



Variation in top-down control of red algae epibiosis in the White Sea

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ABSTRACT: Epibiosis is shaped by a complex interplay of biotic interactions involving hosts, epibionts, and mobile consumers. In temperate waters, consumer control by mesograzers prevents complete overgrowth of seaweeds. In polar waters, the mechanisms determining the abundances of sessile organisms associated with seaweeds are unknown. We empirically assessed the strength of the consumer control effect on the colonization of the sub-arctic red seaweed *Phycodrys rubens* by caging individual plants in the field in the shallow subtidal of the White Sea (65° N). We compared epibiosis on plants in consumer exclusion cages, in cages with the mesopredatory shrimp *Spirontocaris phippisii*, in semi-enclosed cages, and on unmanipulated plants in a cold year (2014) and a warm year (2015). Despite the dramatic interannual variation in consumer control, the mean total cover of epibionts in the absence of consumers never exceeded 15%. While consumers had a substantial effect on the total epibiont cover in the warm year and a nearly negligible effect in the cold year, the total cover of unmanipulated algae was similar in 2014 and 2015. Bryozoans, which were selectively impacted by consumers — particularly shrimp — dominated in both years. However, bryozoan abundance was much lower in 2015, when the abundance of hydroids, sponges, and bivalves — less affected by consumers — increased. Consumer control is not a key factor preventing most *Phycodrys* plants from being heavily overgrown. Yet, smaller plants, which have a higher epibiont cover, may indirectly benefit from consumers. Future climate changes are likely to make the *Phycodrys* epibiosis increasingly top-down regulated.

KEY WORDS: Top-down control · Interannual variation · Predation · Epibiosis · Mesopredator · Shrimp · Red algae · White Sea

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1. INTRODUCTION

Interspecific biotic interactions are key processes determining the structure and dynamics of natural communities. Negative interactions such as competition and consumer control have long been considered critical for understanding and predicting patterns of abundance and diversity in living organisms (Menge & Sutherland 1976). Since most marine benthic communities are constituted predominantly by organisms relying on larval or spore dispersal, the models applied to these systems have usually incorporated an interplay of larval supply and negative interactions

(Connolly & Roughgarden 1999). Though it is widely accepted that the intensity of biotic interactions decreases with latitude (Schemske et al. 2009, Baskett & Schemske 2018), acute competition for stable hard substrate space has been observed from tropical (Chadwick & Morrow 2011) and temperate (Nandakumar 1996) to polar waters (Konar & Iken 2005). Selective predation and grazing have profound direct and indirect effects on species composition and diversity by controlling competitively superior species (Paine 1974) and subordinate consumers (Estes & Palmisano 1974) which, in turn, affect multiple inferior competitors and prey species, respectively. Sub-

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stantial consumer ('top-down') control has also been detected beyond tropical and temperate zones (Quijón & Snelgrove 2005).

The growing recognition of positive interspecific interactions (i.e. facilitation) as an equally powerful driver of community structure (Bruno et al. 2003) prompted recent research on foundation species (FS). FS such as trees, corals, mussels, seagrasses, and seaweeds are strong facilitators ameliorating the effects of environmental stress and negative biotic interactions for the dependent taxa (Ellison 2019). FS decrease consumer pressure by providing refuges (Ware et al. 2019) and reduce competition by generating habitat space (Stachowicz 2001). In particular, common seaweeds develop several square meters of blade surface per one square meter of the bottom (Teagle et al. 2017). Their growing blades are the least space-limited microhabitat in kelp forests, able to host weaker competitors for space (Seed & Harris 1980) and thus potentially increasing species diversity. Although some FS indirectly benefit from their epibionts (Wahl & Hay 1995), algal hosts, when heavily fouled, generally demonstrate growth depletion and suffer from increased herbivory (D'Antonio 1985, Honkanen & Jormalainen 2005). Therefore, consumer control of epibionts by predators and grazers usually has a positive effect on algal hosts (Duffy 1990, Stachowicz & Whitlatch 2005). Overall, biotic interactions behind an observed epibiont assemblage structure can be fairly complex and difficult to disentangle.

While seaweeds and seagrasses act as FS in coastal ecosystems across the globe (Amsler et al. 2014, Olafsson 2016), the knowledge of the functioning of their epibioses is mostly limited to tropical and temperate regions (Duffy 2006, Miller et al. 2015, Moore & Duffy 2016, Freestone et al. 2020, Lamy et al. 2020; but see Amsler et al. 2014). Manipulating the abundance of seagrass- and seaweed-associated mesopredators and mesograzers in the field is technically complicated and thus infrequently attempted (Whalen et al. 2013). Experimental research on red algae as hosts of dependent sessile assemblages is especially scarce despite their wide distribution (Díaz-Tapia et al. 2018) and growing commercial potential (Cabrera et al. 2022).

Red algae can become heavily overgrown, with consumer control being a key process regulating the few systems studied in this respect. In tropical shallow subtidal areas, the foliose red seaweed *Cryptonemia seminervis* supports a sessile community dominated by sponges and bryozoans and covering 50–90% of its surface area. Laboratory experiments show that the red algae covered by bryozoans are preferentially consumed by herbivores (da Gama et al. 2008). In

temperate shallow subtidal habitats, another common foliose red alga, *Chondrus crispus*, is about 50% covered, primarily by ascidians and bryozoans, at the sites with a low abundance of mesograzers (snails), and only 5–10% covered at sites with a high abundance of mesograzers (our approximations based on epibiont/host weight ratios reported by Stachowicz & Whitlatch 2005). Importantly, experimental removal of mesograzers results in a total overgrowth of algae by sessile epibionts, leading to severe growth depletion (Stachowicz & Whitlatch 2005).

In polar subtidal waters, the total cover of epibionts on red algae is relatively low, and the mechanisms that control fouling intensity and structure are mostly unknown (Chava et al. 2019). In the shallow subtidal of the sub-arctic White Sea (65° N), the foliose red alga *Phycodrys rubens* provides substrate for an epiphytic community composed predominantly of bryozoans, serpulid polychaetes, hydroids, and sponges (Chava et al. 2019). *P. rubens* has a lifespan of several years (Schoschina 1996), and most substrate area provided for epibionts is represented by newly grown blades (Chava et al. 2019). These large and distinctly recognizable blades (hereafter referred to as 'young blades') emerge in spring, are colonized by recruits of sessile organisms in summer and fall, and partly degrade in winter, adding to the smaller 'old' part of the plant comprising 1–3 yr old blades. In fall, when the cover of epibionts is highest, it averages 7–10% on young and 24–36% on old blades (Chava et al. 2019). Consequently, competition for space on young blades appears negligible.

It is unclear whether the low cover of *P. rubens* (especially on its newly colonized young blades) is mostly due to consumer control or alternative mechanisms, e.g. recruitment limitation. To investigate this, we manipulated the presence of mobile consumers on *P. rubens* blades in a series of field caging experiments. The mesopredatory shrimp *Spirontocaris phippisii* is one of the most common generalist consumers in subtidal White Sea habitats (Grishankov et al. 1997), feeding on various mobile and sessile epibenthic organisms such as polychaetes, amphipods, mollusks, and bryozoans (Yakovis & Artemieva 2019, 2021, Chava et al. 2024). We used enclosure cages isolating individual plants from any mobile organisms unable to pass 2 mm mesh to assess the effect of consumer control on the epibiosis and enclosures with *S. phippisii* to evaluate its possible role in top-down regulation. Preliminary observations showed a notable interannual variation in *S. phippisii* abundance at our research sites. Considering the strong interannual variation in recruitment rates of sessile organisms in

the White Sea subtidal (Yakovis et al. 2013), we repeated the experiments in 2 consecutive years. A higher epibiont cover in consumer-removal experiments, if detected, would elucidate the role of top-down control in competition decrease and possible protection of the host from overgrowth.

