

# Regional differences and linkage between canopy structure and community composition of rockweed habitats in Atlantic Canada

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**Abstract** *Ascophyllum nodosum* (rockweed) is a dominant, habitat-forming seaweed on intertidal rocky shores in the North Atlantic and commercially harvested in Canada, Maine and Europe. Rockweed plant structure varies regionally, and several morphotypes have been identified in Atlantic Canada alone. Yet the regionality of canopy structure, associated species communities and the link between the two have not been well understood. Using large-scale field surveys and multivariate statistical approaches, we report distinct canopy structures between sites in southwest Nova Scotia and southwest New Brunswick, the two major rockweed harvesting areas in Atlantic Canada, as well as distinct associated community composition. We then demonstrate significant links between canopy and community structure. Importantly, plant and canopy structure, including length, circumference and density, were much better predictors of associated community structure than rockweed biomass, which is often used for single-species monitoring. Adding region or site as predictors further improved model fits. Therefore, measuring plant or canopy

structure would strongly improve insight regarding ecosystem changes. Moreover, incorporating information about regional differences in canopy structure and the dependence of associated communities on those canopies is critical for spatially refined, ecosystem-based management of the rockweed harvest.

## Introduction

Rockweed (*Ascophyllum nodosum*) is a significant ecological component of intertidal rocky shore communities along North Atlantic coasts. In Nova Scotia (NS) and southwest New Brunswick (NB), Canada rockweed and other fucoids cover 80–90% of the intertidal zone maintaining high biomass and primary productivity (Chopin et al. 1996; DFO 1998; Vadas et al. 2004; Worm and Lotze 2006). Thus, rockweed plays important roles in biochemical cycles by storing carbon and cycling nutrients (Schmidt et al. 2011). With their long fronds and branching structure, rockweed plants also create a three-dimensional, forest-like canopy that provides habitat and food for associated plant and animal communities, at both high and low tides (Schmidt et al. 2011; Seeley and Schlesinger 2012). A variety of fish and invertebrate species, some of commercial importance and others of conservation interest, use rockweed canopies (Larsen 2010; Schmidt et al. 2011; Seeley and Schlesinger 2012; Watt and Scrosati 2013a, b).

In addition to its ecological importance, rockweed has also been a commercially important seaweed in NS since the 1960s, for production of alginates, fertilizer and animal feed (Chopin et al. 1996). In NB, commercial harvest of rockweed began in 1995. Considerable monitoring and research efforts have been made to study changes in rockweed plants themselves in response to harvesting; however,

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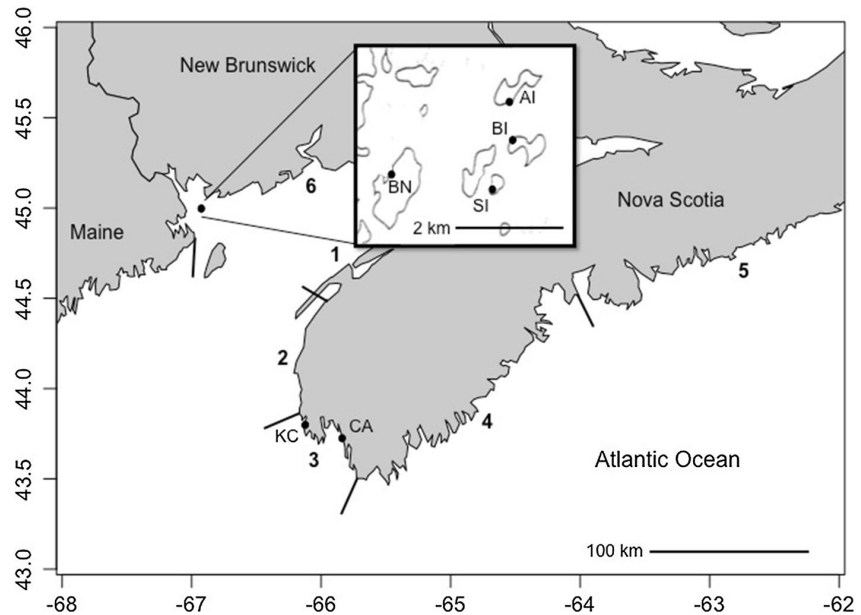
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**Fig. 1** Study sites in southwest Nova Scotia: Central Argyle (CA), Kelley's Cove (KC) and southwest New Brunswick: Adam Island (AI), Barnes Island (BI), Beans Island (BN) and Simpson Island (SI) surveyed in summer 2012. Management areas for *A. nodosum* are indicated as: (1) Annapolis Basin; (2) St. Mary's Bay; (3) Lobster Bay; (4) South shore; (5) Eastern shore; and (6) Southern New Brunswick. Higher concentrations of *Asco-phylum* biomass are found in Lobster Bay (area 3), the region of the South shore adjacent to Lobster Bay (area 4) and the western region of Southern New Brunswick (area 6) (Ugarte and Sharp 2012)



the effects of rockweed harvesting on the overall canopy or habitat structure and the associated fauna and flora have received much less attention (DFO 1998; Rangeley and Davies 2000).

Management of rockweed varies by Canadian province, and new regulations for rockweed harvesting have recently been developed for Maine, USA (Seeley and Schlesinger 2012; DMR 2013). Notably, differences in management regimes across political boundaries are unrelated to the biological makeup or hydrographic conditions of rockweed habitats in different regions. Rockweed beds, similar to other vegetated habitats, have been shown to shift in structure at regional scales because of environmental factors, such as temperature, salinity, substrate type and wave exposure (Baardseth 1970; Keser et al. 1981, 2005; Sharp 1987; McCook and Chapman 1993), as well as in response to human impacts such as nutrient exposure (White et al. 2011).

Despite the phenotypic plasticity of rockweed, few studies have examined whether community composition of rockweed habitats varies by region (see Heaven and Scrosati 2008 for an exception), even though regional differences in community composition are well documented in terrestrial habitats (e.g., Karr and Roth 1971; Wilson 1974; Halaj et al. 2000; Hinsley et al. 2009). Moreover, given the dependence of associated fauna and flora on rockweed habitat (Johnson and Scheibling 1987; Bertness et al. 1999; Ingólfsson and Hawkins 2008), we hypothesize that changes in community composition might be associated with changes in canopy structure at middle elevations surveyed where rockweed canopies modulate extreme

understory temperatures during low tides (Watt and Scrosati 2013a, b). Determining the linkages between canopy structure and community composition will provide insight into how structural changes in foundation species, and thus canopy or habitat structure, might affect associated flora and fauna.

The goals of our study were to (1) quantify variation in the canopy structure and community composition of rockweed habitats at representative sites in southwest Nova Scotia and southwest New Brunswick and (2) examine the linkages between the two. Large-scale field surveys and a multivariate statistical approach were used to address these objectives. Knowledge of regional differences and the linkage between canopy structure and community composition could help inform a spatially refined and ecosystem-based approach to the management of the rockweed harvest. This knowledge is particularly relevant at this time given that industry is currently expanding their harvest (Seeley and Schlesinger 2012).

## Methods

### Study sites

In July 2012, intensive field surveys were performed at six study sites within two major areas of rockweed harvesting: southwest Nova Scotia (NS) and southwest New Brunswick (NB) (Fig. 1, Ugarte and Sharp 2012). In collaboration with Acadian Seaplants Limited (ASL), the main harvester in those regions, we sampled all sites before the annual

rockweed harvest took place (pers. comm., R. Ugarte). All sites had rockweed beds with consistent cover over at least 150 m of shoreline. We selected two sites in NS: Kelley's Cove (KC) and Central Argyle (CA), which are commercially harvested on a regular basis (Fig. 1). In NB, we selected four study sites in the outer Bay of Fundy near Deer Island, with two sites [Adam (AI) and Bean Islands (BN)] subject to a regular commercial rockweed harvest and another two sites [Barnes (BI) and Simpson Islands (SI)] established as harvest exclusion zones (Fig. 1). When only the harvested sites from NB were included in the analyses, the differences in canopy and community structure between the NS and NB sites were the same as when the additional nonharvested NB sites were included; these additional sites were, therefore, used to include a wider range of sites. BN and SI were proximate to finfish aquaculture sites. All four NB sites were previously classified in the same geographic and hydrographic region (MacKay et al. 1979a, b, c; Robinson et al. 1996) and as having the same narrow passage geomorphology (Buzeta and Singh 2008). All six sites had gravel-boulder substrate. Regulations for the rockweed harvest are similar between NS and NB (see Seeley and Schlesinger 2012) with up to 25% of harvestable rockweed biomass removed from NS beds and 17% removed from NB beds annually.

