Canopy-Forming Seaweeds in Urchin-Dominated Systems in Eastern Canada: Structuring Forces or Simple Prey for Keystone Grazers?

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Abstract

Models of benthic community dynamics for the extensively studied, shallow rocky ecosystems in eastern Canada emphasize kelp-urchin interactions. These models may bias the perception of factors and processes that structure communities, for they largely overlook the possible contribution of other seaweeds to ecosystem resilience. We examined the persistence of the annual, acidic (H₂SO₄), brown seaweed Desmarestia viridis in urchin barrens at two sites in Newfoundland (Canada) throughout an entire growth season (February to October). We also compared changes in epifaunal assemblages in D. viridis and other conspicuous canopy-forming seaweeds, the non-acidic conspecific Desmarestia aculeata and kelp Agarum clathratum. We show that D. viridis can form large canopies within the 2-to-8 m depth range that represent a transient community state termed “Desmarestia bed”. The annual resurgence of Desmarestia beds and continuous occurrence of D. aculeata and A. clathratum, create biological structure for major recruitment pulses in invertebrate and fish assemblages (e.g. from quasi-absent gastropods to >150 000 recruits kg⁻¹ D. viridis). Many of these pulses phase with temperature-driven mass release of acid to the environment and die-off in D. viridis. We demonstrate experimentally that the chemical makeup of D. viridis and A. clathratum helps retard urchin grazing compared to D. aculeata and the highly consumed kelp Alaria esculenta. In light of our findings and related studies, we propose fundamental changes to the study of community shifts in shallow, rocky ecosystems in eastern Canada. In particular, we advocate the need to regard certain canopy-forming seaweeds as structuring forces interfering with top-down processes, rather than simple prey for keystone grazers. We also propose a novel, empirical model of ecological interactions for D. viridis. Overall, our study underscores the importance of studying organisms together with cross-scale environmental variability to better understand the factors and processes that shape marine communities.

Introduction

Erect fleshy seaweeds are a dominant component of shallow, rocky benthic communities in polar, subpolar, and cold-temperate seas [1–3]. By creating vertical structure that modifies the light [4,5] and hydrodynamic environments [6,7], seaweeds provide substrate and food for benthic and pelagic organisms [7–9], ultimately modulating predator-prey interactions [10–12]. Because seaweeds generally contribute to increasing marine biodiversity [13–16], any factor that alters their abundance is likely to trigger bottom-up cascades [3,17,18].

A prime example of cold, marine benthic communities organized around the high productivity of erect, fleshy seaweeds is that of the western Antarctic Peninsula. There, three perennial species with contrasting morphologies in the order Desmarestiales, Desmarestia aniceps, Desmarestia menziesii, and Himanthothallus grandifolius, form thick canopies that cover up to 80% of the seabed [2,5]. These foundation species [18], which, presumably, chemically deter dominant grazers [19–21], provide continuous access to vertical structure for the recruitment and growth of highly diverse assemblages of invertebrates [22–24]. This condition contrasts with shallow marine ecosystems at lower latitudes in both hemispheres, where macroherbivores largely control the structure and dynamics of benthic communities [25–27].

Empirical and analytical models of benthic community dynamics for the extensively studied, shallow rocky ecosystems in eastern Canada (Nova Scotia and northwards) emphasize kelp-urchin interactions. These models often include shifts in the distribution and abundance of kelp (mainly Saccharina longissimuris and Alaria esculenta) that can be predicted reasonably well from population shifts in their main predator, the omnivorous green sea urchin, Strongylocentrotus droebachiensis [28–30]. The traditional view that these ecosystems exhibit alternations between two community states, kelp bed and urchin barrens, was recently broadened. It includes, for the Nova Scotia region, a likely transient (multiyear) state dominated by the introduced green seaweed Codium fragile ssp. fragile [31,32]. The latter state, together with improving knowledge about the stability and functional importance of less studied, canopy-forming seaweeds in urchin barrens [11,28,30,33,34], call for a critical reassessment of the generality of phase-shifts and their mechanisms.
Recent studies of acid (H$_2$SO$_4$) production and mortality in the annual Desmarestiales Desmarestia viridis in urchin barrens in Newfoundland show that the acid continuously and irreversibly accumulates within vacuoles as sporophytes grow from recruit to adult (March-June). This build-up lowers the intracellular pH to 0.53 and inevitably culminates into mass releases of acid (July-August) and die-offs (September-October), when mean sea temperature rises above 12°C [35,36]. These and other studies in the northern Gulf of St. Lawrence [11,28] and Nova Scotia ([30,37], P. Gagnon unpublished data) suggest that D. viridis may limit urchin movement and facilitate recruitment in invertebrates and other seaweeds, including kelp. The notion that D. viridis contributes to the development of an ephemeral community state has yet to be scrutinized with integrated studies of the persistence, functional importance, and mechanisms that promote the survival of sporophytes in urchin barrens.

In the present study, we test the overall hypothesis that D. viridis functions as an ephemeral foundation species facilitating recruitment in, and supporting distinct assemblages of, invertebrates in urchin barrens. Specifically, we 1) characterize and relate temporal variability in the abundance of D. viridis and green sea urchins at multiple depths, as well as 2) compare changes in epifaunal assemblages of D. viridis and two other conspicuous, canopy-forming seaweeds in urchin barrens, the non-acidic Desmarestiales Desmarestia aculeata and the grazing-resistant kelp Agarum clathratum throughout an entire growth season (February to October, 2011) in D. viridis. We also 3) conduct two complementary laboratory experiments to assess the vulnerability of D. viridis, D. aculeata, and A. clathratum to grazing by the green sea urchin and how it relates to the seaweed chemical makeup. In light of our findings and related studies, we propose fundamental changes to the study of community shifts in shallow rocky ecosystems and a novel empirical model of ecological interactions for D. viridis in eastern Canada.

**Materials and Methods**

**Study sites and characteristics of seaweeds studied**

This study was conducted with Desmarestia viridis, Desmarestia aculeata, Agarum clathratum, Alaria esculenta, and green sea urchin at, or collected from, two gently sloping, rocky subtidal sites located ~1.4 km apart in Bay Bulls, on the southeastern tip of Newfoundland: Bread and Cheese Cove (BCC, 47°18'35'' N, 52°47'30'' W) and Keys Point (KP, 47°18'15'' N, 52°48'24'' W). All necessary permits for sampling and collecting seaweeds and urchins were obtained prior to sampling in accordance with the Canadian Council of Animal Care guidelines. No specific locational permits were required for seaweed and urchin sampling and collection in Bay Bulls, and no threatened or endangered species were at risk of incidental capture. Seaweed assemblages at both sites are dominated by the kelps Alaria esculenta and Laminaria digitata to a depth of ~2 m, followed by extensive pavements of red coralline seaweeds, mainly Lithothamnion glaciale, to a depth of ~15 m. These pavements, hereafter termed “barren zone” or “barrens” to follow the convention, are colonized year round by the green sea urchin, Strongylocentrotus droebachiensis, as well as D. aculeata. The latter forms small (a few m$^2$), scattered patches on boulder tops and ridges at depths between 2 and 10 m. Desmarestia viridis sporophytes establish annually in both barrens from March to October [35] (Fig. 1). The grazing-resistant kelp A. clathratum [34] forms small, scattered
patches throughout the barrens and large (up to several tens of m²) stands at depths >1.5 m.

