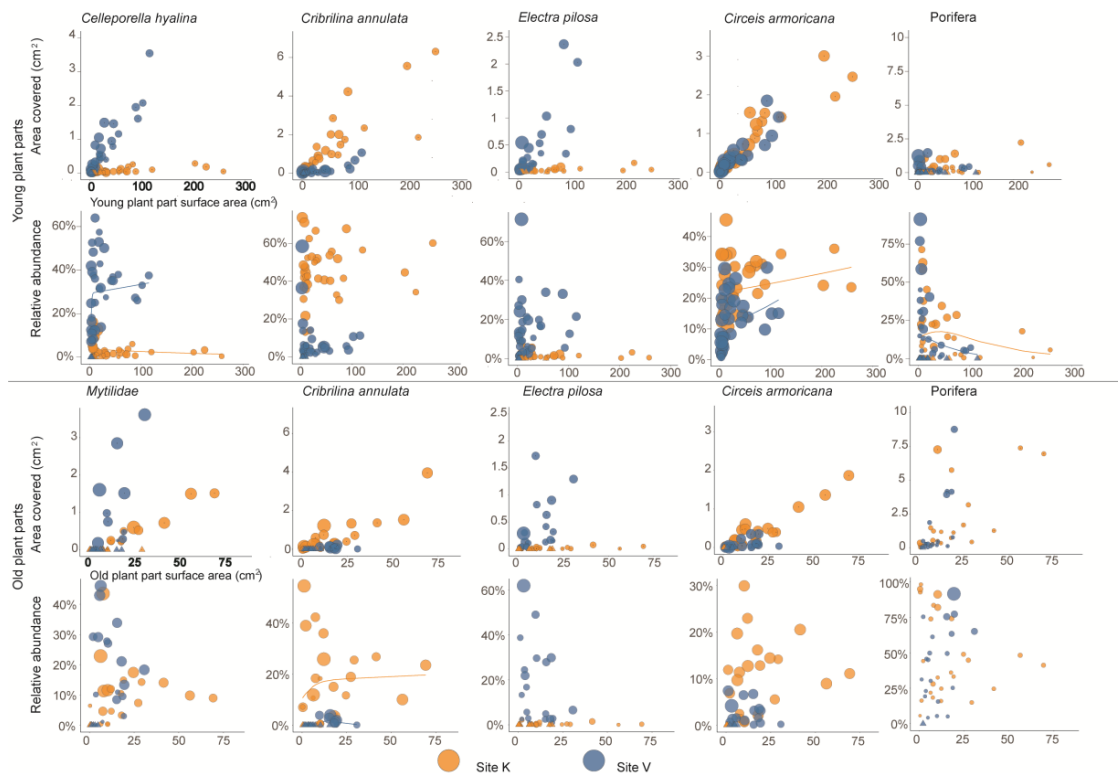


Figure 6. Area covered and relative percent covers of dominant sessile species on young and old parts of *Phycodrys rubens* by plant part surface area in September 2015. Fit lines plotted where plant part area effect or its interaction with Site were significant (see Table 8 for details on models). Dots mark auxiliary non-randomly sampled 5 largest plants per frame (see Methods for details).

#### 4. Discussion

At both locations studied, *Phycodrys rubens* was the dominant seaweed and added substantial substrate space to a habitat. Consistent with our hypotheses plant part age and size both correlated



with species composition and abundances. Old parts were dominated by sponges with total percent cover of epibionts differently affected by surface area depending on the location. Young parts were dominated by bryozoans and spirorbid polychaetes, and had lower total percent cover which was negatively affected by surface area regardless of the location.

Macroalgae as foundation species can host a rich epibiotic community, comprised mostly of epiphytic algae and sessile invertebrates [15]. The number of species and diversity of epibiosis associated with *P. rubens* were similar to other epibiotic assemblages in high latitudes, both on brown [30,45,46] and red algae [13,47]. Species composition was consistent with scarce data on red algae epibiosis in the White Sea, with bryozoans being the most abundant and species-rich group [13,48]. Particularly, bryozoans *Electra pilosa*, *Celleporella hyalina*, *Cribrilina annulata*, and serpulid sedentary polychaetes are common in boreal and arctic epiphytic assemblages associated with kelps and red algae [13,45,47]. However, according to our findings, the epibiosis on *P. rubens* lacked any abundant epiphytic algae, which tend to subdominate alongside bryozoans [45] or predominate [46] in comparable systems. The number of species was similar to the only estimate available for *P. rubens* epibiosis [13].