## Sampling methods

### Environmental parameters

To gain long-term insight into environmental conditions in the two study regions, seasonal sea surface temperature (SST), salinity, chlorophyll *a* (Chl *a*) and nutrient data were acquired from nearby monitoring stations: the Gulf of Maine North Atlantic Time Series (GNATS) (Balch et al. 2008, 2012; <http://seabass.gsfc.nasa.gov/>) data set for Yarmouth, NS and the Department of Fisheries and Ocean (DFO) Buoy Prince 5 directly outside Passamaquoddy Bay, NB (Drinkwater 1987; <http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/hydro/station/yearly-annuelle-eng.html?a=2andy=2013>) as well as SST for Yarmouth, NS and St. Andrews, NB from Advanced Very High Resolution Radiometer (AVHRR) satellite data from NOAA (<http://www.seatemperature.org/north-america/canada/nova-scotia/>).

To directly compare the six study sites, we recorded water temperatures and collected three 1 l water samples during the incoming tide, at high tide and during the outgoing tide with a pipe sampler to capture an average sample of the water column. We repeated the temperature measurements and water collection in August, approximately one month after surveys were conducted in July, in order to obtain better average summer values for each study site.

For each 1 l water sample, three subsampled replicates were analyzed to quantify Chl *a* concentrations and total particulate matter (TPM). For each Chl *a* replicate, 100 ml of water was filtered, in the dark, through a Whatman GF/F (25 mm) filter using a 50-ml syringe and filter holder. The filters were then placed in labeled cryovials and transferred to a liquid nitrogen-cooled Dewar. In the laboratory, filters were transferred to vials containing 10 ml of cooled acetone and were stored in the dark at -20 °C for 24 h. A Turner fluorometer was used to measure the voltage difference associated with each replicate and an acetone blank following the Welschmeyer (1994) technique.

GF/F filters used for the TPM replicates were initially washed to remove impurities and dried for 6 h at 450 °C before being weighed (pre-ash weight). Sample water was filtered with a syringe and filter holder until the filtrate just visibly stained the filter, after which the filters were rinsed twice with 5 ml of isotonic (2%) ammonium formate to expel salt. Filters were stored in foil inside cryovials placed in a liquid nitrogen-cooled Dewar while in the field. In the laboratory, filters were dried at 60 °C for 24 h, reweighed (dry weight) and combusted at 450 °C for 6 h before the final weighing (combusted weight) to determine particulate inorganic and organic matter (PIM, POM).

### Rockweed canopy

At each study site, four 50-m transect lines were laid out parallel to the shore at low tide. Two sets of two transects were laid 4 m apart at middle elevation in each bed, where *A. nodosum* comprised >90% of the fucoids present, with 20–50 m separating the two sets of transects. A weight was attached to each line end to anchor the line, with buoys attached to locate them at high tide. The maximum transect depth, averaged across sites, was  $1.85 \pm 0.15$  m.

Canopy structure measurements were taken during the daytime low tide using five 50 × 50 cm quadrats (spaced every 10 m) along each transect, for a total of 20 quadrats per site. In each quadrat, the number of rockweed plants (i.e., all fronds belonging to a common holdfast) was counted. Since multiple fronds can emerge from each holdfast, we counted plants as separate when holdfasts were at least 0.5 cm distant from each other (pers. comm. Raul Ugarte). Each rockweed plant was measured for its maximum length (cm) and maximum circumference (cm) (at the widest portion of the plant) with a measuring tape and was weighed without blotting (g wet mass) on a portable field scale. Whereas small plants were directly placed on the scale, larger plants were placed in a bucket that had one side cut open (see Ugarte et al. 2006 for a diagram of the weighing setup and a schematic of a rockweed plant). The mass (g) of individual plants was summed up for each quadrat to provide a biomass estimate ( $\text{g m}^{-2}$ ).

In addition, we collected five tissue samples per site from the tips of haphazardly selected rockweed fronds below or above the transects to gain insight into their tissue nutrient content. The tips, cut just below the previous year's air vesicle, reflect the last year of growth and thus contain an integrated measure of the past year's water nutrient profile. The tips were dried for 48 h at 80 °C, ground to a powder and analyzed for tissue nitrogen (N) and carbon (C) content (%) at the University of California Davis Stable Isotope Facility.

Between 10 and 20 plants were also collected from each site in order to establish the relationship between the field measurements of length ( $L$ ), circumference ( $C$ ) and mass ( $M$ ) and the volume and degree of branching of the plants. We submerged plants in tanks in order to record the free-floating maximum diameter, the plant volume (by water displacement), the total volume occupied by the plant [ $\text{plant height} * \pi * (\text{max diameter}/2)^2$ ] and the interstitial volume (total volume – plant volume). Primary to fifth-level branches was counted and recorded.

#### *Associated communities*

At both day- and nighttime high tides, two surveyors swam parallel to each other along the transect lines and recorded the species name and abundance of all fish and large mobile macrofauna (e.g., decapod crustaceans) observed within 1 m of each side of the transect (100 m<sup>2</sup> surveyed area for each transect;  $n = 4$  daytime,  $n = 4$  nighttime). Dive lamps were used for nighttime surveys.

During the daytime high tide, the same surveyors recorded all benthic and epiphytic invertebrates and algae in ten 50 × 50 cm quadrats along each transect at 5-m intervals (for a total of 40 quadrats per site) using SCUBA. Quadrats were placed by divers at pre-marked 5-m intervals along a 50-m transect line that was positioned during low tide. All mobile and certain (sparse) sessile invertebrate species  $\geq 0.5$  cm in size were identified and counted. Divers estimated (1) the proportion of the benthos within the quadrat that was covered by sessile benthic species and (2) the percent of the rockweed frond surfaces that were covered by epiphytic macroalgae and sessile invertebrates. All sides of the rockweed fronds were considered habitable space; therefore, if all sides were covered with epiphytes, this would represent 100% cover. When considering all sessile species, the total percent cover of each quadrat could sum to a value  $>100\%$ .

#### **Data analysis**

##### *Environmental parameters*

Means and standard errors (SE) were calculated for 18 replicates at each site for Chl  $a$  concentrations, total

particulate matter (TPM) and particulate inorganic and organic matter (PIM, POM) as well as for 5 replicates at each site for *Ascophyllum* tissue % nitrogen and % carbon. We used multivariate permutational analysis of variance (PERMANOVA, permutation = 999) to assess whether there was a regional (fixed factor with 2 level) and site (fixed factor nested within region with 6 levels) effect on (1) Chl  $a$  and TPM and (2) % nitrogen and % carbon. If a significant multivariate effect of either factor was detected, we followed up with protected univariate PERMANOVA and pairwise post hoc tests on each of the variables. For TPM, we examined the organic content (POM/TPM \* 100) instead of PIM and POM separately.

##### *Canopy structure*

We used correlation analysis to select the best subset of field measures [plant density ( $D$ ; m<sup>-2</sup>), biomass ( $B$ ; kg m<sup>-2</sup>), individual plant length ( $L$ ; cm), circumference ( $C$ ; cm) and mass ( $M$ ; g)] to represent canopy and plant structure. We also used regression analysis to examine the relationship between field ( $L$ ,  $C$  and  $M$ ) and laboratory (plant volume, total volume, interstitial volume and degree of branching) measurements to see which field measures could be used as a proxy of plant volume and habitat volume and complexity, given that  $B$ ,  $M$  and  $C$  were all highly correlated.  $C$  was the best predictor of plant volume ( $R^2 = 0.62$ ,  $p < 0.0001$ ), total volume ( $R^2 = 0.77$ ,  $p < 0.0001$ ) and the number of branches ( $R^2 = 0.66$ ,  $p < 0.0001$ ); we therefore used  $L$  and  $C$  to represent plant structure and  $L$ ,  $C$  and  $D$  together to represent canopy structure. Since biomass is currently used in rockweed monitoring and management, we analyze it separately as a point of comparison.