Of the three seaweeds in urchin barrens that we investigated for epifaunal assemblages (see below), only one, *D. viridis*, has an annual life cycle. Sporophytes exhibit three phases of change in length at BCC and KP: (1) increase [March to late June], (2) no change [July to mid-August], and (3) decrease [mid-August to late October] [35]. The two other species, *D. aculeata* and *A. clathratum*, are perennials with sporophytes that can live up to at least a few years [35,39] and, in the case of *A. clathratum*, form highly stable patches in urchin barrens [34]. Sporophytes in both *D. viridis* and *D. aculeata* have a highly flexible stipe and a profusely branched frond, which sweeps back and forth over the bottom with wave action [11,40]. This effect is less pronounced in *D. aculeata* because of cortication, during summer, of new tissues arising from the apical parts of the fronds until wave action and sweeping resume, which forces urchins to return to open areas. The few urchins underneath *D. viridis* are basically clinging to the substratum.

Epifaunal assemblages

To assess the functional importance of *Desmarestia viridis*, *Desmarestia aculeata*, and *Agarum clathratum*, we tracked changes in epifaunal assemblages of each species at KP during the entire 2011 growth season in *D. viridis*. Given 1) interspecific differences in ontogeny, morphology, and chemistry of sporophytes outlined above, and 2) marked changes in length, bushiness, and intracellular acidity of *D. viridis* sporophytes within only a few months [35,36], we predicted that epifaunal assemblages in *D. viridis* would be more variable and less diverse than those in the longer-lived, morphologically comparable, non-acidic *D. aculeata*. We also predicted that epifaunal assemblages would be more variable and diverse in *D. viridis* than in the perennial and morphologically less complex *A. clathratum*.

On 18 February, 2011 and every 26 to 35 days until 9 October, 2011 we hand collected (via SCUBA diving) frond tissues from 7 to 10 sporophytes in each seaweed at depths between 6 and 10 m (*D. aculeata*) and 8 and 12 m (*D. viridis* and *A. clathratum*). It was not possible to collect the three seaweeds within a common depth range. Yet, less than 20% of the sporophytes were located in slightly shallower (2 m) water than the rest of the sporophytes. We did not perceive any marked changes in environmental conditions across the 6-to-12 m range. Therefore, we assumed that the effect of depth on epifaunal assemblages, if any, was unlikely to overshadow that of seaweed identity. Tissues from only those sporophytes that showed no, or the least pronounced, external signs of deterioration were collected (frond discoloration and sloughing in *D. viridis* began at the shallower depths in late July). Approximately 10 g of tissues (representing ~5% of the wet weight of the largest sporophytes in July) were cut with scissors from the distal end of each sporophyte. Tissues were placed immediately in rigid 4-L plastic containers (one piece per container) sealed under water to prevent the loss of epifauna. Containers were transported to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland where the content of each container was sieved. Each piece of seaweed was gently groomed to ensure all epifauna ≥250 µm were collected.

Vulnerability to grazing

To assess the vulnerability of *Desmarestia viridis*, *Desmarestia aculeata*, and *Agarum clathratum* to grazing and how it relates to the seaweed chemical makeup, we conducted two complementary experiments with intact sporophyte tissues (Experiment 1) and gelatinized extracts of grinded sporophyte tissues (Experiment 2). We used the green sea urchin as the grazer since it is the dominant consumer of the three seaweeds in eastern Canada [11,34,48], including at our study sites. Experiment 1 tested the hypothesis that in the absence of waves and currents, vulnerability (tissue loss)
to grazing of A. clathratum ( phenolics ) is lower than that of D. viridis (sulfuric acid), which in turn is lower than that of D. aculeata (no known chemical deterrent). We used the kelp Alaria esculenta, which is one of the most consumed seaweeds by S. droebachiensis in the northwestern Atlantic (NWA) [42,48], to test the hypothesis that vulnerability is highest in A. esculenta. We ran the experiment from 15 to 19 July, 2011 with tissues from five sporophytes in each species collected (via SCUBA diving) on 14 July at depths between 2 and 15 m at KP. One piece of ~30 g of tissues was cut with scissors from the apical parts (D. viridis and D. aculeata) or edges of the frond (A. clathratum and A. esculenta) of each sporophyte because in natural habitats urchins typically contact and consume these portions first. Pieces were placed in rigid, 4-L plastic containers (one piece per container) sealed under water to prevent contact of tissues with air at the surface. Tissues from only those sporophytes that showed no, or the least pronounced, external signs of deterioration were collected. Containers were transported to the OSC where their content was transferred to large holding tanks supplied with ambient (7.8±0.5 °C), flow-through seawater pumped in from the adjacent embayment, Logy Bay.

On 15 July (within less than 24 hours of seaweed collection), we cut two pieces of ~10 g (wet weight) from each original sample of ~30 g. Tissue weight was determined with precision with a balance (same model as above) in less than 20 s following emersion. Such inevitable exposure of D. viridis tissues to air had no effect on acidity [35]. One piece of each pair was transferred to either of 20, 75-L glass tanks supplied with flow-through sea water (1 L min⁻¹), and secured to the bottom with 12-g weights attached to the stipe or frond with a plastic cable tie. Ten urchins (3 to 6 cm in test diameter) picked from a pool of individuals collected on 7 July, 2011 at KP and starved for one week to standardize hunger levels, were introduced to each tank and allowed to graze seaweeds for 48 hours. Urchin density in each tank was generally equivalent to that in the barrens at our two study sites. Each piece of seaweed was reweighed at the end. Tissue loss to grazing was corrected for autogenic loss or gain, as determined by applying the procedures above to the second set of 10 g pieces of sporophytes over the following 48 hours, except no urchins were introduced to the tanks. We used the following equation to obtain the corrected tissue loss in each tank [49]:

\[ \text{Tissue loss} = [(T_o \times C_f / C_o) - T_f] \]

where \( T_o \) and \( T_f \) are the initial and final weights of seaweed tissues exposed to urchins, respectively, and \( C_o \) and \( C_f \) are the mean initial and final weights of the corresponding autogenic control, respectively.

The 20 tanks were grouped in five blocks of four tanks. Each tank in each block was randomly assigned one of the four seaweeds, for a total of five replicates per treatment. Each tank was surrounded by opaque canvas to control light conditions. Standardized light intensities were created with an incandescent, 100-watt light bulb (Soft White, General Electric) located at 45 cm above the water surface and controlled with dimmers on a 12-hour light/dark cycle. To increase the sample size, we reran the experiment, including the autogenic controls, twice from 19 to 23 and 23 to 27 July, 2011. We used tissues from two groups of 20 sporophytes (five in each of the four species in each group) collected on 18 and 22 July, and urchins collected on 12 and 14 July starved for one week. As in the first run, treatments in each of the two additional runs were reassigned randomly to tanks in each block to eliminate confounding effects of treatment and block, as well as tank and treatment. Therefore, each treatment was replicated 15 times in total. Temperature in one randomly chosen tank of each treatment was monitored with a temperature logger (≥0.5 °C, HOBO Pendant; Onset Computer Corporation) throughout the experiment.