2. MATERIALS AND METHODS

To test the effect of mobile predators on sessile epifauna of *Phycodrys rubens*, we conducted 2 series of field caging experiments in the shallow subtidal of the White Sea (Velikaya Salma Strait between the Karelian shore and Velikiy Island in the western part of Kandalaksha Bay) in 2014 and 2015. Both series lasted for 2 mo, from late July to late September. The exposure duration was chosen based on the seasonal timing of epifaunal recruitment (Chava et al. 2019) and algal growth pattern (Schoschina 1996). We exposed cages at 2 sites: Site K (near Kamenukha island, 11 m deep, 66° 33.028' N, 33° 9.295' E) and Site V (near Velikiy Island, 12 m deep, 66° 33.437' N, 33° 6.877' E) with different hydrological regimes. Site V was located in the narrowest part of the Velikaya Salma Strait, while Site K was located further seaward, in the wider part of the strait. The flood current at Site V was hence much faster (up to 1.33 m s⁻¹) than at Site K (up to 0.75 m s⁻¹). Detailed descriptions of the sites are given by Chava et al. (2019). Seawater temperatures are similar along the studied part of the Velikaya Salma Strait because of tidal mixing (Mileikovskiy 1970). Temperature data were available for several dates in June, July, and sometimes August in 2009–2016 from an automatic weather station (Aanderaa Instruments, AW 2700) attached to a pier at the White Sea Biological Station (66° 33.177' N, 33° 6.181' E) at 1 m depth. These measurements (Table A1 in the Appendix) show that the summer of 2014 was much warmer (by 2.6°C) than the summer of 2015.

One or 2 d prior to the set-up date, we collected *P. rubens* growing on small cobbles (<15 cm) and *S. phippisii* individuals at Site V in 2014 and at both sites in 2015 and kept them in aerated aquaria until the set-up date. We selected large plants since most sessile epifauna is concentrated on them (see Chava et al. 2019). We fastened each cobble with a plant on it inside a 'cage' (a cylindrical plastic basket 20 cm wide and 30 cm tall covered with 2 mm nylon mesh), 1 plant per cage. We used 4 types of treatments: (1) full cages (=predator enclosures), (2) partial cages, to control for cage effect (similar to full cages but with two 70 × 70 mm openings in the mesh), (3) shrimp cages

(=predator enclosures; similar to full cages but with 3–4 individuals of *Spirontocaris phippisii* added), and (4) ambient controls (see below). Plants were randomly distributed across the treatments. Plants and shrimp were placed inside the cages immediately before the deployment. Shrimp carapace length was 5–8 mm, and their total weight was similar in different shrimp cages. The number of shrimp individuals per cage was chosen based on the previous field manipulations with *S. phippisii* in the White Sea (Yakovis & Artemieva 2019, 2021). The sex of the shrimp used in the experiments was not identified. In July, the cages were anchored to concrete blocks and placed on the bottom in a haphazard pattern. In September, we removed the cages and examined the epibiosis of each plant. In 2014, there were 8 full, 7 partial, and 7 shrimp cages, while in 2015, there were 10 full, 7 partial, and 8 shrimp cages. In 2014, cages were deployed at Site V, and in 2015, they were equally divided between Site V and Site K. While collecting the cages, we also sampled plants around the cages to use them as ambient controls. In 2014, we acquired 7 random plants at Site V. In 2015, we used the largest plants from haphazardly placed 0.25 m² frames (Chava et al. 2019), with the total area of young blades exceeding 5800 mm² (to match the sizes of the plants used in the manipulations). As a result, in 2015, there were 4 ambient controls at Site V and 10 ambient controls at Site K. See Table 1 for a summary of the treatments.

P. rubens thalli develop in such a way that young blades of the current year, which constitute the major part of the thallus, can be easily distinguished from the older part remaining from the previous 1–3 yr (Schoschina 1996) (hereafter 'young' and 'old'). In July, young blades were almost free of any sessile epifauna. Therefore, we did not document the initial state of the experimental plants and examined young blades only at the end of the experiments. For each plant, we documented the surface area of young blades (accurate to 1 mm²), identified all of the sessile organisms attached to young blades (except sponges) to species level, and counted them. We determined the area of each sponge (accurate to 0.1 mm²), calculated the number of units (zooids/polyps) in each hydrozoan or bryozoan colony, and individually measured the opercular diameter of serpulid polychaetes (accurate to 0.05 mm) and the shell length of bivalves. These values were used to estimate the areas covered and the percent cover according to the size–area allometric relationships previously established from subsamples (Chava et al. 2019). Undetermined bryozoan ancestrulae with individual areas less than 0.15 mm² were excluded from further analyses.

Natural density of *S. phippisii* in algal canopy is difficult to assess accurately. Shrimp are traditionally sampled with push nets and beam trawls (Hiddink et al. 2002, Schaffmeister et al. 2006). While these methods have an efficiency of up to 50–60% in sandy or silty habitats and seagrass beds, we could not use them because of the following limitations. Firstly, both of these methods entail the disturbance of the habitat (milder in case of a push net and severe in case of a beam trawl), which was unacceptable since *P. rubens* canopy is fragile and can be easily damaged or torn off the gravel. Secondly, shrimp can easily escape both a trawl and a push net (Schaffmeister et al. 2006), which increases the underestimation of their density. Considering these limitations, we decided to catch all visible shrimp during dives using a hand net or a plastic jar. The efforts were standardized by making individual dives as similar as possible. The same diver spent 45–50 min moving in zigzags at 9–11 m depth during daylight hours 2–4 d prior to the deployment of the cages. The dives were carried out when the strong tidal currents were minimal. According to these rough estimates, the density of *S. phippisii* around Site V in July was 2.5 times higher in 2014 than in 2015. In July 2014, the mean number of shrimps per dive was 9 ± 1 individuals ($n = 6$ dives), while in July 2015 it was 3.5 ± 2 individuals ($n = 8$ dives). The difference was significant ($p = 0.023$, Mann-Whitney *U*-test).

To elucidate possible differences in natural total abundances of epibionts in 2014 and in 2015, we performed univariate permutational analysis of variance (PERMANOVA, Anderson 2001) on Euclidean distances calculated from total percent cover of epibionts on young blades of *P. rubens* at Site V in partial cages and ambient controls. Here and below, we used univariate PERMANOVA (see e.g. Bishop et al. 2012) to substitute univariate ANOVA where obtaining *p*-values by permutation allows avoiding the assumption of normality (Anderson 2017). Compared to other non-parametric methods, it allows a direct additive partitioning of variation for complex models with multiple categorical predictors and covariates (Anderson 2001). Surface area of young *P. rubens* blades significantly affects total cover of epibionts (Chava et al. 2019), so we used the former as a covariate in the analysis.