We then conducted multivariate PERMANOVA to determine whether there were significant differences in canopy structure ( $L$ ,  $C$ ,  $D$ ) between regions and among study sites nested within region. If a significant effect was detected in any factor, we followed up with protected univariate PERMANOVA on each variable individually. We also analyzed mass and biomass individually using univariate PERMANOVA. All morphometric variables were normalized prior to computation of Euclidean distance-based similarity matrices (Anderson et al. 2008). Transect location (shoreward or seaward) was found to not be significant in the initial multivariate PERMANOVAs (site nested within region, fully crossed with transect location); therefore, quadrats from parallel transects were used as replicates ( $n = 20$  per site). Given that site was found to have a significant effect, we also performed post hoc pairwise tests to determine which sites were significantly different from each other.

To improve visualization of the data and corroborate multivariate PERMANOVA results, centroids (i.e., arithmetic means) for canopy structure at each site were computed,

and clusters from a group average cluster analysis were overlaid on the nMDS plot.

#### *Associated community composition*

Given differences in data collection method and whether abundance or percent coverage was recorded, we analyzed three components of the community separately: mobile (and sparse sessile species that we counted rather than estimating coverage, e.g., *Aulactinia stella*) quadrat fauna (abundance  $m^{-2}$ ), sessile quadrat fauna and flora (% cover) and mobile transect fauna (abundance  $m^{-2}$ ). The sessile species were also further divided into benthic and epiphytic (on rockweed) assemblages.

For each community component, we first calculated average ( $\pm$ SE) abundance and % cover of individual species across 4 transects or 40 quadrats per site. We used nested univariate PERMANOVA to identify significant differences between regions and sites (nested in region) in total abundance ( $m^{-2}$ ) or total % cover as well as species richness. We then used nested multivariate PERMANOVAs on a zero-adjusted Bray–Curtis similarity matrix for each component to assess the effects of site(re) and region on community composition. For mobile transect species, time of day (day or night) was found to not be significant in initial multivariate PERMANOVAs (site nested within region, fully crossed with time of day); therefore, day and night transects were used as replicates ( $n = 8$  per site). Species-level abundance and cover data for each component were square root transformed in order to downweight the influence of abundant species and allow for a contribution to the resemblance matrix from rarer species (Anderson et al. 2008). Where site was found to have a significant effect, we also performed post hoc pairwise tests to determine which sites were significantly different.

To determine which species contributed most consistently to regional or site differences, a similarity percentages (SIMPER) analysis was performed on each community component (Clarke and Gorley 2006). nMDS plots with superimposed clusters from cluster analyses using group averages were used to visualize differences in community composition. All PERMANOVA, nMDS, cluster and SIMPER analyses were conducted using PRIMER (version 6.1.11) with PERMANOVA+ (version 1.0.1, PRIMER-E, Plymouth).

#### *Linking canopy structure to community composition*

Canonical correspondence analysis (CCA) was used to quantify statistical associations between species assemblage patterns and plant and canopy structure (plant length, circumference, density and biomass). CCA is a nonlinear eigenvector ordination technique that constrains the axes

so that they are linear combinations of the environmental variables (ter Braak 1986). A matrix of explanatory morphometric variables was used to determine the amount of variation in the species data that related to changes in the canopy structure. We used the ‘vegan’ package in R v2.3.0 (R Foundation for Statistical Computing) in which the Chi-square-transformed species data matrix is subjected to weighted linear regression on constraining variables and the fitted values undergo correspondence analysis done using singular value decomposition. The percentage of species variance explained by each CCA model was calculated as the ratio of the sum of the canonical eigenvalues of the CCA to the total inertia (sum of all unconstrained eigenvalues of CA). Statistical significance of each of the constrained canonical axes of the CCA model was tested with a Monte Carlo permutation test (999 unrestricted permutations).

Second, to determine the relationship between plant or canopy structure and aggregated community measures (i.e., abundance, richness) as well as individual species (SIMPER-identified species or other species of ecological interest), we first used generalized linear models (GLMs) with normal, Poisson or negative binomial distributions. In cases where residuals were over-dispersed, or data contained many zeros, generalized additive models (GAMs) or Hurdle models were used, which were developed to handle zero-inflated data (Wood 2006). Models were fitted to (1) quadrat (mobile and sessile) species richness, (2) richness of mobile (quadrat), benthic sessile and epiphytic sessile components, (3) abundance or % cover of mobile (quadrat), benthic and epiphytic sessile components and (4) abundance or % cover of individual species using various sets of plant and canopy variables as predictors. Species counts from transects were not fitted because of the low level of replication (eight transects per site). Site or region was also added as a predictor to increase model fits.

## Results

### Environmental parameters

Long-term SST readings at the two monitoring locations demonstrated that annual minimum and maximum SST (NS: 3.0–13.5 °C; NB: 2.9–13.3 °C) and July average and maximum SST (NS: 11.9, 14.6 °C; NB: 11.8, 14.1 °C) were similar between regions over recent years (NS 1999–2013; NB 2005–2012); however, the yearly average was 2 °C lower in southwest NS (8.3 °C) than southwest NB (10.3 °C) (DFO Prince 5 data retrieved 2014, NOAA data retrieved 2015). Temperature readings from our dive computers in the field at the NS ( $13 \pm 1$  °C) and NB ( $12 \pm 1$  °C) study sites in July were similar and consistent



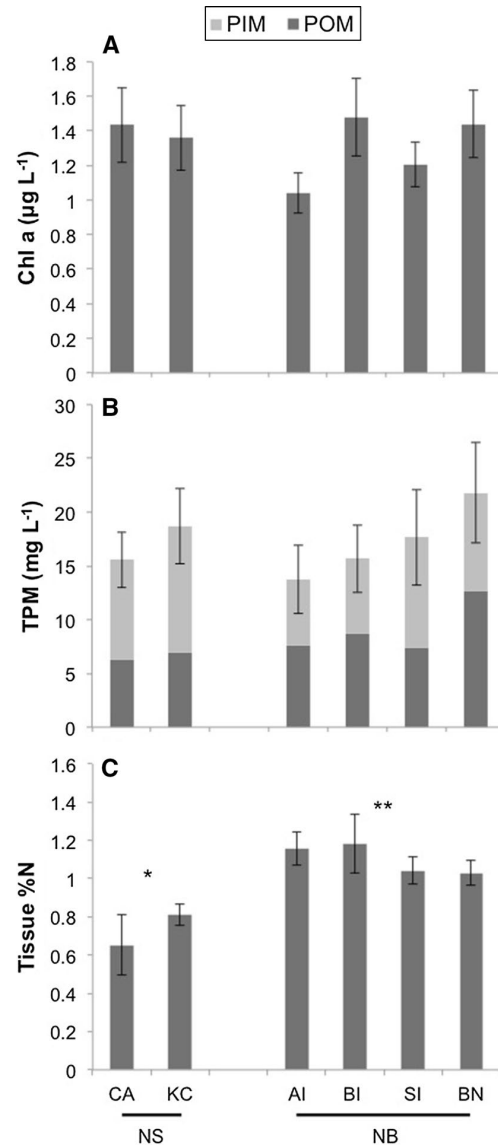
with July values for the two regions from the previous decade, with slightly higher summer temperatures in NS than NB (Balch et al. 2012, DFO Prince 5). Similarly, salinity measures did not differ between the regions (average 31.5–32‰; Drinkwater 1987; Balch et al. 2012, DFO Prince 5). Average Chl *a* values appear to be slightly higher in long-term monitoring series for NB ( $3.5 \pm 0.7 \mu\text{g l}^{-1}$ ) than in NS ( $1.8 \mu\text{g l}^{-1}$ ; Drinkwater 1987; Balch et al. 2012); however, our multivariate analysis did not find a significant effect of region (pseudo- $F_{1,89} = 0.311$ ,  $p = 0.75$ ) or site nested within region (pseudo- $F_{4,89} = 0.73$ ,  $p = 0.65$ ) on water column particulates (Chl *a* and TPM). Although, the % organic content of the TPM was significantly higher in NB ( $51.46 \pm 4.32\%$ ) than in NS ( $40.89 \pm 2.73\%$ ) (region pseudo- $F = 12.315$ ,  $p = 0.003$ ; site(re) pseudo- $F = 0.763$ ,  $p = 0.541$ ).