Experiment 2 examined the unique contribution of seaweed chemical makeup to grazer deterrence. It also provided an indirect test for urchin-perceived differences in non-chemical traits among seaweeds in Experiment 1, including tissue toughness, which cannot be separated from the chemical makeup without altering the structural integrity of tissues. Experiment 2, therefore, tested the hypothesis that vulnerability to grazing depends primarily on the chemical makeup, with the same expectation in species ranking than in Experiment 1. As in Experiment 1, we used A. esculenta as a reference with the expectation that it is the most vulnerable of the four species. We ran the experiment from 27 to 31 July, 2011 with tissues from four sporophytes in each species collected (via SCUBA diving) on 25 July at depths between 2 and 15 m at KP. Procedures for collection, transportation, and maintenance of sporophytes in the laboratory were similar to those in Experiment 1. Water temperature during acclimation in the holding tanks was 8.8±0.5 °C.

On 27 July (within less than 48 hours of seaweed collection), we cut one piece of ~10 g (wet weight, measured with the same balance as above) from each original sample of ~30 g. Each piece weighed from 9.8 to 10.2 g and was crushed for 60 s in 100 mL of distilled water with a high-speed blender (model Magic Bullet; Homeland Housewares). The blend was suctioned through a 25-μm filter paper (model 1004-070; Whatman) to remove particulates. Eighty (90) mL of the filtrate (extract) were agitated and warmed on a heating plate (model VMS-C7 S1; VWR International) after adding 2 g of granulated agar (product BP1423-500; Fisher Scientific) to it. The resulting extract-agar solution was poured into two circular, 50-mL Petri dishes and allowed sufficient time to cool. Each solidified disk was removed from its dish and weighed with a balance (same model as above). We prepared eight additional disks, each made up of 40 mL of distilled water and 1 g of agar, to verify that urchins consumed, and hence were not repelled by, the raw agar medium without seaweed extracts (procedural control). One disk of each pair with seaweed extracts, and four disks with no extracts, were each transferred to one of 20, 75-L glass tanks supplied with flow-through sea water (1 L min⁻¹) and secured to the bottom with 5-g weights. Ten urchins (3 to 6 cm in test diameter) picked from a pool of individuals collected on 18 July, 2011 at KP and starved for one week, were introduced to each tank and allowed to graze disks for 48 hours. Each disk was reweighed at the end. Disk loss to grazing was corrected for artificial loss or gain as determined by applying the procedures above to the second set of disks over the following 48 hours in the absence of urchins. We used the same equation as in Experiment 1 to obtain the corrected disk loss in each tank.
Figure 2. Mean (±SE) Desmarestia viridis cover and urchin (Strongylocentrotus droebachiensis) density at 2 (A, B), 3 (C, D), 4 (E, F), and 8 (G, H) m depths, and averaged across all depths (I and J) at Bread and Cheese Cove (BCC) and Keys Point (KP) from 8 March to 13 October, 2011. Each data point in panels A to H is the average cover of D. viridis or urchin density in 10 quadrats (0.8 m² each) from two transects (20 to 25 m) at each depth. The seeming lack of standard error on some data points is due to low data variation. Solid and dashed horizontal lines are the average D. viridis cover and urchin density, respectively, from 8 April to 23 September (12 data points; see “Materials and methods” for the details of restriction of the statistical analyses to these points). The number in parentheses within each panel is the ratio of urchin density to D. viridis cover, also from 8 April to 23 September.

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Table 1. Summary of three-way ANOVA (applied to raw data) examining the effect of Site (BCC and KP), Depth (2, 3, 4, and 8 m), and sampling Date (12 dates) on the cover of Desmarestia viridis on the seabed from 8 April to 23 September, 2011 (see “Materials and methods” for the details of the two error terms).

| Source of variation             | df | SS      | MS       | F-value  | P         |
|---------------------------------|----|---------|----------|----------|-----------|
| Site                            | 1  | 2760.48 | 2760.48  | 130.43   | <0.0001   |
| Depth                           | 3  | 6385.47 | 2128.49  | 100.57   | <0.0001   |
| Date                            | 11 | 6162.65 | 560.24   | 26.47    | <0.0001   |
| Site × Depth                    | 3  | 2121.58 | 707.19   | 33.42    | <0.0001   |
| Site × Date                     | 11 | 1998.81 | 181.71   | 8.59     | <0.0001   |
| Depth × Date                    | 33 | 6847.43 | 207.50   | 9.80     | <0.0001   |
| Site × Depth × Date             | 33 | 3607.22 | 109.31   | 5.16     | <0.0001   |
| Error (among transect)          | 96 | 2031.71 | 21.16    | 0.19     |           |
| Error (within transect)         | 768| 84192.02| 109.63   |          |           |
| Corrected total                 | 959|         |          |          |           |

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a temperature logger (same model as above) throughout the experiment. Mean water temperature during trials was comparable between Experiment 1 (6.1 ± 0.2°C) and Experiment 2 (8.3 ± 0.1°C).

Statistical analysis

We used a three-way ANOVA with the factors Site (two study sites: BCC and KP), Depth (four sampling depths: 2, 3, 4, and 8 m), and sampling Date (12 sampling dates from 8 April to 23 September, 2011), to examine effects of site, depth, and time on the mean cover of Desmarestia viridis. Data acquired in March and October were excluded from the analysis (these data are nevertheless presented graphically) because mortality of D. viridis sporophytes in these months is highly variable and largely affected by factors other than urchin grazing [35]. Site was a fixed factor because the two sites were selected specifically for their locations (opposite sides of Bay Bulls), and bathymetry (gently sloping, rocky substrate). The analysis was applied to the raw data on individual frames taken from each pair of video transects at each depth (2 sites × 4 depths × 12 dates × 2 transects × 5 frames; n = 960). F-ratios were formed according to expected mean squares, as in Quinn and Keough [50]. We partitioned the error term into among and within transect variation and formed the F-ratios of the main effects and their interactions over the MS error among transect to avoid confounding effect of transects (Table 1) [50]. We then used simple linear regression analysis [51] to relate D. viridis cover to urchin density for each depth at each site. Each regression model (eight in total) was based on 12 data points. Each point was calculated from the 10 frames of each pair of transects for a given site, depth, and date. All regressions were applied to the raw data.

Values for density of epifaunal taxa on D. viridis, Desmarestia aculeata, and Agarum clathratum were 4th-root transformed prior to multivariate analysis because of differences of up to three orders of magnitude within and among the months sampled (February to October). We used non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrices calculated from these transformed data to visualize distances among epifaunal assemblages [52]. Inspection of the nMDS plot (see Results) from all monthly averages of samples in the three seaweeds [n = 7 to 10, except 3 for A. clathratum in February, for a total n = 221] directed the following approach to data analysis. We used a one-way analysis of similarity (ANOSIM) with the factor Seaweed (D. viridis, D. aculeata, and A. clathratum) to test for significant differences in assemblages among the three seaweeds (data pooled across all months, separated by seaweed) [52]. We also used a one-way ANOSIM with the factor Group (1 [data pooled across seaweeds for February to August] and 2 [data pooled across seaweeds for September and October]) to test for significant differences in assemblages between the first seven and last two months. The latter two ANOSIMs yielded significant differences, which we further investigated by analyzing each seaweed separately. Inspection of the nMDS plot of each seaweed from monthly samples [n = 80 (D. viridis), 77 (D. aculeata), and 64 (A. clathratum)] also directed the use of a one-way ANOSIM to test for significant differences in assemblages between Group 1 and Group 2 (same grouping as above). This was followed by a one-way analysis of similarity percentage (SIMPER) in each of Group 1 and Group 2 to assess the degree of similarity of assemblages among sampling events. Lastly, we used two one-way SIMPER analyses with the factor Seaweed (D. viridis, D. aculeata, and A. clathratum) to identify taxa important in distinguishing the assemblages associated with each seaweed, one for February to October (entire duration of the study) and one for September and October (when epifaunal abundance and diversity changed markedly, see Results).