To assess the effects of treatments on total cover of epibionts, we also used univariate PERMANOVA on Euclidean distances. Separate analyses were conducted for 2014 (with one site) and 2015 (with 2 sites). Treatment (fixed) and young plant part area (covariate) were used as predictors for 2014; in addition, site (fixed) was used for 2015. To test the same effects on the multivariate community structure, we analyzed

square-root transformed percent cover of high-order taxa using multivariate PERMANOVA based on Bray-Curtis dissimilarities. We also performed separate univariate PERMANOVAs on Euclidean distances to test these effects for major fouling taxa in the community, that is, sponges, hydroids, bivalves, bryozoans, and polychaetes. Where the treatment effect was significant and variances were homogeneous (see below), we examined pairwise differences between treatment levels with the following set of contrasts:

(1) ambient controls vs. partial cages to check for the artifacts of caging procedure (hereafter 'A vs. P'),

(2) (ambient controls and partial cages) vs. full cages (=predator enclosures) to test the effects of excluding any kind of predators larger than 2–3 mm (hereafter '(A & P) vs. F'),

(3) (ambient controls and partial cages) vs. shrimp enclosures to test the effect of *S. phippisii* predation compared to natural predation level (hereafter '(A & P) vs. S'),

(4) shrimp cages vs. full cages to test the effect of *S. phippisii* predation compared to predator absence (hereafter 'S vs. F').

To check for homogeneity of variances between the levels of the factors included in the analyses, we performed the PERMDISP test (Anderson 2006). In case of significant heterogeneity of variances, we considered the results not reflecting the difference between means, since PERMANOVA does not distinguish the difference between variation in location and scale.

In order to visualize the differences between treatments and contributions of particular taxa, we used non-metric multidimensional scaling (nMDS) based on the Bray-Curtis index similarity matrix. We performed the procedure separately for 2014 and 2015 and for the 2 years combined.

Calculations were conducted in PRIMER 6.0 software with the PERMANOVA add-on and in R v.4.3.1 (R Core Team 2023). Means are reported \pm SE.

3. RESULTS

3.1. Background

Mean abundances of all taxa by year, site, and treatment levels are summarized in Table 1. Total cover of sessile organisms in ambient controls and partial cages was similar. It was also similar between years at Site V, which was sampled both in 2014 and in 2015 (Tables 1 & 2). Mean \pm SE total cover (ambient controls and partial cages pooled) at Site V was $7.41 \pm 1.79\%$ in 2014 and $6.20 \pm 0.59\%$ in 2015; it was slightly

Table 1. Mean \pm SE percent cover of epibionts on young *Phycodrys rubens* blades by year, site, and treatment level in the field experiments. Site K: near Kamenukha Island; Site V: near Velikiy Island (see Section 2 for details); N: number of replicates. Epiphytic algae and cirripeds were extremely scarce, and their mean cover (never exceeding 0.0002 and 0.009%, respectively) is omitted. Note that only a single polychaete species (*Circeis armoricana*) was recorded

Treatment	Site	Year	N	Porifera	Coelenterata	Polychaeta	Bivalvia	Bryozoa	Tunicata	Total
Ambient control	V	2014	7	0.21 \pm 0.21	0.22 \pm 0.16	1.21 \pm 0.42	0.02 \pm 0.02	6.29 \pm 1.83	<0.01	7.95 \pm 2.58
Ambient control	K	2015	10	0.41 \pm 0.20	0.14 \pm 0.02	1.48 \pm 0.15	0.14 \pm 0.05	3.10 \pm 0.44	0.02 \pm 0.01	5.30 \pm 0.59
Ambient control	V	2015	4	0.30 \pm 0.10	0.62 \pm 0.18	1.23 \pm 0.27	0.50 \pm 0.16	4.61 \pm 0.68	0	7.26 \pm 0.51
Full cage	V	2014	8	0.42 \pm 0.42	0.06 \pm 0.04	1.60 \pm 0.27	0	12.55 \pm 0.99	0.05 \pm 0.03	14.68 \pm 1.21
Full cage	K	2015	5	0.12 \pm 0.09	0.07 \pm 0.03	0.92 \pm 0.18	0.02 \pm 0.02	5.19 \pm 0.86	0.05 \pm 0.04	6.38 \pm 0.97
Full cage	V	2015	5	0.08 \pm 0.06	0.39 \pm 0.14	0.68 \pm 0.06	0.07 \pm 0.05	4.67 \pm 0.62	0.02 \pm 0.02	5.91 \pm 0.59
Partial cage	V	2014	7	0	0.04 \pm 0.03	0.92 \pm 0.26	0.01 \pm 0.004	5.91 \pm 2.39	<0.01	6.88 \pm 2.67
Partial cage	K	2015	4	0.04 \pm 0.01	0.01 \pm 0.01	0.62 \pm 0.10	0.01 \pm 0.01	3.19 \pm 0.78	<0.01	3.88 \pm 0.87
Partial cage	V	2015	3	0.07 \pm 0.07	0.24 \pm 0.07	0.85 \pm 0.17	0.07 \pm 0.04	3.54 \pm 0.20	0.01 \pm 0.01	4.79 \pm 0.43
Shrimp cage	V	2014	7	0.04 \pm 0.03	0.25 \pm 0.16	0.72 \pm 0.16	0.03 \pm 0.02	6.21 \pm 2.21	0.02 \pm 0.02	7.28 \pm 2.42
Shrimp cage	K	2015	4	0.16 \pm 0.09	0.06 \pm 0.03	0.12 \pm 0.05	0.01 \pm 0.01	0.31 \pm 0.16	<0.01	0.66 \pm 0.26
Shrimp cage	V	2015	4	0.01 \pm 0.01	0.47 \pm 0.13	0.09 \pm 0.02	0.10 \pm 0.06	0.77 \pm 0.21	0	1.45 \pm 0.36

lower at Site K in 2015 ($4.89 \pm 0.50\%$). Bryozoans dominated ambient controls and partial cages, contributing on average from 58 to 84% of the total cover depending on site and year, with the most abundant species being *Juxtacribulina annulata*, *Celleporella hyalina*, and *Electra pilosa*. Serpulid polychaetes (particularly *Circeis armoricana*) were the second most abundant group, contributing from 14 to 29% of the total cover. Sponges, hydroids, and bivalves each contributed up to 8%, while all other taxa taken together contributed less than 1%. At Site V (ambient controls and partial cages pooled), there were notably more bryozoans in 2014 ($83 \pm 2\%$) than in 2015 ($68 \pm 4\%$, $p = 0.002$, Mann-Whitney *U*-test), while the relative abundance of serpulid polychaetes was similar in the 2 years ($15 \pm 2\%$ and $17 \pm 2\%$, respectively, $p = 0.322$).

Sites V and K (compared in 2015) differed slightly in species composition (ambient controls and partial cages pooled): there were more hydrozoans at Site V ($7 \pm 1\%$) than at Site K ($2 \pm 1\%$, $p = 0.004$, Mann-

Whitney *U*-test), while serpulid polychaetes were more abundant at Site K ($25 \pm 2\%$) than at Site V ($17 \pm 2\%$, $p = 0.025$). Relative abundances of bryozoans, sponges, bivalves, and other taxa did not differ significantly at these 2 sites.

3.2. Experiment

Total cover of sessile organisms displayed contrasting responses to manipulations in 2014 and 2015. In 2014, when ambient abundance of shrimp was higher, the exclusion of predators had a strong impact: the mean total cover in full cages was twice as high ($15 \pm 1\%$) as in all other treatments, where it was similar (Fig. 1, Tables 1 & 3). The variances were homogeneous (PERMDISP, $F = 0.64$, $p = 0.835$). Treatment effect was significant. Both contrasts involving full cages were significant, while the contrasts comparing ambient controls with partial cages and both of them with shrimp cages were insignificant (Table 3). In 2015, when ambient abundance of shrimp was lower, the exclusion of predators made no difference: shrimp cages demonstrated a significantly lower total cover than all other treatments, which were similar (Fig. 1, Tables 1 & 4). The variances were homogeneous (PERMDISP, $F = 1.87$, $p = 0.188$). Treatment effect was significant regardless of site. Both contrasts involving shrimp cages were significant, while the contrasts comparing ambient controls with partial cages and both with full cages were insignificant (Table 4).