In marine benthic habitats substrate space is commonly in short supply [4,49]. It is either released from occupants by disturbance events, clearing ‘Type I patches’ *sensu* Sousa [50], or created anew by habitat engineers like seaweeds or bivalves, which serve as substrate for epibiosis (‘Type II patches’). *P. rubens* blades are typical Type II patches. Species composition and abundances of the residents of such a patch can generally result from the interplay of colonization history and further survival driven by interspecific interference and predation or grazing [51]. Colonization history, in turn, is most affected by propagule supply and larval selectivity, while interspecific interactions depend on space deficiency and relative competitive ability; substrate longevity should affect both.

Our results revealed the relationships between the plant part age, total cover and species composition of *Phycodryas*-associated epibiotic community. Substrate age can directly result in a higher number of species and total cover on older plant parts: these have been exposed to potential colonizers for longer (from 1 to 3 years) and could accumulate the results of recruitment, which often has strong interannual variation [52,53]. This, however, can only affect species with a long enough lifespan. The colony lifespan at least of the two dominant bryozoans, *E. pilosa* and *C. annulata*, is limited mostly by substrate lifetime and reaches up to 2–3 years. Both species definitely can make it through winter [54,55] as their zooids hibernate during the cold season and emerge again with rising water temperature. Though the data on longevity of sponges in our study region is scarce, the lifespan of common species, *Myxilla incrustans* and *Iophon piceus*, in the White Sea is reported to exceed 4 years [56]. Taking into account that sponges are generally longest-living animals [57], the species inhabiting *Phycodryas* (presumably *Mycale* sp. and *Halichondria sitiens*) are likely to last long and successfully overcome the cold season. Mytilid bivalves found on *P. rubens* (*Musculus discors* and *Modiolus modiolus*) are also perennial: *M. discors* has a lifespan of 2–5 years [58], and *M. modiolus* can last for 50 years or more [59]. However, these species do not necessarily stay always attached to a same substrate: like other mytilids they can use macroalgae as a transitional habitat for juveniles [60,61]. Another dominant bryozoan, *C. hyalina*, in contrast, has an annual lifespan [62]. Similarly, largest individuals of a serpulid polychaete *C. armoricana* are found on the thalli *Laminaria* that renew each year [63]. Interestingly, consistent with these species-specific differences in life histories, relatively short-living *C. armoricana* and *C. hyalina* in September on at least at one site had higher abundances on young plant parts compared to old ones. The dominants with longer lifespan were either more abundant on old parts or not affected by substrate age (Table 4).

Old parts of *P. rubens* are closer to the bottom than young ones, potentially causing the difference in flow velocity and illumination. However, possible consequences of this difference are complicated. Decreased flow beneath macroalgae resulting in increased sedimentation affects feeding performance and lowers growth rates in bryozoans, bivalves and cirripedes, at the same time being beneficial for serpulid polychaetes and sponges [64,65]. Flow intensity also affects larval settlement of sessile

invertebrates (reviewed in reference [61]). While settling bryozoans *Bugula turrita* and *Tubulipora* sp. or a serpulid polychaete *Pseudochitinopoma occidentalis* prefer the zones of reduced flow velocity and turbulence, a hydroid *Tubularia crocea* is attracted by higher velocities [66,67]. The difference in lighting conditions resulting in microalgal turf development intensity may be beneficial for sponges or ascidians [64,68], but disadvantageous for serpulids [64]. On *Fucus serratus* several epiphytic sponges are more abundant on relatively rigid fibrous basal segments of *Fucus serratus* due to selective settling or differential early survival [7,69].

Heavier fouling itself can further facilitate some species to colonize old *Phycodrys* parts. Extensively covered by epibionts old parts become more rigid and rugged, which may favor other epibionts. Primary epibionts commonly provide more suitable substrate for the secondary ones than a basibiont, developing ‘fouling cascades’ [70]. Intensive fouling can reduce the amount of anti-fouling chemicals released by algae [14] which also can provide positive feedback for subsequent arrivals. On the other hand, settling larvae of many invertebrate species strictly prefer younger parts of marine macroalgae [71–75]. This mechanism allows the vulnerable postlarval stages to occupy the most long-living and unfouled part of the basiphyte. In particular, bryozoans *Membranipora* sp. and *Scrupocellaria reptans* prefer basal growing parts of kelp [71,73], while *Alcyonidium hirsutum* and *Flustrellidra hispida* settle mostly on the frond tips—the youngest parts of *Fucus serratus* [72]. A spirorbid polychaete *Neodexiospira brasiliensis* selects the youngest regions when settling on seagrasses species [75], while *Spirorbis corallinae* and *S. pagenstecheri* show the same pattern on *Laminaria digitata* [71].