We used two-way ANOVAs (one for each group of organisms) with the factors Seaweed (three seaweeds: D. viridis, D. aculeata,
and A. clathratum) and Month (nine levels: February to October) to examine temporal changes within and between seaweeds in the density of individuals in the six numerically dominant (i.e. with a peak density ≥900 individuals kg⁻¹ seaweed in any month) invertebrate taxa (Bivalvia, Gastropoda, Copepoda, Amphipoda, Polychaeta, and Isopoda), and fish and gastropod egg masses. Raw invertebrate taxa (Bivalvia, Gastropoda, Copepoda, Amphipoda, Polychaeta, and Isopoda), and fish and gastropod egg masses. Raw invertebrate taxa (Bivalvia, Gastropoda, Copepoda, Amphipoda, Polychaeta, and Isopoda), and fish and gastropod egg masses. Raw invertebrate taxa (Bivalvia, Gastropoda, Copepoda, Amphipoda, Polychaeta, and Isopoda), and fish and gastropod egg masses. Raw

We used three two-way ANOVAs with the factors Seaweed (four seaweeds: D. viridis, D. aculeata, A. clathratum, and A. excelsa) and Month (nine levels: February to October) to examine temporal changes in the Shannon diversity index ($H'$), Pielou's evenness index ($J'$), and species richness (S) of epifauna. The latter three analyses were applied to the raw data (n = 221). We used a one-way ANOVA with the factor Seaweed (four seaweeds: D. viridis, D. aculeata, A. clathratum, and A. excelsa) to examine differences in the proportion of seaweed tissue weight loss (relative to initial weight) to urchin grazing (Experiment 1). Likewise, we used a one-way ANOVA with a similar structure and a fifth level (the procedural control) within the factor Seaweed, to examine differences in the proportion of agar-embedded seaweed extracts weight loss (relative to initial weight) to urchin grazing (Experiment 2). We treated both analyses as a particular case of the generalized linear models with a binomial distribution of the response variable (ratio of final to initial weight) [54,55]. No binomial variation was detected. Prior to running these one-way ANOVAs, we used two three-way ANOVAs with the additional factors Run (each of three or five runs of replicates in Experiment 1 and Experiment 2, respectively) and Block (each of five or four blocks of tanks in each run in Experiment 1 and Experiment 2, respectively), to determine whether results differed between runs and blocks. There was no significant interactions between the factors Run and Block in both analyses (Factor = Run x Block, $\chi^2 = 2.12, p = 0.98$ [Experiment 1]; $\chi^2 = 0.78, p = 0.99$ [Experiment 2]). Therefore, we applied the two one-way ANOVAs to the pooled data from all runs in each experiment.

In all ANOVAs and regression analyses, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by examining the normal probability plot of the residuals [56]. To detect differences among levels within a factor, we used Tukey HSD multiple comparison tests (comparisons based on least-square means) [51]. A significance level of 0.05 was used. All analyses were conducted with JMP 7.0 and Minitab 16, except multivariate analyses, which were carried out with Plymouth Routines in Multivariate Ecological Research (PRIMER) v6.1.10.

### Results

#### Distribution and abundance of *D. viridis* and urchins

Patterns of *Desmarestia viridis* and urchin abundances at 2, 3, 4, and 8 m depths at BCC and KP from March to October, 2011 suggested a general increase in *D. viridis* cover and decrease in urchin density with increasing depth (Fig. 2). The highest mean cover of *D. viridis* ranged from 8% at 2 m to 21% at 8 m at BCC, and from 6% at 2 m to 25% at 8 m at KP. The highest mean urchin density ranged from 152 individuals m⁻² at 2 m to 70 individuals m⁻² at 8 m at BCC, and from 199 individuals m⁻² at 2 m to 54 individuals m⁻² at 8 m at KP (Fig. 2). In general, the overall cover (all depths pooled) of *D. viridis* at both sites: 1) increased steadily from March to mid-July; 2) decreased slowly to intermediate values from mid-July to late September; and 3) further decreased dramatically to extinction by mid-October (Table 1, Fig. 2). The latter decrease was when mean sea temperature peaked above 10°C [35] and urchins were below ~75 individuals m⁻² (Fig. 2). Yet, cover showed some differences between sites among depth, being generally higher at KP than BCC at all depths except at 2 m where it was similar between sites (Table 1, Fig. 2).

Regression analysis revealed significant, negative relationships explaining 33% to 48% of the variation between *D. viridis* cover and urchin density at 3 and 4 m at BCC, and at 3, 4, and 8 m at KP (no significant relationship for the other combinations of site and depth; Table 2, Fig. 3). The urchin density to *D. viridis* cover ratio is a proxy for *D. viridis* vulnerability to urchin grazing; the greater the ratio, the more urchins per unit of *D. viridis* cover, and hence higher the theoretical vulnerability [40]. This ratio was 1.4 times greater at KP (49.8) than BCC (34.4) at 2 m, yet between 1.8 and 3.1 times lower at KP than BCC at greater depths, i.e. a reverse difference between sites that increased from 3 to 8 m (Fig.

### Table 2. Results of simple linear regression analyses (applied to raw data) examining the relationship between *Desmarestia viridis* cover and urchin (Strongylocentrotus droebachiensis) density (x, urchins m⁻²) at 2, 3, 4, and 8 m depths at each of the two study sites, Bread and Cheese Cove (BCC) and Keys Point (KP) from 8 April to 23 September, 2011.

| Site | Depth (m) | Equation for *D. viridis* cover (%) | $R^2$ | $F_{(1,10)}$ | p |
|------|----------|------------------------------------|-------|-------------|---|
| BCC  | 2        | 7.00–0.031 x                        | 0.169 | 2.027       | 0.19 |
|      | 3        | 6.40–0.056 x                        | 0.482 | 9.29        | 0.012 |
|      | 4        | 7.92–0.088 x                        | 0.352 | 5.44        | 0.042 |
|      | 8        | 16.55–0.23 x                        | 0.253 | 3.89        | 0.096 |
| KP   | 2        | 2.70–0.00028 x                      | <0.0001 | <0.001      | 0.99 |
|      | 3        | 33.074–0.28 x                       | 0.407 | 6.85        | 0.026 |
|      | 4        | 12.044–0.17 x                       | 0.334 | 5.023       | 0.049 |
|      | 8        | 20.93–0.48 x                        | 0.453 | 8.27        | 0.017 |

Each regression is based on 12 data points. Each point is the mean *D. viridis* cover and corresponding mean urchin density calculated from the 10 frames of each pair of transects for a given site, depth, and date.