Long-term nutrient measurements indicate higher background nutrient levels in NB relative to NS (Balch et al. 2008, DFO Prince 5). Multivariate PERMANOVA revealed a significant regional effect (pseudo- $F = 6.01$ ,  $p = 0.005$ ) on % tissue carbon and nitrogen that was driven by the significantly higher % tissue nitrogen content (pseudo- $F = 14.82$ ,  $p = 0.003$ ) measured in rockweed plants from NB compared to NS (Fig. 2c). No effect of site nested within region was detected in any analysis ( $p > 0.69$ ) nor was there a regional effect for percent tissue carbon (pseudo- $F = 0.571$ ,  $p = 0.451$ ).

### Plant and canopy structure

Multivariate PERMANOVA detected a significant effect of region and site, on canopy structure (*L*, *C*, *D*; Table 1), with region explaining 46.1% and site 13.0% of the variation, respectively (region pseudo- $F = 68.875$ ,  $p \leq 0.001$ ; site(re) pseudo- $F = 3.031$ ,  $p \leq 0.001$ ). The canopy structures of CA and KC in NS were not different from each other, but were significantly different from all NB sites (post hoc:  $p \leq 0.0021$  for all eight comparisons). Within NB, the only significant difference was observed between BI and BN ( $p = 0.027$ ). The nMDS plot (Fig. 5a) illustrates the two distinct clusters for the centroids of canopy structure: one tighter cluster for the two NS sites and a second for the four NB sites in which BN is distanced from the remaining three sites.

Protected univariate PERMANOVAs on the three measures indicated a clear difference in plant structure and density between regions, with plants having significantly greater length (region pseudo- $F = 55.598$ ,  $p \leq 0.001$ ; site(re) pseudo- $F = 6.531$ ,  $p \leq 0.001$ ) and circumference (region pseudo- $F = 157.1$ ,  $p \leq 0.001$ ; site(re) pseudo- $F = 1.182$ ,  $p = 0.322$ ) at our study sites in NS than in NB (Fig. 3a–c), whereas plant density was significantly higher



**Fig. 2** **a** Average summer chlorophyll *a* concentration (Chl *a*) ( $\pm$ SE,  $n = 18$ ), **b** total particulate matter (TPM) divided into inorganic (PIM) and organic (POM) components ( $\pm$ SE,  $n = 18$ ) and **c** average tissue percent nitrogen ( $\pm$ SE,  $n = 5$ ) for all six study sites in two regions, Nova Scotia (NS) and New Brunswick (NB). Asterisks (\*) indicate significant differences between regions

(region pseudo- $F = 30.977$ ,  $p \leq 0.001$ ; site(re) pseudo- $F = 1.351$ ,  $p = 0.278$ ) in NB (Fig. 3d). Univariate analyses of plant mass and biomass separately also showed lower values in NB than in NS (region pseudo- $F = 8.187$ ,  $p \leq 0.001$ ; site(re) pseudo- $F = 0.953$ ,  $p = 0.443$ ; region pseudo- $F = 9.12$ ,  $p = 0.003$ ; site(re) pseudo- $F = 0.632$ ,  $p = 0.65$ , respectively; Fig. 3e).

**Table 1** Nested multivariate PERMANOVA (permutations = 999) results for the effect of region and site on canopy structure [length (*L*), circumference (*C*), density (*D*)] and the species composition of different community components

	Source	df	Pseudo- <i>F</i>	<i>P</i>	Sqrt- <i>V</i>
Canopy structure ( <i>L</i> , <i>C</i> , <i>D</i> )	Region	1	68.875	<b>≤0.001</b>	1.526
	Site (region)	4	3.031	<b>≤0.001</b>	0.431
	Residuals	114			1.353
Mobile (quadrat) species	Region	1	20.740	<b>≤0.001</b>	15.672
	Site (region)	4	7.479	<b>≤0.001</b>	14.661
	Residuals	234			36.431
Sessile (quadrat) species	Region	1	24.625	<b>≤0.001</b>	19.732
	Site (region)	4	11.717	<b>≤0.001</b>	21.702
	Residuals	234			41.927
Epiphytic (sessile) species	Region	1	8.097	<b>≤0.001</b>	7.510
	Site (region)	4	9.336	<b>≤0.001</b>	13.292
	Residuals	234			29.116
Benthic (sessile) species	Region	1	25.748	<b>≤0.001</b>	19.454
	Site (region)	4	11.971	<b>≤0.001</b>	21.152
	Residuals	234			40.388
Mobile (transect) species	Region	1	14.396	<b>≤0.001</b>	4.656
	Site (region)	4	2.024	<b>0.028</b>	2.102
	Residuals	42			5.876

Sqrt-*V* values are unbiased estimates of the contribution to variance of region or site and the residuals in the model. Significant *p* values are shown in bold

### Associated species richness and abundance

Both region and site significantly affected richness of mobile quadrat species, with richness at BN being significantly lower than at all other sites and driving the regional difference in richness (region pseudo-*F* = 4.558, *p* = 0.035, site(re) pseudo-*F* = 12.030, *p* ≤ 0.001) (Fig. 4a). Similarly, sessile species richness differed significantly by region and by site, and richness at CA was significantly lower than at all other sites and the driver of lower richness in NS (region pseudo-*F* = 9.701, *p* ≤ 0.001, site pseudo-*F* = 17.829, *p* ≤ 0.001) (Fig. 4b). There was a significant difference in mobile transect species richness between NS and NB (Fig. 4c), with lower values in NS, while site had no significant effect (region pseudo-*F* = 17.968, *p* ≤ 0.001, site pseudo-*F* = 2.311, *p* ≤ 0.078).

Patterns in overall species abundances across sites were more varied. For mobile quadrat fauna abundance, there was a significant effect of region and site, with lower abundance in NB and BN having the lowest abundance (region pseudo-*F* = 15.387, *p* ≤ 0.001, site pseudo-*F* = 11.846, *p* ≤ 0.001) (Fig. 4d). *Littorina littorea* and *L. saxatilis* were more abundant at the two NS sites and AI, while *L. obtusata* was most abundant at SI (Suppl 1. Figure 1). For sessile species cover, there was a significant effect of region

and site, with higher cover in NS, highest cover at KC and lowest at SI and BN (region pseudo-*F* = 7.339, *p* = 0.004, site pseudo-*F* = 15.686, *p* ≤ 0.001) (Fig. 4e). These differences were mainly caused by the high cover of *Semibalanus balanoides* at KC and low cover of *Hildenbrandia rubra* at SI and BN (Suppl 1. Figure 2). The abundance of mobile transect fauna was significantly lower in NS, as indicated by a significant region but not site effect (region pseudo-*F* = 31.033, *p* ≤ 0.001, site pseudo-*F* = 0.999, *p* ≤ 0.404) (Fig. 4f). This was largely caused by *Carcinus maenas*, *Gasterosteus aculeatus* and ctenophores (*Pleurobrachia pileus* and a large unidentified ctenophore) being more abundant in NB than in NS sites (Suppl 1. Figure 3). Fish abundances were very low across all sites.