Table 2. Effect of year on the total epibiont cover on young *Phycodrys rubens* blades at Site V. Univariate PERMANOVA on Euclidean distances between total cover of sessile organisms on young blades of *P. rubens* in partial cages and ambient controls in 2014 and 2015. A: ambient controls; P: partial cages; Area: total area of young blades of a plant

Source of variation	df	SS	Pseudo- <i>F</i>	<i>p</i>	Unique permutations
Area (fixed, covariate)	1	0.0028	0.8026	0.295	9778
Treatment (fixed, A vs. P)	1	<0.0001	0.0015	0.974	9865
Year (fixed, 2014 vs. 2015)	1	0.0011	0.3114	0.638	9868
Treatment \times Year	1	0.0004	0.1064	0.745	9841
Residuals	16	0.0555			
Total	20	0.0604			

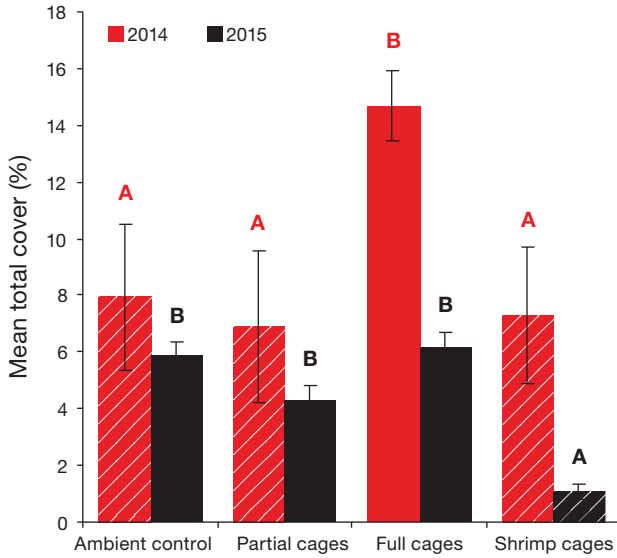


Fig. 1. Mean total cover of epibionts (\pm SE) on young *Phycodrys rubens* blades by treatment in 2014 and 2015. Fill pattern and capital letters indicate homogeneous groups within the years according to PERMANOVA contrasts (Tables 3 & 4). Partial fill denotes the groups with the lower mean total cover. Sites pooled in 2015

Multivariate community structure showed a generally similar response. In 2014, predator exclusion altered the taxonomic composition so that full cages grouped separately from the other treatments on nMDS plots (Fig. 2). The variances were homogeneous (PERMDISP, $F = 3.15$, $p = 0.117$). Treatment effect and both contrasts involving full cages were significant, while the contrasts comparing ambient controls with partial cages and both of them with shrimp cages were insignificant (Table 5). In 2015, shrimp cages clearly grouped separately from all

other treatments (Figs. 3 & 4). The variances, however, were heterogeneous (PERMDISP, $F = 6.65$, $p = 0.004$), rendering the results of PERMANOVA uninformative (Table 6).

Both in 2014 and 2015, bryozoans were a major contributor to the differences in epibiont cover between treatments, while the proportion of hydrozoans and bivalves mostly varied between sites and years (Figs. 2–4). Consistently, univariate analyses revealed the significant effect of manipulations on the mean percent cover only in bryozoans (Tables 1, 7, & 8). In polychaetes (2014), bivalves (2014), hydroids (both years), and sponges (both years), the treatment effect was insignificant, while polychaetes and bivalves in 2015 showed heterogeneous variances (PERMDISP, $F = 3.88$, $p = 0.032$ and $F = 6.87$, $p = 0.030$, respectively). In 2014, predator exclusion made mean bryozoan cover in full cages twice as high as in all other treatments (Table 1, Fig. 5). The variances were homogeneous (PERMDISP, $F = 0.88$, $p = 0.769$). Treatment effect was significant, and so were both contrasts involving full cages, while the contrasts comparing ambient controls with partial cages and both of the latter with shrimp cages were insignificant (Table 7). In 2015, full cages also displayed a higher mean bryozoan cover than partial cages and ambient controls, while, in contrast, shrimp enclosures had much fewer bryozoans than any other treatment (Table 1, Fig. 5). The variances were homogeneous (PERMDISP, $F = 2.26$, $p = 0.130$). Treatment effect was significant, and the only insignificant contrast was the one comparing partial cages and ambient controls (Table 8).

Table 3. Effect of predator abundance manipulations on the total epibiont cover on young *Phycodrys rubens* blades in 2014. Univariate PERMANOVA on Euclidean distances between total cover of sessile organisms on young blades of *P. rubens* in the 2014 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; ** $p < 0.01$; *** $p < 0.001$. PERMDISP: $F = 0.64$, $p = 0.835$

Source of variation	df	SS	Pseudo- F	p	Unique permutations
Area (fixed, covariate)	1	0.0174	5.7137	0.0281**	9800
Treatment (fixed)	3	0.0371	4.0519	0.0158**	9953
Contrast A vs. P	1	0.0001	0.0291	0.8599	9823
Contrast (A & P) vs. F	1	0.0299	9.3622	0.0025**	9852
Contrast (A & P) vs. S	1	0.0001	0.0291	0.8987	9848
Contrast S vs. F	1	0.0223	23.719	0.0001***	9829
Residuals	24	0.0732			
Total	28	0.1221			

4. DISCUSSION

Although we found dramatic inter-annual variation in the consumer control of sessile organisms covering young blades of *Phycodrys rubens*, their mean total cover never exceeded 15% even after consumer removal. This clearly shows that, in contrast to a comparable epibiosis of *Chondrus crispus* in temperate waters (Stachowicz & Whitlatch 2005), it is not top-down regulation that prevents young *P. rubens* blades from heavy overgrowth. In the warm year (2014), mobile consumers substantially shaped the community, and their removal doubled the total

Table 4. Effect of predator abundance manipulations on the total epibiont cover on young *Phycodrys rubens* blades in 2015. Univariate PERMANOVA on Euclidean distances between total cover of sessile epifauna on young blades of *P. rubens* in the 2015 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; *** $p < 0.001$. PERMDISP: $F = 1.87$, $p = 0.188$

Source of variation	df	SS	Pseudo- F	p	Unique permutations
Area (fixed, covariate)	1	0.0007	3.40	0.0702	9832
Treatment (fixed)	3	0.0096	14.74	0.0001***	9958
Contrast A vs. P	1	0.0002	0.92	0.3439	9816
Contrast (A & P) vs. F	1	0.0002	0.84	0.3588	9811
Contrast (A & P) vs. S	1	0.0075	42.48	0.0001***	9826
Contrast S vs. F	1	0.0054	24.81	0.0004***	9873
Site	1	0.0006	2.68	0.1088	9825
Treatment \times Site	3	0.0007	1.01	0.4000	9948
Residuals	30	0.0065			
Total	38	0.0234			

abundances of sessile organisms. According to our rough estimates, in 2014 there were also more mesopredatory shrimp in the surrounding habitat. In the extremely cold year (2015), when there were apparently fewer shrimp around, consumer removals had an almost negligible effect on the total cover at both sites. Consumers unequally impacted different sessile epibenthic taxa, targeting mostly bryozoans, which were heavily preyed upon both in 2014 and

in 2015. At the same time, bryozoans were much less abundant in 2015, when there were more sponges, hydroids, and bivalves, than in 2014. Greater consumer control in the warm year and low consumer control, combined with less potential prey, in the cold year resulted in a remarkably similar total percent cover in a natural community.