With several times higher total percent cover (up to 36% in September on Site V, see Table 2) and much longer existence term, the epibiosis on old plant parts must experience the pressure of interspecific interference. While competition can hardly shape community structure on young parts having total cover within 10%, on old parts the importance of overgrowth interactions is quite expectable. In tropical epibioses species abundances and composition are commonly determined by the relative competitive strength of epibionts [76–78]. Almost nothing is known though of the competitive hierarchies among benthic sessile invertebrates in polar regions. Yet, the strong dominance of sponges, which is the most important feature of old *Phycodrys* blades compared to young ones (Figure 1, Figure 2) is seemingly caused by their highly competitive strength. Indeed, based on the studies in temperate and tropical waters higher taxonomic groups have the following competitive hierarchy: ascidians (mostly colonial) and sponges are superior in relation to bryozoans, and the latter are better competitors for space than cirripedians, polychaetes and hydroids [79].

In particular, on coral reefs at Rio Bueno, Jamaica, sponges are the strongest overgrowth competitors for space which results in their ultimate dominance on older regions of coral undersurfaces, with young coral edges left for inferior competitors including cheilostome bryozoans [80]. Alongside remarkable resistance to environmental stresses (e.g., references [81,82]) sponges can exhibit strong allelochemical effects on their competitors [76,83,84].

Consistent with our observations on the *Phycodrys*-associated community, epibiosis on macroalgae commonly varies across a single thallus age-, structure- or function-dependently [30,74,85–90]. On *Lobophora variegata* (a brown alga) community structure strongly depends on the blade side. Upper- and undersides show different species composition, and undersides also harbor greater numbers of individuals. The supposed advantages of an underside include (i) providing potential shelter from herbivorous grazers, (ii) hosting several species of secondary basiphytes, (iii) containing lower amounts of defensive substances, which serve as anti-fouling and anti-grazing agents [85]. Epibiosis on a common brown kelps *Saccharina latissima* and *Laminaria digitata* show the decrease in species diversity on older parts of the lamina [30]. One of possible reasons for such a decline is that the distal (and oldest) part of the lamina is mostly exposed to physical stress and tissue decay. Algal epiphytes of a kelp *Ecklonia radiata* are, in contrast, most abundant on oldest parts of the thalli [86]. While the authors propose the length of time spent in water as a principal determinant of these age-related differences, the position in the water column and surface rugosity are also considered important.

In addition to plant parts' age, epibiosis on *P. rubens* was also related to their surface area. At both sites, total percent cover on young plant parts dropped on larger plants, while the proportion of solitary organisms, number of species and diversity increased. On old plant parts (which were several times smaller than young parts) the effect on total cover was location-specific, species diversity was constant, while the number of species also increased with substrate surface area. Similarly, in the epibiosis of *Fucus serratus*, plant size affects abundances and within-plant distribution of sponges and tunicates [91]. In marine benthic communities there are also other Type II biogenic habitat patches where epibiosis is affected by substrate surface area. The relationship between patch size and community structure is best studied in the systems with strong competition for substrate space. There the larger the patch, the higher the probability that one would be colonized by poorly-recruiting strong competitors (tunicates or sponges), causing space monopolization [51]. Patch size thus shifts the principal structuring process from colonization to interspecific interference. On young *P. rubens* parts total percent cover is much lower, and the role of competition for space unlikely is important. Consistently, the relative abundances of potentially strong competitors (modular organisms, especially sponges) did not increase, but, on the contrary, decreased on larger plants (Table 8, Figure 6). Our results suggest that the effect of substrate size on the epibiosis of relatively large and lightly fouled young parts is driven by recruitment limitations of dominant species. It looks like only a polychaete *Circeis armoricana* of top abundant species had a strong enough propagule supply in 2015 to maintain nearly constant percent cover despite the substrate size and sampling location (Figure 6). Other dominants underperformed either at one of the sites (bryozoans) or on both (sponges). A bryozoan *Celleporella hyalina* had also smaller mean colony size on larger plants. This may either reflect that substrate size affects colony growth or results from seasonal variation in recruitment: largest plants could be colonized during the heaviest settlement peak, which might coincidentally be the latest leading to smaller (younger) colonies. Settlement and survival conditions on larger plants can be less advantageous compared to smaller ones: a major part of young blades in large plants is located further from the bottom than in small ones, and consequently is more exposed to the flow. Increased flow velocity may in turn negatively affect larval settlement, colony growth and feeding in many epibiotic species (reviewed in reference [7]).