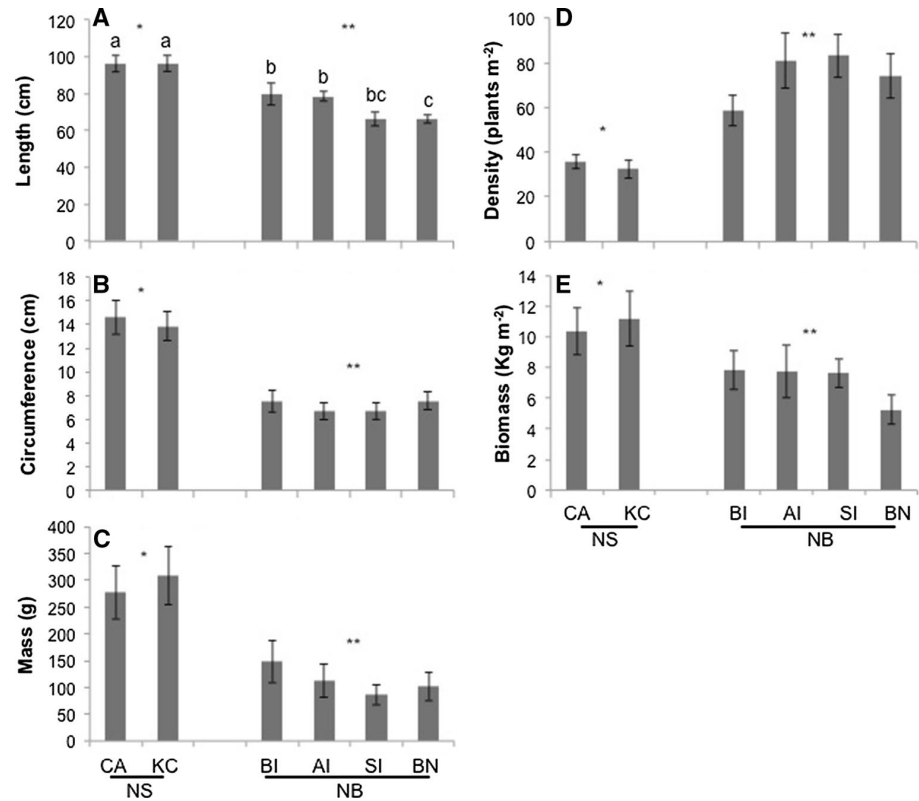
### Associated community composition

Nested multivariate PERMANOVAs detected a significant effect of region and site, respectively, on the composition of mobile quadrat species (Table 1), with region explaining 23.4% and site 22.0% of the variation. The composition of quadrat species did not differ significantly between the NS sites, but most pairwise comparisons between NS and NB sites were significantly different (*p* ≤ 0.0015), except that AI and BI did not differ from CA. In NB, species composition did significantly differ between BI and SI (*p* = 0.0075), and BN was significantly different from the other three NB sites (*p* ≤ 0.0002) (see Suppl. 2 for all PERMANOVA post hoc results). The nMDS plot (Fig. 5b) corroborates that BN is segregated from all other sites, whereas the NS sites—CA in particular—are more similar to the NB sites. The main species identified by SIMPER contributing >10% to differences among sites include *L. littorea*, *L. obtusata* as well as limpets and *C. maenas* in some cases (Suppl. 3).

For the composition of sessile species, there was a significant effect of region and site (Table 1). Site explained 26.0% and region 23.7% of the variation. The percent cover of sessile species did not differ between three of the sites in NB: AI, BI and SI, but all other comparison of sites showed significant differences (*p* ≤ 0.0001) (Suppl. 2). Figure 5c shows a cluster of the NB sites that is similar to that seen for the canopy structure (Fig. 5a). There is no cluster for the NS sites; however, they are more removed from the NB sites than any of these are from each other. The main species identified by SIMPER contributing >10% to differences among sites include *H. rubra* and *S. balanoides*, as well as *Fucus* spp., *Ulva* spp. and a cyanobacteria–algal mat (Suppl. 4).

When separating benthic and epiphytic sessile communities, there were also significant effects of site and region (Table 1). However, the patterns of similarities and dissimilarities as well as SIMPER-identified species for benthic

**Fig. 3** Average rockweed plant and canopy parameters ( $\pm$ SE,  $n = 20$ ): **a** plant length, **b** plant circumference, **c** plant mass, **d** density and **e** biomass across all six study sites in two regions, Nova Scotia (NS) and New Brunswick (NB). Lowercase letters indicate significant differences between sites. Asterisks indicate significant differences between regions



and epiphytic species, respectively, were similar to those observed across all sessile species and are therefore not reported in order to reduce redundancy.

Regarding the composition of transect species, multivariate PERMANOVAs (site nested in region, fully crossed with time of day) detected a significant effect of site ( $p \leq 0.03$ ) and region ( $p \leq 0.001$ ), but not for time of day. Night and day transects were therefore pooled, and nested PERMANOVA also detected significant site and region effects (Table 1). Region explained 36.8% and site 16.6% of variation. There was no difference between the NS sites, and most NB sites were significantly different from the NS sites ( $p < 0.016$ ), except AI was not significantly different from KC (Suppl. 2). Within NB, BN and BI were significantly different from one another ( $p = 0.0024$ ). The nMDS plot (4D) demonstrates two distinct clusters for NS and NB sites, as seen for the canopy structure (Fig. 5a). Within the NB sites, SI and BI group most closely together. The two principal species identified by SIMPER as contributing to differences among sites were *C. maenas* and *P. pileus* (Suppl. 3).

### Linking canopy structure to community composition

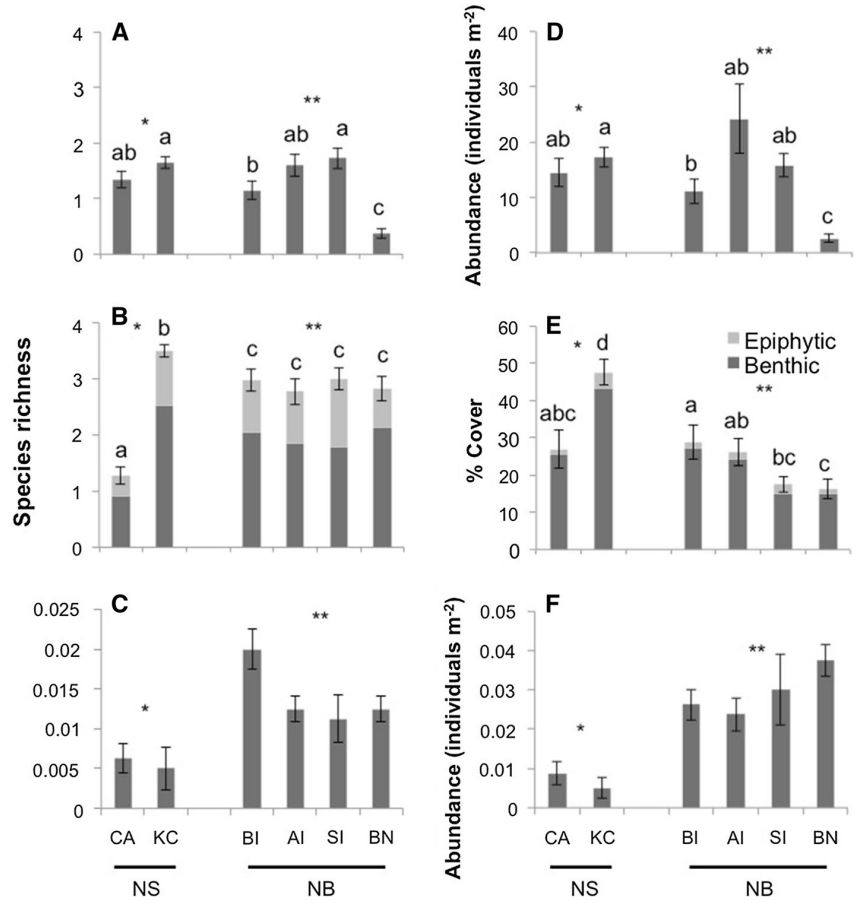
The CCA for canopy structure ( $L, C, D$ ) explained more of the variation in community composition than plant

structure ( $L, C$ ),  $B$  or ( $B, D$ ) (Table 2, Suppl. 4). The CCA of mobile quadrat community using canopy structure ( $L, C, D$ ) as explanatory variables produced an ordination in which the constrained axes explained 5.9% of the variance (CCA1  $F = 3.048$ ,  $p = 0.050$ ). For sessile quadrat community, canopy structure ( $L, C, D$ ) produced constrained axes that explained 5.1% of the variance (CCA1  $F = 3.469$ ,  $p = 0.003$ ; CCA2  $F = 2.072$ ,  $p = 0.045$ ). The CCA of mobile transect community using canopy structure ( $L, C, D$ ) produced an ordination in which the constrained axes explained 15.5% of the variance in the mobile transect community (CCA1  $F = 4.244$ ,  $p \leq 0.001$ ). In contrast,  $B$  produced ordinations that explained only 1.1–5.9% of the variation in these three community components and only the ordination for mobile transect community was significant (CCA1  $F = 2.246$ ,  $p = 0.002$ ).