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These results, together with the 1.5-fold greater overall ratio (all depths pooled) at BCC than KP (Fig. 3), suggest that the theoretical vulnerability of *D. viridis* to urchin grazing was generally higher and more uniform across depth at BCC. At both sites, urchin grazing on *D. viridis* from March to July was limited to only a few scattered days when wave action, and hence the wave-induced sweeping motion of sporophytes, was virtually null. However, we witnessed dramatic increases in urchin grazing on *D. viridis* in early August, which persisted, especially at greater depths, until complete disappearance of *D. viridis* in October.

**Epifaunal assemblages**

Epifaunal assemblages on *Desmarestia viridis*, *Desmarestia aculeata*, and *Agarum clathratum* from 18 February to 9 October, 2011 at KP consisted of 41 taxa; 38 invertebrates and three chordates (all juvenile fish), in eight phyla (Table S1). To minimize data variation and skewing, we excluded: 1) chordates, which were highly mobile and often moved away while collecting seaweed tissues; 2) copepods, which were relatively abundant on *Desmarestia* spp. throughout the survey; and 3) juvenile crab *Hyas* sp. and nemertean *Tetrastemma* sp., which were rare, on average between zero and one individual per seaweed in any month. For practical reasons, fish (unidentified species) and gastropod (*Lacuna vincta*) egg masses were considered distinct epifaunal entities as opposed to real taxa. Masses (one count per mass) and the 35 remaining taxa were included in the following nMDS, ANOSIM, and SIMPER analyses.

Inspection of the nMDS plot from all monthly averages of samples suggested little difference in the direction of change of epifaunal assemblages among seaweeds throughout the study (Fig. 4A). There was some overlap among assemblages of the three seaweeds (ANOSIM: R = 0.411, p = 0.001) that appeared more pronounced between the two Desmarestiales than between *A. clathratum* and the two Desmarestiales (Fig. 4A). We also noted a marked difference in assemblages of the three seaweeds taken together between the first seven (February to August) and last two (September and October) months (ANOSIM: R = 0.704, p = 0.001; Fig. 4A). The sudden shift in assemblages from August to September coincided well with the end of a rapid (~2 weeks) increase in mean daily sea temperature, from ~6°C to ~12°C, and accelerating release of acid to the environment by, and decay of, *D. viridis* (Fig. 1) [35,36]. Differences in assemblages between the first seven (Group 1) and last two (Group 2) months were highest in *D. viridis* (ANOSIM: R = 0.736, p = 0.001), followed by...
D. aculeata (ANOSIM: R = 0.629, p = 0.001) and A. clathratum (ANOSIM: R = 0.508, p = 0.001) (Fig. 4 B-D). Assemblages in each seaweed exhibited higher similarity percentages in Group 2 than Group 1, ranging from 62% (D. aculeata) to 68% (A. clathratum), and from 44% (D. viridis) to 48% (A. clathratum), respectively.

SIMPER analysis of data from February to October (entire survey) showed that the snail Lacuna vincta contributed the most to similarities in epifaunal assemblages in the three seaweeds, from 23% (D. viridis and D. aculeata) to 34% (A. clathratum), followed by the caprellid amphipod Ischyrocerus anguipes and mussel Mytilus sp. (Table 3). Most of the dissimilarity between D. viridis and D. aculeata was caused by L. vincta, I. anguipes, the snail Margarites helicinus, and gammarid amphipod Stenothoe brevicornis, which were all more abundant (up to two orders of magnitude) on D. viridis (Table 3). Patterns of dissimilarity between D. viridis and A. clathratum were comparable, with the exception that Mytilus sp., fish egg masses, and the amphipods Pontogenia inermis and Calliopus laeviusculus were more abundant on D. viridis (Table 3). The polychaete Spirorbis borealis and bryozoan Lichenopora sp. were generally more abundant on A. clathratum than on the two Desmarestiales, thus also contributing to the majority of the differences in epifaunal assemblages among seaweeds. SIMPER analysis of data in September and October (when seaweeds formed distinct clusters) identified L. vincta as the numerically dominant species in D. viridis, Mytilus sp. in D. aculeata, and S. borealis and Lichenopora sp. in A. clathratum.

The density of bivalves, gastropods, copepods, polychaetes, and egg masses (gastropods and fish) differed among seaweeds over time, as shown by the significant interaction between the factors Seaweed and Month (two-way ANOVAs, Table 4). Although copepods were generally more abundant (up to one order of magnitude in most months) than amphipods, these were the only two common taxa from February to October on D. viridis, and to a lesser extent on D. aculeata (they were largely absent from A. clathratum) (Fig. 5). There was a remarkable increase from virtual absence prior to September, to >150 000 gastropod and >230 000 bivalve recruits kg$^{-1}$ of D. viridis and D. aculeata in October, respectively. Likewise, polychaetes remained low on the two Desmarestiales throughout the survey but increased by three orders of magnitude on A. clathratum from August to September (Fig. 5). Isopod density also increased significantly in the last two months regardless of seaweed (Table 4, Fig. 5). Gastropod eggs...
generally increased in also differed significantly among seaweeds over time (Table 5). It generally peaked between 0.7 and 0.9 from May to June in all seaweeds (Fig. 6). Evenness in the two Desmarestiales decreased rapidly, by at least three times, in the last two months, whereas it decreased only slightly in \textit{D. viridis} in August and September, and again in \textit{A. clathratum} in October, when their density was twice higher than in any other month (Fig. 5). \textit{Desmarestia viridis} was the preferred seaweed for deposition of eggs by fish; egg masses increased by two orders of magnitude from April to May, followed by a steady monthly decline to near absence in September (Fig. 5).

The Shannon diversity index differed significantly among seaweeds over time (Table 5). It was generally highest in \textit{A. clathratum} from February to May, in \textit{D. aculeata} in June and July, in \textit{D. viridis} in August and September, and again in \textit{A. clathratum} in October (Fig. 6). There was a two-fold increase in diversity from March to April in all seaweeds, four-fold decrease from August to October in the two Desmarestiales, and two-fold decrease from April to October in \textit{A. clathratum} (Fig. 6). The Pielou’s evenness index also differed significantly among seaweeds over time (Table 5). It generally peaked between 0.7 and 0.9 from June to August in all seaweeds (Fig. 6). Evenness in the two Desmarestiales decreased rapidly, by at least three times, in the last two months, whereas it decreased only slightly in \textit{A. clathratum} (Fig. 6). Declines in diversity and evenness from August to October were largely caused by marked increases in recruits of gastropods (\textit{L. vincta} and \textit{Margarites helicinus}) in \textit{D. viridis}, and bivalves (\textit{Mytilus} sp. and \textit{Hiaticulenta arctica}) in \textit{D. aculeata}. Species richness also differed significantly among seaweeds over time (Table 5). It generally increased in \textit{D. viridis} from \(~4\) to 12 species from March to September (LS means, \(p<0.001\)) and decreased in \textit{D. aculeata} from \(~13\) to 7 species from April to September (LS means, \(p<0.001\)) (Fig. 6). Richness was less variable throughout in \textit{A. clathratum}, ranging from \(~5\) (August) to 8 (February to April) species (Fig. 6).