Selective predation is a powerful driver of community composition, but much of its power comes from the indirect positive effects on inferior competitors in the presence of strong competition (Paine 1974). In temperate waters, generalist mesopredatory shrimp can selectively target bryozoans, preventing them from monopolizing artificial hard substrates (Dumont et al. 2011).

Mesograzers remove dominating bryozoans from the red seaweed (Stachowicz & Whitlatch 2005), while grazing chitons similarly restrict bryozoan presence in marina dock fouling (Nydam & Stachowicz 2007). In our study, bryozoans dominated on young *Phycodrys* blades and were a primary target for consumers, whereas subdominant tubeworms and other less abundant groups were less targeted. However, indirect benefits for inferior competitors in this particular microhabitat are improbable, because the

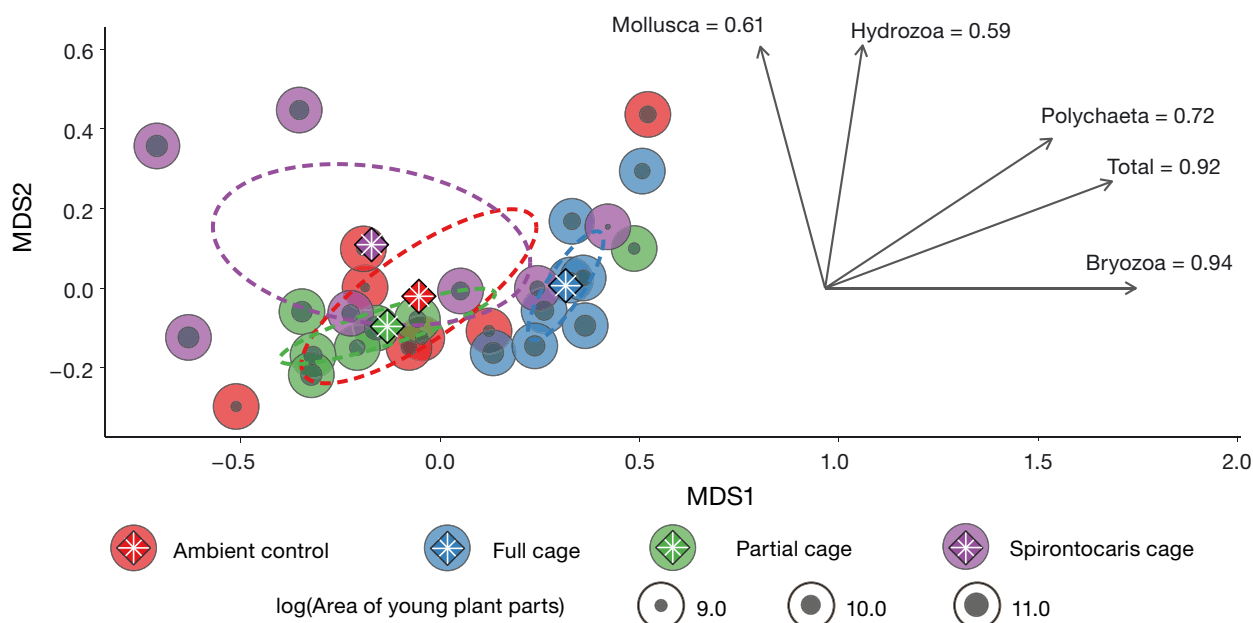


Fig. 2. Multivariate structure of the epibiosis on young *Phycodrys rubens* blades by treatment in 2014. Non-metric multidimensional scaling (nMDS) on square-root transformed standardized total cover of high-order taxa in 2014. Bray-Curtis dissimilarity. Diamonds are centroids, ellipses denote SE. Vectors show significant correlations of standardized percent cover by taxa with nMDS axes

Table 5. Effect of predator abundance manipulations on the multivariate community structure of the epibiosis on young *Phycodrys rubens* blades in 2014. PERMANOVA on square-root transformed Bray-Curtis dissimilarities between standardized cover of high-order taxa in the 2014 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; *** $p < 0.001$. PERMDISP: $F = 3.15$, $p = 0.117$

Source of variation	df	SS	Pseudo- F	p	Unique permutations
Area (fixed, covariate)	1	1607	3.22	0.0202	9945
Treatment (fixed)	3	4906	3.28	0.0004***	9926
Contrast A vs. P	1	777	1.31	0.2639	9949
Contrast (A & P) vs. F	1	2777	6.06	0.0008***	9951
Contrast (A & P) vs. S	1	431	0.67	0.6223	9953
Contrast S vs. F	1	2651	6.64	0.0001***	9954
Residuals	24	11958			
Total	28	18007			

low total cover clearly indicated the lack of competition. While *Spirontocaris phippisii* is unlikely to be the only mesopredator in the system, our results obtained in 2014 indicate that it is a key one. Although this shrimp is omnivorous (Birkely & Gulliksen 2003, Yakovis & Artemieva 2019, 2021), a recent microcosm study (Chava et al. 2024) revealed that, owing to its feeding habits, it has a much stronger impact on bryozoans than on co-dominant serpulid tubeworms. Unitary tubeworms outperform modular bryozoans against shrimp because of the superior ability of tubeworms to outgrow predation pressure, especially from

large shrimp individuals (Chava et al. 2024). This is consistent with our results showing the relative vulnerability of bryozoans in the field. Caged shrimp, in fact, had a similar impact on the community in 2014 and 2015, reducing the average bryozoan percent cover by 4–6% compared to predator enclosures, but in 2015 this meant a near elimination of bryozoans (Fig. 5). The 4–6% reduction closely matched the natural predation rate in 2014. In 2015, the reduction of bryozoan cover in ambient controls and partial cages compared to enclosure cages was about 2%, consistent with the estimated inter-annual difference in ambient shrimp abundance.

Our design has a limited capability to assess spatial variation of consumer control, since the latter was much stronger in 2014, when we exposed all cages at a single site. However, bryozoans were impacted by consumers in both years, and neither location nor its interaction with treatment affected bryozoan cover in 2015. Thus, compared to its interannual variation and taxonomic selectivity, the difference in the consumer control strength between the 2 sites was negligible. *Chondrus* epibiosis shows extensive spatial variation of the consumer control strength associated with patchy distribution of mesograzers snails (Stachowicz