The effects of substrate size observed on relatively small and close to the bottom (compared to young ones) old *Phycodrys* parts are less interpretable. Here, much higher total percent cover strongly increased with the substrate surface area at Site V and slightly decreased at Site K. *Cribrilina annulata* was the only dominant species with relative abundance affected, and the effect was also location-specific, but inverse. While sponges constituted more than a half of average total cover on old blades, their relative abundances exhibited no relationship with substrate size. Importantly, in contrast to young plant parts, which clearly have developed within the recent season, old parts comprise the blades of variable undetermined age, possibly different for the two sites. This, together with a plethora of other factors, including the location-specific difference in flow regime, could contribute to the observed inconsistency in plant size effect between the sampling locations. The relationship between the substrate area and the number of species was positive both on young and on old plant parts. This result is rather obvious. Indeed, larger plants have a higher probability of hosting rare species with limited propagule supply, and at the same time are more complex due to a higher number of blades, while patch size and habitat complexity are both known to increase the species number [92].

The proportion of young and old parts and the size of an individual plant reflects the ontogenetic stage of *P. rubens* and local growth conditions. In addition to the limited data on potential community-wide effects of ontogenetic variation in an ecosystem engineer for seaweeds [90], the examples from terrestrial habitats are available. For instance, species diversity and composition of lichens epiphytic on ash trees changes significantly with tree age [93]. In tropical rainforests species richness of ants and herbivore insects increases with host tree size, which also affects species composition [29]. Similarly, the observed effects of individual *P. rubens* properties on the associated epibiosis show how the demography of this ecosystem engineer can generate a spatial structure for the entire community.

The patterns documented here can result from multiple interacting processes. A survey of interannual variation in community structure is seemingly needed to interpret the observations on epibiosis covering old blades, where the traces of multiple previous years accumulate. While only manipulative experiments can reveal causal relationships behind the correlations we found, understudied systems like the one described first need observations to provide the context for further experiments [94]. *Phycodryx rubens* grows in easily accessible shallow subtidal, where the disturbance level is low. An individual plant commonly has a small rock or gravel as a substrate, thus offering a convenient unit for field and laboratory manipulations. Epibenthic community associated with *P. rubens* is thus potentially a perfect system for further experiments aimed towards isolating the contributions of colonization, interspecific interference and possible grazing to the patterns observed.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/11/5/80/s1>, Figure S1: Size structure of *Phycodryx rubens* and its proportion compared to other red macroalgal species in September 2015 and 2016 by site and frame, Table S1: Average number and wet weight of foliose red algae per 1 m<sup>2</sup> of the bottom in September–October by species and year, Table S2: Contribution of 20 largest *Phycodryx rubens* plants to approximated total area in a frame and total wet weight in September–October by year, site and frame, Table S3: Approximated surface area of *Phycodryx rubens* per 1 m<sup>2</sup> in September–October by plant part age, site and year, frames pooled, Table S4: Mann-Whitney U-tests comparing total cover of the epibiosis on *Phycodryx rubens* in September 2015 between the two replicate frames by site and plant part age, Table S5: Kolmogorov–Smirnov and Mann-Whitney U-tests comparing total plant surface areas and the proportion of young blades' surface of *Phycodryx rubens* between the pairs of replicate frames in September 2015 by sampling site, Table S6: Effects of plant part age, month, and location on total cover of *Phycodryx rubens* epibiosis (alternative analysis with Frame factor included), Table S7: Effects of plant part age, month, and location on multivariate community structure of epibiosis on *Phycodryx rubens* (alternative analysis with Frame factor included), Table S8: Effects of plant part size and location on total cover on young and old plant parts of *Phycodryx rubens* in September 2015 (alternative analysis with Frame factor included), Table S9: Effects of plant part size and location on the number of species and diversity on young and old plant parts of *Phycodryx rubens* in September 2015 (alternative analysis with Frame factor included), Table S10: Effects of plant part size and location on multivariate community structure of epibiosis on young and old plant parts of *Phycodryx rubens* in September 2015 (alternative analysis with Frame factor included), Table S11: Effects of and plant part size and location on mean individual size of 5 top abundant species on young and old plant parts of *Phycodryx rubens* in September 2015, Supplementary File 1: Raw data.

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