Vulnerability to grazing

Analysis of data from Experiment 1 showed that the loss of sporophyte tissues to urchin grazing was similar between \textit{Desmarestia viridis} and \textit{Desmarestia aculeata} and between \textit{D. viridis} and \textit{Agarum clathratum}, and at least 59\% less in any of these three seaweeds compared to \textit{Alaria esculenta} (one-way ANOVA [generalized linear model]: Factor = Seaweed, \(\chi^2 = 12.01, p = 0.0074, \text{Fig. 7}\)). Analysis of data from Experiment 2 with agar-embedded extracts of grinded sporophyte tissues showed a slightly different outcome whereby grazing on \textit{D. viridis} was significantly lower than on \textit{D. aculeata} but similar to \textit{A. clathratum} (one-way ANOVA [generalized linear model]: Factor = Seaweed, \(\chi^2 = 11.64, p = 0.020, \text{Fig. 7}\)). As in Experiment 1, grazing was highest on \textit{A. esculenta}, followed by \textit{D. aculeata} with a difference of 27\% between the two (\(\chi^2 = 10.81, p = 0.001\)). The loss of agar-embedded extracts of \textit{D. viridis} and \textit{A. clathratum} was similar to that of the procedural control with no seaweed extracts (Fig. 7), supporting the notion that the chemical makeup of both seaweeds was not particularly attractive to urchins.

**Table 3.** Epifauna accounting for \(\geq 5\%\) of the similarity within each of the three seaweed species (diagonal) and for \(\geq 5\%\) of the dissimilarity between two seaweeds as determined by SIMPER analysis of data from February to October, 2011. 

|                | \textit{Desmarestia viridis} | \textit{Desmarestia aculeata} | \textit{Agarum clathratum} |
|----------------|-----------------------------|-------------------------------|----------------------------|
| \textit{Desmarestia viridis} | Lacuna vincta (23.6)         |                               |                            |
| \textit{Ischyrocerus anguipes} | (23.3)                      |                               |                            |
| \textit{Pontogoneia inermis}  | (7.1)                       |                               |                            |
| \textit{Mytilus sp.}          | (6.5)                       |                               |                            |
| \textit{Calliope laeviusculus} | (6.1)                       |                               |                            |
| Fish egg masses              | (5.5)                       |                               |                            |
| \textit{Desmarestia aculeata} | Mytilus sp. (10.7)          | \textit{L. vincta} (23.3)     |                            |
| \textit{L. vincta*}           | (8.2)                       | \textit{Mytilus sp.} (23.1)    |                            |
| \textit{I. anguipes*}         | (7.9)                       | \textit{C. laeviusculus} (11.8)|                            |
| \textit{P. inermis}           | (6.5)                       | \textit{I. anguipes} (8.0)     |                            |
| \textit{C. laeviusculus}      | (6.2)                       | \textit{M. helicinus} (5.4)    |                            |
| \textit{Margarites helicinus*} | (5.7)                       |                               |                            |
| \textit{Stenothoe brevicornis*}| (5.6)                       |                               |                            |
| \textit{Agarum clathratum}    | \textit{L. vincta} (9.0)    | \textit{Mytilus sp.*} (14.9)  | \textit{L. vincta} (33.5)  |
| \textit{P. inermis*}          | (8.2)                       | \textit{C. laeviusculus*} (8.1)| \textit{I. anguipes} (23.8)|
| \textit{I. anguipes*}         | (7.4)                       | \textit{C. laeviusculus*} (6.4)| \textit{S. borealis} (18.5)|
| \textit{C. laeviusculus*}     | (7.0)                       | \textit{S. borealis} (6.2)    | \textit{Mytilus sp.} (7.3) |
| \textit{Mytilus sp.*}         | (6.8)                       | \textit{Lichenopora sp.} (5.2)| \textit{Lichenopora sp.} (6.8)|
| \textit{M. helicinus*}        | (5.8)                       | \textit{M. helicinus} (5.1)   | \textit{M. helicinus} (6.2) |
| \textit{S. brevicornis*}      | (5.6)                       | \textit{L. vincta*} (5.1)     |                            |
| Fish egg masses              | (5.4)                       |                               |                            |
| \textit{Spirorbis borealis}   | (5.1)                       |                               |                            |

For each grouping, epifaunal taxa are listed in order of decreasing percentage contribution (bracketed values) to similarity or dissimilarity among seaweed. The density of epifauna with an asterisk is higher on the seaweed given at the top of the table.

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were consistently uncommon on \textit{D. viridis}. They were predominately deposited on \textit{A. clathratum} in May and June, on \textit{D. aculeata} in July and August, and again on \textit{A. clathratum} in October, when their density was twice higher than in any other month (Fig. 5). \textit{Desmarestia viridis} was the preferred seaweed for deposition of eggs by fish; egg masses increased by two orders of magnitude from April to May, followed by a steady monthly decline to near absence in September (Fig. 5).
This study uncovers biological, ecological, and functional aspects of the annual, brown seaweed *Desmarestia viridis* that advocate fundamental changes to the study of community shifts in shallow, rocky ecosystems in eastern Canada.

### Table 4. Summary of two-way ANOVAs (applied to raw data) examining the effect of Seaweed (*Desmarestia viridis*, *Desmarestia aculeata*, and *Agarum clathratum*) and Month (each of nine sampling months: February to October, 2011) on the density of individuals in the six numerically dominant invertebrate taxa, and gastropod (*Lacuna vincta*) and fish (unknown species) egg masses at Keys Point (see caption of Fig. 5 for species in each taxa).

| Taxa          | Source of variation | df | MS       | F-value | p     |
|---------------|---------------------|----|----------|---------|-------|
| Bivalvia      | Seaweed             | 2  | 231405   | 1.70    | 0.21  |
|               | Month               | 8  | 179180   | 1.11    | 0.41  |
|               | Seaweed × Month     | 16 | 164396   | 4.69    | <0.01 |
|               | Error               | 194| 35018    |         |       |
|               | Total               | 220|          |         |       |
| Gastropoda    | Seaweed             | 2  | 153513   | 1.07    | 0.37  |
|               | Month               | 8  | 196991   | 1.17    | 0.37  |
|               | Seaweed × Month     | 16 | 170934   | 3.67    | <0.01 |
|               | Error               | 194| 46623    |         |       |
|               | Total               | 220|          |         |       |
| Copepoda      | Seaweed             | 2  | 8302.59  | 19.40   | <0.01 |
|               | Month               | 8  | 2059.23  | 4.81    | <0.01 |
|               | Seaweed × Month     | 16 | 2115.64  | 4.94    | <0.01 |
|               | Error               | 194| 427.92   |         |       |
|               | Total               | 220|          |         |       |
| Amphipoda     | Seaweed             | 2  | 263.85   | 20.35   | <0.01 |
|               | Month               | 8  | 36.92    | 2.85    | <0.01 |
|               | Seaweed × Month     | 16 | 13.49    | 1.04    | 0.42  |
|               | Error               | 194| 12.97    |         |       |
|               | Total               | 220|          |         |       |
| Polychaeta    | Seaweed             | 2  | 6.33     | 1.79    | 0.19  |
|               | Month               | 8  | 5.82     | 1.42    | 0.26  |
|               | Seaweed × Month     | 16 | 4.17     | 3.36    | <0.01 |
|               | Error               | 194| 1.24     |         |       |
|               | Total               | 220|          |         |       |
| Isopoda       | Seaweed             | 2  | 0.28     | 1.01    | 0.38  |
|               | Month               | 8  | 0.68     | 2.66    | 0.043 |
|               | Seaweed × Month     | 16 | 0.25     | 0.71    | 0.79  |
|               | Error               | 194| 0.36     |         |       |
|               | Total               | 220|          |         |       |
| Fish egg masses | Seaweed          | 2  | 0.29     | 3.51    | 0.052 |
|                | Month               | 8  | 0.11     | 1.18    | 0.37  |
|                | Seaweed × Month     | 16 | 0.098    | 4.16    | <0.01 |
|                | Error               | 194| 0.024    |         |       |
|                | Total               | 220|          |         |       |
| Gastropod egg masses | Seaweed  | 2  | 0.032    | 1.62    | 0.22  |
|                     | Month               | 8  | 0.017    | 0.81    | 0.61  |
|                     | Seaweed × Month     | 16 | 0.022    | 1.75    | 0.040 |
|                     | Error               | 194| 0.012    |         |       |
|                     | Total               | 220|          |         |       |