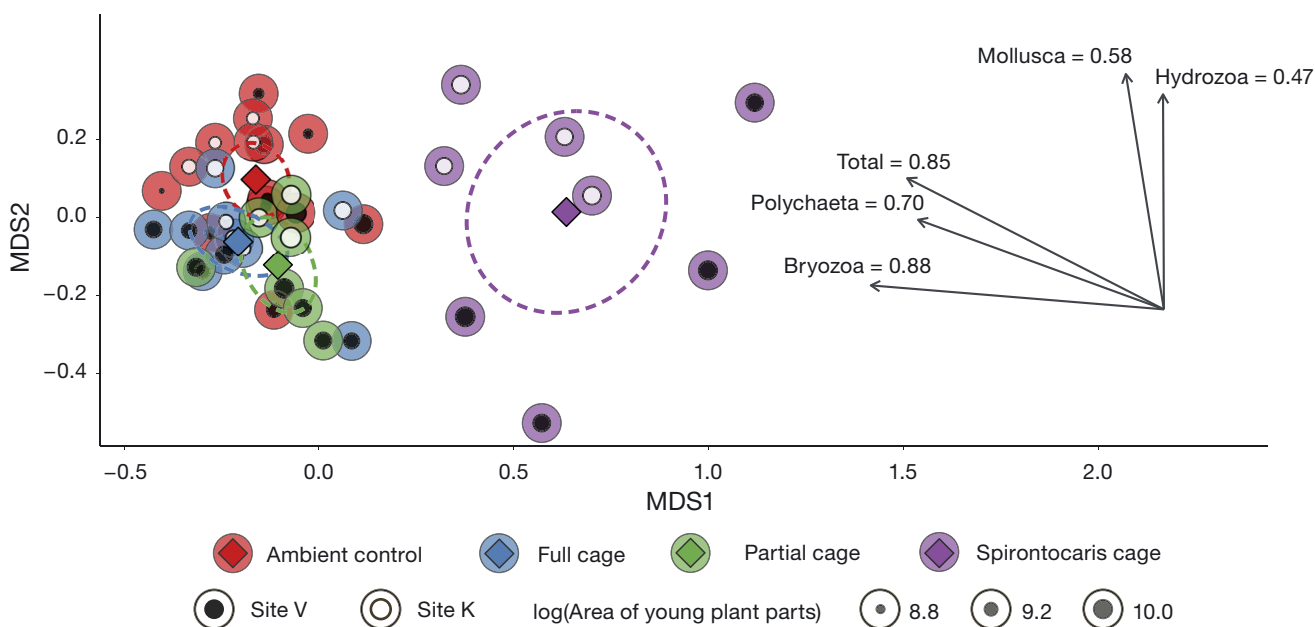


Fig. 3. Multivariate structure of the epibiosis on young *Phycodrys rubens* blades by treatment in 2015. Non-metric MDS (nMDS) on square-root transformed standardized total cover of high-order taxa in 2015. Bray-Curtis dissimilarity. Diamonds are centroids, ellipses denote SE. Vectors show significant correlations of standardized percent cover by taxa with nMDS axes

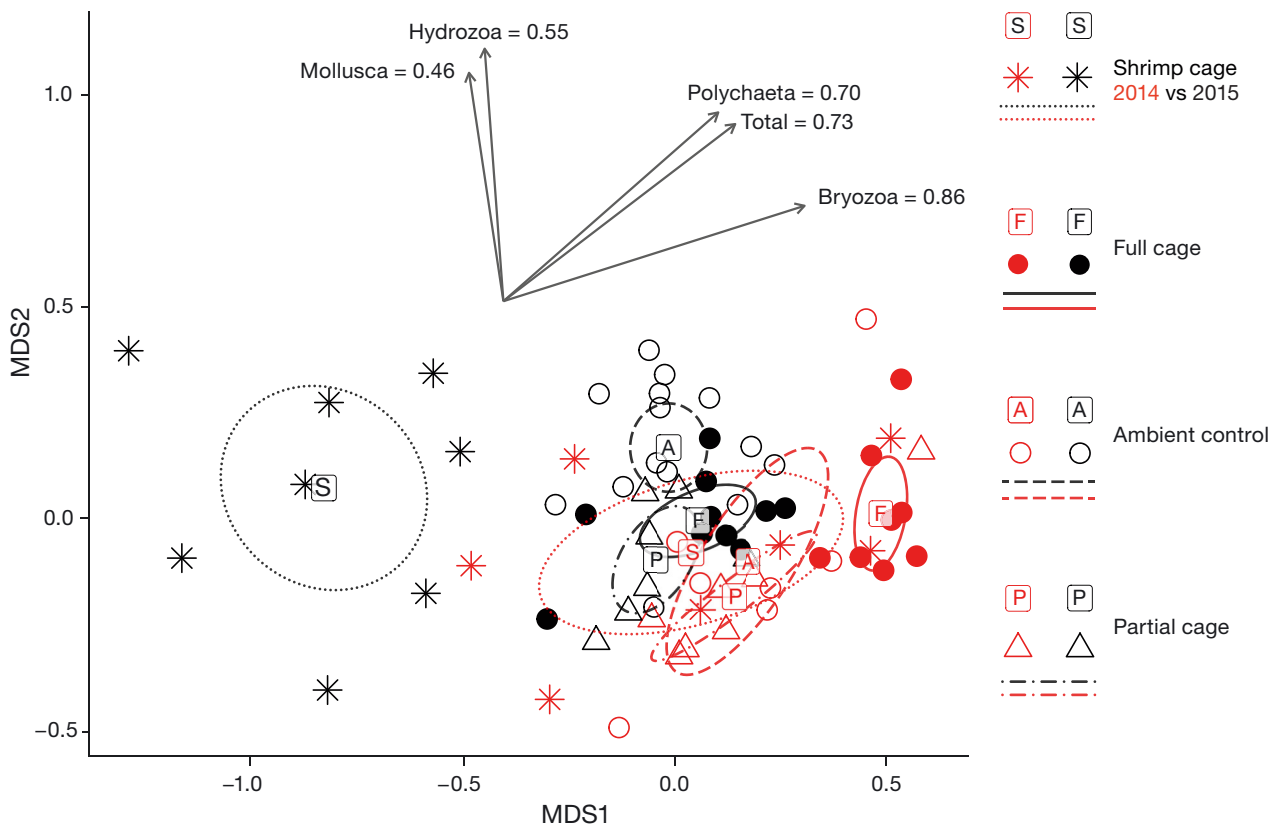


Fig. 4. Multivariate structure of the epibiosis on young *Phycodrys rubens* blades by treatment in 2014 and 2015. Non-metric MDS (nMDS) on square-root transformed standardized total cover of high-order taxa in 2014. Bray-Curtis dissimilarity. Squares with letters inside are centroids, ellipses denote SE. Vectors show significant correlations of standardized percent cover by taxa with nMDS axes

Table 6. Effect of predator abundance manipulations on the multivariate community structure of the epibiosis on young *Phycodrys rubens* blades in 2015. PERMANOVA on square-root transformed Bray-Curtis dissimilarities between standardized cover of high-order taxa in the 2015 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; ** $p < 0.01$, *** $p < 0.001$. PERMDISP: $F = 6.65$, $p = 0.004^{**}$

Source of variation	df	SS	Pseudo- F	p	Unique permutations
Area (fixed, covariate)	1	370	0.89	0.5102	9940
Treatment (fixed)	3	11225	8.99	0.0001***	9907
Contrast A vs. P	1	1018	3.58	0.0004***	9953
Contrast (A & P) vs. F	1	1527	4.47	0.0002***	9935
Contrast (A & P) vs. S	1	7552	16.45	0.0001***	9953
Contrast S vs. F	1	5424	9.81	0.0001***	9945
Site	1	5403	12.98	0.0001***	9952
Treatment \times Site	3	1657	1.33	0.1611	9914
Residuals	30	12489			
Total	38	33440			

& Whitlatch 2005). However, shrimp are much more mobile than snails. While the spatial distribution of shrimp can also be patchy, at least when shaped by the patches of FS providing prey and refuge from

predators (Shinomiya et al. 2017), they generally tend to show spatial abundance variation at a larger scale (Boddeke 1976, Koeller 2000). Since we studied only 2 sites, there is a good chance that, despite the difference in the tidal flow, they were too similar in terms of consumer abundance to detect spatial variation in top-down control of *Phycodrys* epibiosis.