Using GLMs, and in cases of over-dispersed residuals GAMs or Hurdle models, we found that plant structure ( $L, C$ ) was nearly always a better predictor for patterns in the richness and abundance of community components and abundances of SIMPER species than was rockweed biomass ( $B$ ). Moreover, canopy structure ( $L, C, D$ ) generally predicted more deviation in species patterns than plant structure ( $L, C$ ) alone, explaining 19% to as much as 90% of the deviance overall (Table 3). Adding region (NB, NS)



**Fig. 4** Average species richness (a–c) and abundance (d–f) of mobile quadrat species (a, d;  $n = 40$ ), sessile benthic and epiphytic species (b, e;  $n = 40$ ) and mobile transect species (c, f;  $n = 8$ ) at each of the six study sites in two regions, Nova Scotia (NS) and New Brunswick (NB). Data are means and SE; lowercase letters indicate significant differences between sites. Asterisks (\*) indicate significant differences between regions



**Table 2** Summary table for the CCAs of community components (mobile quadrat, sessile quadrat and mobile transect communities), showing ANOVA results for the axis tests to determine significance of constrained axes

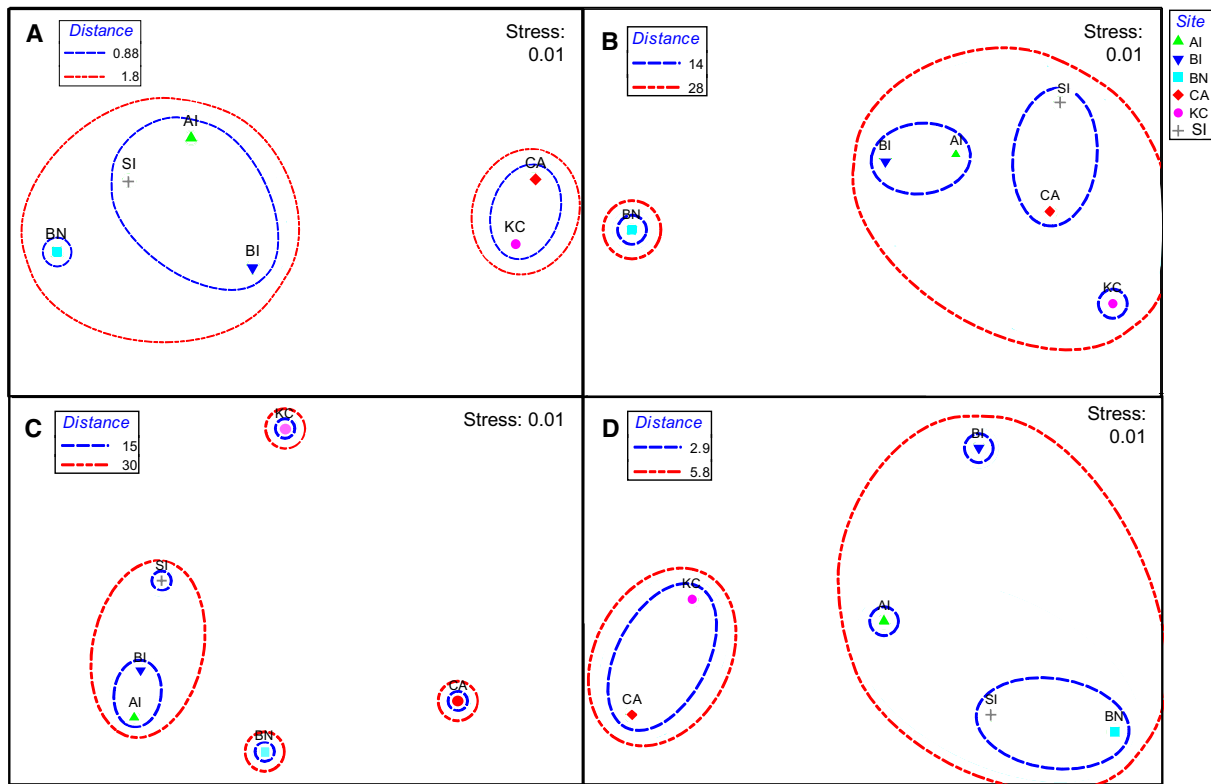
	<i>L, C</i>		<i>L, C, D</i>		<i>B</i>		<i>B, D</i>	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Mobile quadrat								
CCA1	3.045	0.070	3.048	<b>0.050</b>	1.946	0.281	2.216	0.220
CCA2	1.114	0.706	1.532	0.508			1.306	0.608
CCA3			0.671	0.933				
Sessile quadrat								
CCA1	3.378	<b>0.003</b>	3.469	<b>0.003</b>	1.260	0.244	2.700	<b>0.009</b>
CCA2	0.459	0.909	2.072	<b>0.045</b>			1.057	0.355
CCA3			0.457	0.915				
Transect								
CCA1	3.841	<b>0.001</b>	4.244	<b>0.001</b>	2.246	<b>0.002</b>	2.908	<b>0.001</b>
CCA2	1.051	0.333	1.406	0.100			0.596	0.855
CCA3			0.576	0.850				

Significant *p* values are shown in bold. Results are reported for the following combination of predictors: plant structure [plant length (*L*) and circumference (*C*)]; canopy structure [plant length (*L*), circumference (*C*) and density (*D*)] and rockweed biomass (*B*) as a second measure of canopy structure. For full CCA results on total and constrained inertia and percent constrained inertia and eigenvalues for each CCA axis and percent of associated variance see Supplement 4

**Table 3** Output from best models using structural components of the rockweed canopy and site (*S*) as predictors for richness or abundance of community components and SIMPER species

	Biomass ( <i>B</i> )	Canopy structure ( <i>L, C, D</i> )	Canopy structure and site ( <i>S</i> )	Best model fit
	Best model	Best model	Best model	
Quadrat (mobile and sessile) richness				
SP	NS	NS	<i>C</i> and <i>S</i> <sup>a</sup>	GLM
DE	50.7%	50.4%	60.0%	
Mobile (quadrat) species richness				
SP	NS	NS	<i>S</i> <sup>a</sup>	GLM
DE	50.7%	51.2%	50.7%	
Benthic sessile richness				
SP	NS	<i>D</i>	<i>D</i> <sup>a</sup>	GLM
DE	50.7%	51.9%	56.4%	
Epiphytic sessile richness				
SP	NS	NS	<i>C</i> and <i>S</i> <sup>a</sup>	GLM
DE	50.4%	50.5%	56.1%	
Quadrat fauna abundance				
SP	<i>B</i>	All	All	GAM
DE	6.4%	35.3%	43.4%	
Benthic % cover				
SP	<i>B</i>	All	All	GAM
DE	6%	35%	49.3%	
Epiphytic % cover				
SP	<i>B</i>	All	All	GAM
DE	5.3%	19.2%	26.2%	
Littorinids ( <i>L. littorina, L. saxatilis</i> )				
SP	<i>B</i>	All	All	GAM
DE	7.3%	43.2%	50.1%	
<i>Littorina obtusata</i>				
SP	<i>B</i>	All	All	GAM
DE	12.2%	57.9%	64.6%	
<i>Semibalanus balanoides</i>				
SP	<i>B</i>	All	All	GAM
DE	24.2%	53.7%	85.7%	
Cyanobacteria–algal mat				
SP	<i>B</i>	All	All	GAM
DE	23.4%	47.1%	67.2%	
<i>Lithothamnion glaciale</i>				
SP	<i>B</i>	All	<i>L, C</i> and <i>S</i> <sup>a</sup>	GAM
DE	25.8%	89.9%	85.1%	
<i>Hildenbrandia rubra</i>				
SP	<i>B</i>	All	All	GAM
DE	5.7%	28.5%	39%	
Red foliose algae				
SP	<i>B</i>	<i>C, D</i>	NA	GAM
DE	49.0%	74.9%		
<i>Ulva</i> spp.				
SP	<i>B</i>	All	<i>L, C</i> and <i>S</i> <sup>a</sup>	GAM
DE	20.8%	85.9%	66.4%	
<i>Dynamena pumila</i>				
SP	<i>B</i>	All	<i>L, C</i> and <i>S</i> <sup>a</sup>	GAM
DE	9.9%	61.4%	66.4%	
<i>Fucus</i> spp.				
SP	<i>B</i>	All	All	GAM
DE	30.9%	61.7%	65.3%	