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### Discussion

The need to consider a transient community state: "*Desmarestia bed"

We showed that *D. viridis* can form a transient canopy from March to October over bare or coralline seaweed-encrusted rocky substratum within the 2-to-8 m depth range in Bay Bulls, Newfoundland. The canopy covered, on average, ~25% of the
seabed in 2011, and up to ~90% in 2012 and 2013. Interestingly, this depth range is also where destructive grazing of kelp beds by urchin fronts typically occur in eastern Canada [28,30]. The initiation of the *D. viridis* canopy in March and April was when significant wave height and sea temperature were nearing annual maxima and minima, respectively, and urchin displacement and grazing were greatly limited. During the same period, *D. viridis* sporophytes exhibited relatively high mortality (up to 40% biweekly) and growth (~4 to 6% daily increase in length), and the intracellular acidity also increased rapidly [35,36]. These observations suggest that recruits depend on the severity of the physical environment to escape grazing while they invest resources in the establishment of *D. viridis*, as implied by between- and within-site differences in *D. viridis* cover, and inverse relationships between *D. viridis* cover and urchin density at 3 and 4 m at BCC, and at 3, 4, and 8 m at KP.

In a concurrent study, we found that significant wave height was generally higher at KP than at BCC from March to early July and from mid-August to October (no difference between sites from early July to mid-August) [35]. These patterns and the generally decreasing water flows from 2 to 8 m that we perceived during our dives at both sites, may partly explain the observed site- and depth-specific differences in *D. viridis* and urchin abundances. This suggestion is corroborated by the experimental demonstration that moderate, wave-induced sweeping motion of *D. viridis* sporophytes provides mechanical protection against urchin grazing up to a threshold of 136 to 194 urchins m\(^{-2}\) [40]. Accordingly, we think that 1) high wave action at 2 m at BCC and KP largely prevented urchins from moving and grazing fast-sweeping *D. viridis* sporophytes; 2) moderate wave action at 3 and 4 m at BCC, and from 3 to 8 m at KP, provided *D. viridis* with efficient mechanical protection against urchin grazing at relatively low urchin densities; and 3) low wave action at 8 m at BCC did not induce sufficient sweeping in *D. viridis*, which was readily grazed by urchins, even at low densities.

As noted above, we witnessed the establishment of a virtually continuous *D. viridis* canopy in 2012 and 2013 throughout much of the 3-to-8 m depth range at our two study sites. This phenomenon certainly is not unique to our study sites. Canopies of *D. viridis* frequently develop in urchin barrens, often right below the lower edge of kelp beds, throughout the extensive (7542 km\(^2\)) coast of Newfoundland and Labrador ([38,57,58,59], P. Gagnon personal observations). This is also the case in the northern Gulf of St. Lawrence [11,28,33,42] and Nova Scotia [30,31]. In these regions, the cover of *D. viridis* often momentarily exceeds 70% on vertical surfaces (e.g. boulders and rock walls), while nearing 100% on horizontal surfaces [see aforementioned references]. Using data from 41 stations at 26 sites along the coasts of northeastern Newfoundland, southern Labrador, and eastern Quebec, Asley and Hayek [57] show that *D. viridis* can form up to 39% of the total seaweed biomass within the 2.5-to-10 m depth range. They also show that *D. viridis* and the kelp *Agarum clathratum* overwhelmingly dominate the lower half to two-thirds of the subtidal macrophyte zone in the Newfoundland-Labrador-Quebec region [57], which Gagnon et al. [34] further corroborate.

Therefore, we propose that *D. viridis* recruitment, especially in years of higher productivity, results in the creation of an ephemeral, or transient, community state termed “*Desmarestia bed*”, adding to the kelp bed and urchin barren states in eastern Canada. Several studies in eastern Canada and the Aleutian (northern Pacific) and Svalbard (Arctic Ocean) archipelagos suggest that *D. viridis* sporophytes function as “giant sweepers” that retard or prevent the formation of urchin fronts at the lower edge of kelp beds [40,43,48,60]. In eastern Canada, the predictable annual outbreak and die-off of *D. viridis* sporophytes could then represent a cyclical, natural disturbance that disrupts urchin-kelp interactions, ultimately allowing kelp beds to re-establish over the barrens. Longer-term studies of the relationships between the physical environment, *D. viridis* and urchin abundances, and the frequency and extent to which kelp beds re-establish over barrens colonized or not by *Desmarestia beds*, are needed to determine the importance of *D. viridis* to ecosystem resilience [61,62].

The need to elevate *D. viridis* to the rank of foundation species

We showed that the quick development of *Desmarestia* beds in urchin barrens creates biological structure for major recruitment pulses in characteristic invertebrate and fish assemblages. Most recruitment pulses measured at KP (and observed at BCC), including the herbivorous snail *Lucana vinca* from quasi-absent to >150 000 recruits kg\(^{-1}\) *D. viridis*, were restricted to only a few weeks in August and September. At this time mean sea temperature fluctuated around the lethal 12°C for *D. viridis*: the sulfonic acid was released from *D. viridis* to the environment, the sporophytes entered the senescence phase, and urchins began to massively graze *D. viridis* ([35,36], this study). Such annual, synchronous decay in *D. viridis* also occur throughout the rest of Newfoundland and Labrador, the northern Gulf of St. Lawrence, and Nova Scotia, [11,30,57], P. Gagnon unpublished data). It suggests complex, environmentally- (largely temperature) driven cascades. In this case, a self-defended, fast-growing seaweed suddenly turns into a highly vulnerable prey for numerically dominant benthic (e.g. urchin) and epifaunal grazers (e.g. *L. vinca*, see below). We found that fish egg masses occurred almost exclusively on *D. viridis*, whereas *L. vinca* and other invertebrates deposited eggs or recruited almost exclusively on the two longer-lived, perennial seaweeds *Desmarestia aculeata* and *A. clathratum*. These patterns further suggest ontogenetic partitioning in the use of habitat-forming species among invertebrates.