To our knowledge, substantial inter-annual variation in consumer control strength has never been previously detected in a seaweed epibiosis, although it is common in various other freshwater and marine systems in tropical and temperate zones (Heck & Wilson 1987, Hairston 1988, Posey et al. 1995, Navarrete 1996). The known mechanisms of

this variation range from relatively infrequent climatic events such as El Niño–Southern Oscillation to gradual long-term trends like oligotrophication (Meserve et al. 2003, Kerimoglu et al. 2013). Ambient abiotic

Table 7. Effect of predator abundance manipulations on the percent cover of bryozoans on young *Phycodrys rubens* blades in 2014. Univariate PERMANOVA on Euclidean distances between total cover of bryozoans on young blades of *P. rubens* in the 2014 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. PERMDISP: $F = 0.88$, $p = 0.769$

Source of variation	df	SS	Pseudo- F	p(perm)	Unique permutations
Area (fixed, covariate)	1	0.0133	6.28	0.022*	9832
Treatment (fixed)	3	0.0291	4.60	0.011	9957
Contrast A vs. P	1	0.0005	0.15	0.718	9857
Contrast (A & P) vs. F	1	0.0231	10.99	0.001**	9863
Contrast (A & P) vs. S	1	0.0001	0.05	0.827	9862
Contrast S vs. F	1	0.0163	17.31	<0.001***	9850
Residuals	24	0.0507			
Total	28	0.0879			

Table 8. Effect of predator abundance manipulations on the percent cover of bryozoans on young *Phycodrys rubens* blades in 2015. Univariate PERMANOVA on Euclidean distances between total cover of bryozoans on young blades of *P. rubens* in the 2015 field experiment. Significant effects and contrasts are highlighted in **bold**. A: ambient controls; P: partial cages; F: full cages; S: shrimp enclosures; Area: total area of young blades of a plant; *** $p < 0.001$. PERMDISP: $F = 2.26$, $p = 0.130$

Source of variation	df	SS	Pseudo- F	p	Unique permutations
Area (fixed, covariate)	1	0.0003	1.49	0.2296	9825
Treatment (fixed)	3	0.0070	13.64	0.0001***	9957
Contrast A vs. P	1	<0.0001	0.02	0.9006	9829
Contrast (A & P) vs. F	1	0.0011	5.39	0.0273	9835
Contrast (A & P) vs. S	1	0.0041	32.55	0.0001***	9831
Contrast S vs. F	1	0.0039	21.57	0.0005***	9852
Site	1	0.0002	1.07	0.3111	9803
Treatment \times Site	3	0.0005	0.87	0.4584	9945
Residuals	30	0.0052			
Total	38	0.0150			

conditions can switch a system from top-down to bottom-up regulation and back (Hoekman 2010). Temporal limitations of our experiments make it impossible to distinguish a causation from fluctuation, but given the contrasting water temperatures in 2014 and 2015, the abiotic regulation of consumer control seems highly probable. Importantly, according to the long-term records of water temperatures in the White Sea (at Station D1 in the Chupa Inlet of the Kandalaksha Bay, 66° 19.836' N, 33° 40.098' E; data from: Usov et al., <https://www.st.nmfs.noaa.gov/copepod/timeseries/ru-10101/>), the summer of 2015 was the coldest since 2010, while the summer of 2014 was the sixth warmest since 1991. This means that our experiments were by chance made under contrasting conditions

with respect to the summer water temperature range (Fig. 6). Below we discuss the processes shaping epibiosis and the possible effects of climatic differences between years.

Community composition and abundances of sessile epibenthic organisms colonizing newly developed seaweed blades generally result from larval supply (recruitment) and subsequent growth of epibionts, their competition, substrate provision by the host, consumer control, and physical disturbance. Physical disturbance frequency is low in subtidal habitats (Palmer et al. 1996); there were no traces of wave action at our 11–12 m deep sites. Shielding associated organisms from abiotic stress, which is commonly provided by FS in the intertidal (Bruno et al. 2003, Olafsson 2016), does not appear to be important in a subtidal habitat. In fact, the assemblages associated with *Phycodrys* blades may be even more accessible to mesopredators than those on underlying gravel and rocks shielded by *Phycodrys* canopy.

Competition for space is also uncommon on young *Phycodrys* blades, as indicated by 8% mean total cover on random natural plants in 2014 (Table 1) and 7–10% in 2015 (Table 2 in Chava et al. 2019). This is in contrast with comparable systems from tropical and temperate waters (Stachowicz & Whitlatch 2005, da Gama et al. 2008). At the same time, red seaweed productivity is highly sensitive to water temperature (Paalme et al. 2011). *Phycodrys* grows twice as fast at 10°C as at 4°C (Gordillo et al. 2022). The area of young *Phycodrys* blades per square meter of the bottom at Sites V and K was, accordingly, 2–4 times lower after the extremely cold summer of 2015 than after the contrastingly warm following summer (Fig. 6), while the density of the plants remained similar (Chava et al. 2019). Given that the summer of 2014 was also extremely warm, *Phycodrys* growth at our research sites supplied substrate at a rate well exceeding the cumulative recruitment and growth capacity of the epibionts both in high-productive and low-productive years. However, this excess is apparently limited to large and average-sized *Phycodrys* plants. Total cover on individual hosts is negatively

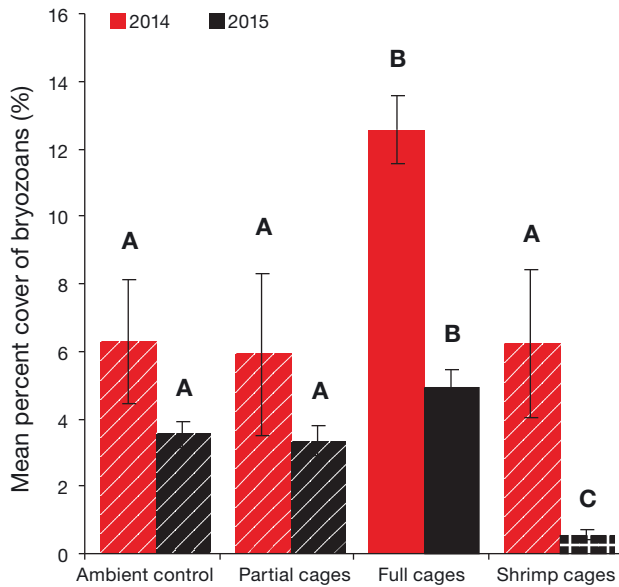


Fig. 5. Mean percent cover of bryozoans (%), \pm SE on young *Phycodrys rubens* blades by treatment in 2014 and 2015. Fill pattern and capital letters indicate homogeneous groups within the years according to PERMANOVA contrasts (Tables 7 & 8). Solid fill denotes the groups with the highest mean bryozoan cover, crosshatched partial fill denotes the group with the lowest mean bryozoan cover. Sites pooled in 2015