Significant predictors (SP), % deviance explained (DE) and model type (GLM, GAM) are reported for models with best results. Not significant (NS) indicates that none of the predictor variables had a significant effect. Results are reported for the following combination of predictors: rockweed biomass (*B*); canopy structure [plant length (*L*), circumference (*C*) and density (*D*)]; and canopy structure and site (*S*). Predictor variables are sometimes excluded when the model over-fits the data<sup>a</sup>



**Fig. 5** Multidimensional scaling (nMDS) plots showing centroids for similarity matrices using Euclidean distances for **a** canopy structure (*L*, *C*, *D*,  $n = 20$ ), and Bray–Curtis similarity matrices for **b** mobile (quadrat) species composition ( $n = 40$ ), **c** sessile species ( $n = 40$ )

and **d** mobile (transect) species ( $n = 8$ ) at each of the six study sites. The *solid* and *broken lines* indicate Euclidean or Bray–Curtis-derived distances from a cluster analysis also conducted on the centroids

and especially site (*S*) into a model as a predictive factor often helped explain an additional 5–10% of deviance (Table 3). Some models over-fit the data, likely because data are so scarce for these species; therefore, where appropriate, a predictor variable was removed from the model to reduce over-fitting (Table 3).

Summarizing the patterns of change, the models suggest that mobile quadrat species abundance and richness and cover of *S. balanoides* were greater in canopies like those we surveyed in southwest NS, which had less densely packed rockweed with larger plants and greater biomass. In turn, the models suggest more *Littorina obtusata* (often located in the canopy) and greater cover of *Lithothamnion* sp., *Ulva* spp. and *Dynamina pumila* in canopies like those surveyed in southwest NB, which had a more densely packed canopy with smaller plants and lower biomass. Furthermore, *Elachista fucicola* and *Fucus* spp. were more abundant in an intermediate canopy of less dense, smaller plants and red foliose algae were found in denser or intermediate canopies with larger plants. Inconclusive patterns were determined for Littorinids (*L. littorea*, *L. saxatilis*), *C.*

*maenas*, cyanobacteria–algal mats and *H. rubra*, likely due to their ubiquitous presence and high abundance relative to other species.

## Discussion

Using large-scale field surveys and multivariate statistics, we established clear differences in canopy structure and associated community composition of rockweed beds between the sites surveyed in southwestern Nova Scotia and southwestern New Brunswick. Additionally, CCAs showed a significant dependence of associated communities on the three-dimensional structure of rockweed habitats. CCAs and individual general linear and additive models further showed that plant and canopy structure explained a greater degree of the pattern in community composition, aggregated community abundance and richness and individual species than rockweed biomass alone. While environmental parameters certainly explain a large portion of the underlying regional differences in canopy

and community structure, the significant link between the two has important implications for the ecosystem-based management of rockweed.

### Environmental parameters

The observed regional differences in plant and canopy structure between our study sites in southwestern NB and NS are likely due to differences in underlying environmental factors. The growth rate of *A. nodosum* is temperature dependent, and a substantial amount of its growth occurs in late spring and summer (Baardseth 1970; Mathieson et al. 1976). Although average sea surface temperature (SST) was 2 °C lower in NS than in NB, average and maximum July temperatures were slightly higher in NS. These higher summer temperatures may in part account for higher growth and larger rockweed plants in NS.

Several other physical factors are known to affect rockweed abundance and growth (Baardseth 1970; Keser et al. 1981, 2005; Vadas and Wright 1986; McCook and Chapman 1993). While salinity and substrate type were similar across our study sites, wave exposure and tidal height differed. Tidal range was lower in Yarmouth, NS (4.5 m) than near Deer Island, NB (5.6 m) (Durand et al. 2008), generally creating higher water movements in NB. Our NB sites are nestled in among other islands (e.g., Deer Island and the West Isles) in the outer Bay of Fundy that create a narrow passage geomorphology (Buzeta and Singh 2008), slowing water movement around the island sites. Modeled current speeds around these sites do not exceed 1 m s<sup>-1</sup> on rising or falling tides (Durand et al. 2008). In comparison, our NS sites were located in embayments and generally exposed to low wave action and currents, except when directly hit by onshore winds. The overall calmer conditions at our NS sites may contribute to the observed larger plants at these locations.

Long-term nutrient concentrations indicate higher levels of nitrate and phosphate in NB (Balch et al. 2012; DFO retrieved 2014), and this was reflected in significantly higher % tissue nitrogen content in our rockweed plants from NB than NS. Nutrient loading can both directly and indirectly affect rockweed's abundance and morphology (Worm and Lotze 2006; White et al. 2011). While rockweed plants near finfish aquaculture sites in southwest Nova Scotia were larger (more massive) than those at control sites (White et al. 2011), rockweed cover has been lower at sites exposed to nutrient loading (Worm and Lotze 2006). We also found significantly higher % organic TPM and higher long-term Chl *a* measurements in NB (Balch et al. 2012; DFO retrieved 2014), although direct field measures of Chl *a* in July and August were comparable. These results indicate generally higher nutrient availability, primary productivity and turbidity in NB, which may help

explain the higher abundance of filter-feeding hydroids and bryozoans, and opportunistic green filamentous algae and *Ulva* spp. we observed in NB.

### Canopy structure and community composition

Our results demonstrate distinct differences in the structure of the rockweed canopy between our selected sites in southwest NS and southwest NB. Plants were significantly smaller and more densely packed at the sites in NB than in NS and form distinct clusters of canopy structure in the two regions (Fig. 5a). There are several morphotypes of rockweed across Atlantic Canada, and we were not able to represent all of these in this survey. We instead selected sites from the two most heavily harvested areas in NS and NB to test their differences. Because we were limited to a surveillance of two sites in NS and four sites in NB, we designated site as a fixed factor in our experimental design so as not to over-generalize our findings to the entirety of each region. In the following we, therefore, discuss differences between sites belonging to the two different regions.

Our method of verifying the representativeness of our field measurements as indicators of canopy structure is not without problems. For instance, we measure maximum circumference in the field and maximum diameter in the laboratory to calculate total volume occupied by the plant, while the volume associated with each plant in the field will likely be impinged upon by neighboring plants. However, the strength of the relationships between circumference and plant volume, and even with the more spatially complex degree of branching, gave us confidence in our choice of maximum circumference as a variable.

Differences in canopy structure likely translate into differences in the associated species community, as first proposed and demonstrated in terrestrial environments (e.g., MacArthur and MacArthur 1961; Karr and Roth 1971; Wilson 1974; Halaj et al. 2000). For example, canopy cover and height are both important for bird species composition, while branch density and arrangement influence arthropod species composition (Halaj et al. 2000; Hinsley et al. 2009). In the marine realm, relating three-dimensional habitat structure to species assemblages is a more recent development and measures of habitat spatial complexity remain diverse and habitat dependent (e.g., Gunnill 1982; Hacker and Steneck 1990; Gee and Warwick 1994; Kelaher 2003; Kovalenko et al. 2012). So far, no studies have aimed to quantitatively link canopy and community structure in rockweed habitats; however, a logical extension for rockweed beds would suggest that plant and canopy structure might affect associated mobile and sessile benthic and epiphytic assemblages.