By forming large aggregations relative to the size of the organisms that they facilitate, marine foundation species markedly increase environmental heterogeneity, often transforming a two-dimensional, featureless landscape into a complex, three-dimensional structure [18]. Our study supports the notion that *D. viridis*, and perhaps *D. aculeata* and *A. clathratum*, facilitate recruitment
shows that Be´gin et al. [33], the present study draws opposite conclusions. It
sporophytes can actually be heavily
A. clathratum
Margarites
sporophytes provide density-
U. pinnatifida
preferred kelp Alaria esculenta. That the two experiments provided fairly similar results with regards to the ranking of seaweeds, suggests that in the absence of waves and currents vulnerability to grazing in D. viridis and A. clathratum, and to a lesser extent in D. aculeata, depends primarily on the chemical makeup. Morphological or structural differences [e.g. tissue toughness] if any, were not sufficient to cause the observed differences in grazing. These experiments were not designed to identify the chemical compounds at the origin of the observed differences in grazing. Nevertheless, results of the two experiments taken together indicate that the chemical makeup of D. viridis and A. clathratum helps retard urchin grazing compared to D. aculeata and A. esculenta. They corroborate other studies that suggest that the sulfuric acid in D. viridis, and phenolics in A. clathratum, act as chemical deterrents to grazing [11,40,43–45]. Further research is needed to determine the relative importance of the chemical makeup and wave-induced sweeping motion of fronds to the survival of these seaweeds in urchin barrrens.

A novel empirical model of ecological interactions for D. viridis
Several studies have helped elevate the ecological significance of unusual morphology and acid (H₂SO₄) production of D. viridis in eastern Canada. The wave-induced sweeping motion and chemical makeup of D. viridis sporophytes provide density-dependent protection against grazing [40]. This natural protection ultimately enables the species to form extensive canopies in urchin barrrens [28,30,57], this study] that enhance the recruitment of other seaweeds [11]. The constitutive and irreversible accumulation of acid as sporophytes grow from recruits to adults inevitably culminates into dramatic mass releases of acid and die offs, when mean sea temperature rises above 12 °C (the species is intolerant to temperature above ~12°C) [35,36]. These and the present studies

| Source of variation | df | MS   | F-value | p     |
|---------------------|----|------|---------|-------|
| Diversity (H')      |    |      |         |       |
| Seaweed             | 2  | 0.016| 0.15    | 0.85  |
| Month               | 8  | 3.85 | 37.83   | <0.01 |
| Seaweed × Month     | 16 | 0.70 | 6.90    | <0.01 |
| Error               | 194| 0.10 |         |       |
| Total               | 220|      |         |       |
| Evenness (J')       |    |      |         |       |
| Seaweed             | 2  | 0.15 | 10.78   | <0.01 |
| Month               | 8  | 0.99 | 71.31   | <0.01 |
| Seaweed × Month     | 16 | 0.13 | 9.60    | <0.01 |
| Error               | 194| 0.014|         |       |
| Total               | 220|      |         |       |
| Species richness (S)|    |      |         |       |
| Seaweed             | 2  | 62.20| 18.58   | <0.01 |
| Month               | 8  | 19.15| 5.72    | <0.01 |
| Seaweed × Month     | 16 | 41.16| 12.29   | <0.01 |
| Error               | 194| 3.35 |         |       |
| Total               | 220|      |         |       |

Table 5. Summary of two-way ANOVAs (applied to raw data) examining the effect of Seaweed (Desmarestia viridis, Desmarestia aculeata, and Agarum clathratum) and Month (each of nine sampling months: February to October, 2011) on the Shannon diversity index (H'), Pielou’s evenness index (J'), and species richness (S), of seaweed epifauna at Keys Point.

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provide the empirical evidence needed to propose a novel model of ecological interactions for the species that can serve as a foundation for future studies of community shifts in rocky subtidal ecosystems in eastern Canada.

According to this model (Fig. 8), small (\(10\) to \(15\) cm in length) \(D.\) viridis recruits exhibit highest specific growth rates (SGR) in early March, when the cover and amplitude of the wave-induced sweeping motion are lowest, and mortality and grazing by urchins are moderate. As recruits grow to adult-size (\(50\) to \(60\) cm) sporophytes in July, SGR and intracellular pH decrease (the latter being indicative of sulfuric acid production and accumulation) at a decelerating rate. Mortality decreases as a result of increasing cover and sweeping, which further reduces urchin grazing. The rapid increase in mean sea temperature in June and July to above \(10\)°C marks the onset of mass release of acid to the environment (as shown by increasing pH), and senescence (as shown by sudden declines in cover and SGR) until all sporophytes disappear in October. The sudden increase in urchin grazing on decaying sporophytes in August and September precipitates mortality and decline in cover. Throughout its existence as a sporophyte, \(D.\) viridis provides a suitable surface for deposition of eggs by fish, as well as to distinct assemblages of mobile epifauna throughout the senescence phase. These patterns of variation mainly reflect conditions at the two study sites in the present study. Patterns may change slightly with location because of the importance of the thermal environment to the biology of \(D.\) viridis (see above) and latitudinal variation in sea temperature in eastern Canada [35,63–65].

Summary and future research directions

The present and related studies demonstrate the ability of \(D.\) viridis to form relatively large (10s to 100s of m\(^2\)) canopies, namely \(D.\) beds, in shallow rocky ecosystems in eastern Canada. These canopies, together with those of two co-occurring, longer-lived seaweeds in urchin barrens, \(D.\) aculeata and \(A.\) clathratum, can host high abundances of recruits, juveniles, and adults in at least 41 invertebrate and fish taxa, indicating a strong foundational potential. The annual resurgence and high spatial and temporal predictability of \(D.\) beds and associated epifauna represent a third community state adding to the much more studied kelp bed and urchin barrens states. In light of our findings and the patterns they suggest, we propose that canopy-forming seaweeds in so-called urchin barrens play an underappreciated role in the overall ecosystem dynamics. In particular, we think that the traditional view that shallow rocky subtidal ecosystems in eastern Canada alternate between two community states, kelp beds and urchin...
The dominant environmental controls (temperature and urchin grazing) are shown as open rectangles and dashed lines, *D. viridis* traits (cover/sweeping, specific growth rate [SGR], pH, and mortality) as gray ellipses and solid lines, and epifauna (fish eggs, bivalves [B], herbivorous gastropods [G], and predatory polychaetes [P] and isopods [I]) as solid rectangles and dotted lines. Numbers above rectangles and ellipses are the sources of information for temporal variation: 1 [present study]; 2 [28]; 3 [30]; 4 [35]; 5 [57]; 6 [36] (see “Discussion” for a detailed description of the model).

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### Supporting Information

#### Table S1 Mean density (individuals [or egg masses] kg⁻¹ seaweed) of invertebrates and fish on *Desmarestia viridis*, *Desmarestia aculeata*, and *Agarum clathratum* sporophytes sampled monthly from 10 February to 9 October, 2011. Standard error is given below each mean in *italics.*

| Species               | Jan  | Feb  | Mar  | Apr  | May  | Jun  | Jul  | Aug  | Sep  | Oct  |
|-----------------------|------|------|------|------|------|------|------|------|------|------|
| Fish eggs             |      |      |      |      |      |      |      |      |      |      |
| Mean density          |      |      |      |      |      |      |      |      |      |      |
| (individuals/kg seaweed) |      |      |      |      |      |      |      |      |      |      |
| SGR                   |      |      |      |      |      |      |      |      |      |      |
| pH                    |      |      |      |      |      |      |      |      |      |      |
| Mortality             |      |      |      |      |      |      |      |      |      |      |

(DOCX)

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### Author Contributions

Conceived and designed the experiments: CB PG. Performed the experiments: CB PG. Analyzed the data: CB PG. Contributed reagents/materials/analysis tools: PG CB. Wrote the paper: CB PG.

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