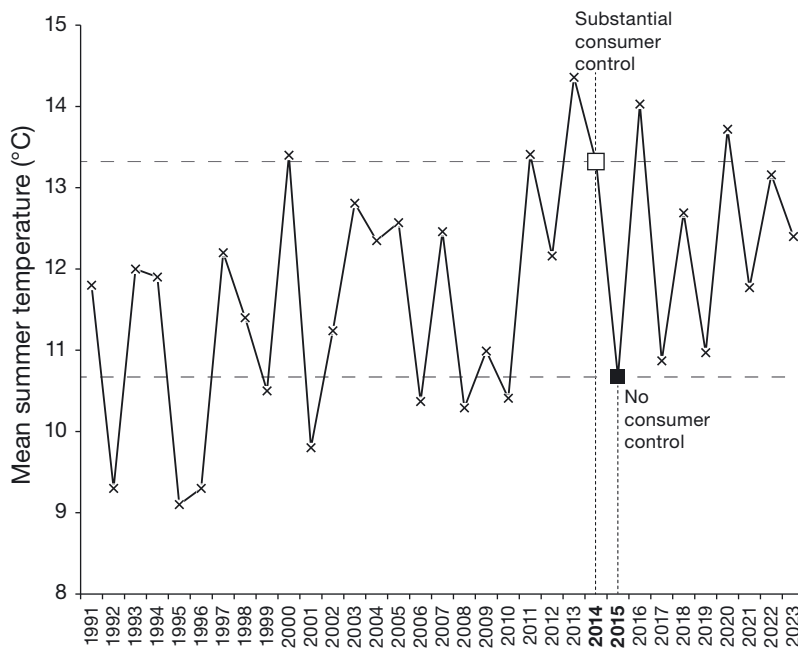


Fig. 6. Mean summer water temperatures in the White Sea in 1991–2023. Measured at Station D1 in the Chupa Inlet of Kandalaksha Bay ($66^{\circ} 19.836' N$, $33^{\circ} 40.098' E$), averaged across 0.5–10 m depths (data from Usov et al., <https://www.st.nmfs.noaa.gov/copepod/time-series/ru-10101/>). The 2 years of the field experiments are highlighted in **bold**

correlated with their size, reaching 25–40% on young blades of small plants (Chava et al. 2019; Fig. 3). Heavy overgrowth and its regulation by consumers may hence cause size-selective pressure on the population structure of the host. Competition for space and consequent indirect effects of consumers targeting dominant competitors seem important on old *Phycodrys* blades and underlying rocks where the cover of sessile organisms is several times higher (Chava et al. 2019, V. Verzhbitsky pers. comm.).

Our results show that lower natural bryozoan abundances in 2015 were not caused by large mesopredators. There are still some other potential consumers that can pass through a 2 mm mesh, e.g. turbellarians, nudibranchs, and polychaetes (Lidgard 2008). Since we did not observe many of these, we assume that in years with weak consumer control, the community assembly is mostly driven by supply-side processes (i.e. recruitment, see Underwood & Keough 2001 for review) and further shaped by growth rate variations in response to ambient conditions. Larvae and juveniles of sessile organisms are usually sensitive to fluctuations in temperature (Ushakova 2003, Saunders & Metaxas 2007, Bitschovsky et al. 2011). Lower temperatures can also cause limited nutrient supply to mature epibionts restricting both their growth and reproductive potential (Seed & Hughes 1992, Gibson et al. 2001).

Substantial taxonomic variation of seasonal recruitment timing in Arctic waters (Meyer et al. 2017) suggests that climatic variables can unequally affect different taxa, causing interannual shifts in community composition. The established residents surviving from the previous years on the neighboring stable substrates, like old *Phycodrys* parts and rocks, must also affect larval supply and settlement patterns (Meyer et al. 2017). Consequently, the abiotic drivers from previous years imprint in the community history of the adjacent less ephemeral microhabitats and would also shape the epibiosis of young *Phycodrys* blades.

The observed difference in the community composition in the 2 study years encompasses a lower percent cover of predation-sensitive bryozoans associated with the decreased mesopredator abundance and consumer control strength in the colder year. This may be either a coincidence or the re-

sult of a causal relationship. Shrimp population dynamics in temperate and polar zones is commonly driven by water temperatures, which affect hatching and juveniles (van der Veer & Bergman 1987, Beukema 1992, Oh et al. 1999, Aschan & Ingvaldsen 2009, Koeller et al. 2009, Richards et al. 2012, Beukema & Dekker 2014, 2020), and is bottom-up controlled by food availability (Salama & Hartnoll 1992, Hufnagl et al. 2010). Fish predation (Tiews 1978, Koeller 2000, Wieland et al. 2007, Jónsdóttir 2017), which is in turn regulated by marine mammals (Temming & Hufnagl 2015), can also affect shrimp. However, based on the limited available data, *Spirontocaris* is not known to be a part of fish diet in the White Sea (Gerasimova & Podrazhanskaya 1991, Ershov 2010). Colder water in summer 2015 is thus consistent with lower shrimp abundance. Yet, considering that *Spirontocaris* has a lifespan up to 5 yr (Vogt 2019 based on Węśławski 1987), its population structure can accumulate the effects of climatic variables from different years. While the variation in relative abundance of bryozoans may cause bottom-up control of shrimp abundance, it is also likely that both are driven by the same climatic variables (see Saunders & Metaxas 2007, Beukema & Dekker 2014). At least, the reproductive cycles of other organisms from higher trophic layers, including predatory shrimp, have apparently evolved to use environmental triggers correlated with the abundance of potential prey, minimizing direct bottom-up trophic control (Koeller et al. 2009). However, a much greater observation effort would be necessary to detect the interannual correlation between climatic variables and abundances of shrimp and bryozoans.

The strength of biotic interactions, including consumer control, generally decreases with latitude (Schemske et al. 2009, Baskett & Schemske 2018), although the supporting data are geographically limited. Among the communities shaped by FS, tropical and temperate seagrass beds show the latitudinal gradient of predation strength (Freestone et al. 2020). However, direct consumer control and trophic cascades also affect at least some communities associated with FS in polar waters (Yakovis & Artemieva 2019, 2021). We showed that consumer control is not a critical factor preventing a sub-polar seaweed host from extensive overgrowth. Our findings suggest that consumer control of epibiosis is triggered by higher water temperatures. This means that a future increase of top-down regulation due to the ongoing rapid climatic changes in Arctic and sub-Arctic areas (McCrystall et al. 2021) may be predicted. In addition, a large interannual variation range of consumer control (from substantial to negligible) re-

vealed in our study indicates that the data obtained in one year of observations or experiments in polar waters should be treated with caution.

5. CONCLUSIONS

We can draw the following conclusions from this study. (1) Consumer control of community composition in a sub-arctic seaweed epibiosis can show strong interannual variation. Exclusion of consumers doubled the total cover in 2014 but had no effect on it in 2015, when the summer was about 3°C colder than in the previous year. (2) Consumers, particularly the mesopredatory shrimp, primarily affected bryozoans both in 2014 and 2015. There were fewer bryozoans on unmanipulated plants in the colder year, apparently because of the lower recruitment rate. (3) Compared to temperate and tropical waters, consumer control in a polar sea is not critical for the protection of an algal host from being heavily overgrown. However, top-down regulation of epibiosis appears to be triggered by higher water temperatures. In the face of climate change, top-down regulation may become a more important factor, especially in smaller host plants with higher epibiont cover.

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Appendix

Table A1. Water temperatures (°C) near the experimental sites in summer 2009–2016. Measured at 66° 33.177' N, 33° 6.181' E in Velikaya Salma Strait, Kandalaksha Bay, at 1 m depth. The 2 years of the field experiments are highlighted in **bold**. The warmest and coldest values for each date are highlighted in yellow and blue, respectively

Year	5 June	25 June	5 July	25 July	5 August	25 August
2009	6.1	9.4	11.1	11.7	14.2	11.6
2010	6.1	10.3	11.5	12.3	14.7	9.4
2011	6.9	12.2	13.1	15.2	14.8	
2012	5.4	11.1	10.3	10.2	12.3	11.1
2013	9.6	12.6	15.2	13.7		
2014	7.9	10.1	10.0	16.3	16.5	13.1
2015	5.3	7.2	9.4	10.6	12.1	12.2
2016	8.5	11.7	13.7	14.6		

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