We found higher richness and abundance of mobile transect fauna, including fish and crabs, at our NB sites,

whereas abundance and richness of other mobile and sessile species were more variable. Richness and abundance of the community components were low; however, together they defined community composition for all three components that differed significantly between the sites in NB and NS (Fig. 5).

The minimum size (0.5 cm) of mobile species surveyed means that smaller organisms were overlooked; however, since we used a standardized survey method across all sites, our results should be consistent and thus comparable across our sites. Similarly, dive lights used during night dives may affect the behavior of fish beyond the widely observed diver effect that would apply during day and night (e.g., St John et al. 1990; Bozec et al. 2011; Dickens et al. 2011). Calibrations between day and nighttime observations are not possible in this study, given the very low richness and abundances of mobile fishes and crustaceans. However, since we used consistent survey methods across sites, our estimates of community structure should be comparable across sites.

Some of these regional differences in the associated community can likely be attributed to differences in the above-mentioned environmental factors or differences in anthropogenic influences. Interestingly, within NB canopy and community composition at Bean Island (BN) separates from the other three sites (Fig. 5), which may be explained by the additional impact of long-term finfish aquaculture in its proximity. However, some differences in community composition may also be attributed to differences in canopy structure. Indeed, using CCA, we found that rockweed plant and canopy structure, including measures of plant length, circumference and density, accounted for a significant degree of the multivariate pattern in the composition of mobile transect and quadrat macrofauna, as well as the sessile assemblages. In all cases, plant ( $L, C$ ) and canopy ( $L, C, D$ ) structure accounted for more of the variation in the assemblages than did biomass ( $B$ ) alone. The percentage of explained variance tends to be low for ecological data, often around the 10% range; the values of 5–15% of variance explained by canopy structure are, therefore, reasonable for the data type (ter Braak and Verdonschot 1995).

Investigating the link between rockweed canopy structure and associated species more closely using GLMs, GAMs and Hurdle models, we found that plant structure ( $L, C$ ), and even more strongly canopy structure ( $L, C, D$ ), routinely outperformed biomass ( $B$ ) as a predictor of community component and species abundance. This is of particular interest because biomass is regularly used as a metric for monitoring rockweed beds and for assessing bed recovery after harvesting (Ugarte et al. 2006; Trott and Larsen 2012; DFO 2013). Although this may be sufficient for assessing changes in rockweed biomass in a single-species context, it

does not capture plant or canopy structure and thus does not help to assess habitat or ecosystem changes to the degree that other measures of canopy structure would. Adding region or site as predictors was a way of including a proxy for environmental variability in the models, which further improved explanation of the patterns of variation for most species. Nevertheless, plant or canopy structure variables on their own were able to account for more than 19%—and in some cases up to 90%—of the pattern in nine species of interest, while region or site in most cases only added an additional 5–10% of the variance explained. These results strongly emphasize the importance of canopy structure for associated community structure.

Using these canopy measures may help identify areas of ecological importance or interest for conservation and management. Regions with a canopy structure associated with higher species diversity or greater abundance of vulnerable species, for instance, might warrant greater protection, for example by decreasing the allowed annual harvested biomass of rockweed or the frequency of harvest. Our field sampling and model results suggest higher abundance of smaller, slow-moving mobile and sessile (quadrat) species (e.g., littorinids, barnacles) in less dense canopies with larger plants, as at our sites in NS; this is possibly due to more open space for settlement (Bologna and Heck 2002). In contrast, we found higher abundances of larger mobile (transect) fauna (e.g., fish, crabs) in dense canopies with smaller plants as at our sites in NB, which may be explained by predator avoidance or enhanced food supply (Heck and Wetstone 1977; Edgar 1990). Similar patterns have been observed between the more open edge compared to the denser interior of rockweed and seagrass meadows (Schmidt et al. 2011).

Unfortunately, we did not encounter a great variety or abundance of larger, commercially important fish or invertebrates, except a few herring (*Clupea harengus*), pollock (*Pollachius pollachius*) and rock crab (*Cancer irroratus*) in NB. This low abundance and diversity of fish in rockweed beds in regions, where historically juvenile and adult fish have been abundant (e.g., Rangeley and Kramer 1995a, b, Lotze and Milewski 2004), will make any examination of changes in fish communities challenging. Interestingly, the most abundant large mobile species was the invasive green crab *C. maenas*, which was introduced to North America in the early 1800s (Grosholz and Ruiz 2002). While results of the GLM were inconclusive for *C. maenas*, abundance data (Suppl. 1 Figure 1) illustrate that the green crab was more abundant in the dense canopies of the NB sites than the NS sites. In the quadrat community, greater numbers of *L. littorea* and *L. saxatilis* were found in NS, and more *L. obtusata*, often located in the canopy, at two NB sites with the densest canopies (AI and SI). The periwinkle *L. littorea* is commercially harvested in NB (Lotze and Milewski 2004), which may



help explain the lower numbers observed there. This species is also affected as bycatch in the rockweed harvest together with *L. obtusata*; however, this effect is minimal compared to the commercial harvest of periwinkles (Ugarte et al. 2010).

Another species of interest among the sessile species is the opportunistic green alga *Ulva* spp., found in greater abundance at the sites in NB, which is also the region with higher nutrient availability (Lavery et al. 1991). The contribution of nutrient exposure is captured in the predictor variable 'Region' in the regression models; however, canopy structure (*L*, *C*, *D*) alone accounts for 86% of the deviance explained for *Ulva* spp. (Table 3). Thus, the regional difference in nutrient exposure could be affecting canopy structure itself (e.g., Worm and Lotze 2006), thereby constituting an indirect effect on community structure.

### Management implications

This work has two important implications for resource management. First, the link between canopy structure and associated community structure could be used to inform an ecosystem-based management approach. A number of studies mapping relationships between terrestrial canopies and species assemblages discuss these relationships in the context of management implications, such as for forestry (e.g., Dellasala et al. 1996; Annand and Thompson 1997; Fuller and Green 1998; Robinson and Robinson 1999; Ishii et al. 2004). Given that the structural complexity of canopies influences the forest's productivity and biodiversity, including an assessment of the three-dimensional structure into management plans is needed to maintain ecosystem functions and biodiversity (Ishii et al. 2004). The same case can be made for the management of rockweed harvesting. So far, regulation of the rockweed harvest in North America remains a single-species approach (Seeley and Schlesinger 2012), despite long-standing discussion about possible ecosystem effects (DFO 1998; Rangeley and Davies 2000). Concern surrounding the rockweed harvest has been focused on the effects of cutting and removing the plants themselves, as evidenced by existing harvest regulations, and monitoring efforts by industry mainly consider rockweed biomass (Seeley and Schlesinger 2012; DFO 2013; DMR 2013). While this may be appropriate from a single-species management perspective that aims to keep rockweed biomass and harvest constant, it does not provide insight into changes in canopy structure and associated species communities. Our work demonstrates significant relationships between plant and canopy structure and the abundance and composition of associated species. Thus, plant and canopy metrics, like length and circumference combined with plant density, not only give a better indication of the habitat structure of the rockweed bed, and they also provide a much stronger predictor of the associated community assemblage. Therefore, including plant and canopy measures into

monitoring and management efforts would strongly improve our ability to apply ecosystem-based management.

Secondly, the strong site differences between southwest NS and southwest NB documented in canopy and community structure highlight the need for a spatially refined management framework. Although current harvest regulations slightly differ among the major harvest regions in NS, NB and Maine (Seeley and Schlesinger 2012), they are related to political boundaries rather than environmental differences. The work described here indicates that differences exist in canopy structure and community composition between sites in southwest NS and NB, which should be recognized in a spatial management framework.

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### Compliance and ethical standards

**Conflict of interest** All authors declare no conflict of interest.

**Ethical approval** All applicable national and institutional guidelines for the care and use of animals were followed.

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