

# Regional consistency of intertidal elevation as a mediator of seaweed canopy effects on benthic species richness, diversity, and composition

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**ABSTRACT:** Through a regional-scale study, we tested the hypothesis that seaweed canopies affect benthic species richness, diversity, and composition differently depending on intertidal elevation. The theory behind that prediction recognizes that macroalgal canopies (composed mainly of *Ascophyllum nodosum* and secondarily of *Fucus* spp. on the studied shores) limit temperature and desiccation stresses in understory habitats during low tides at high and intermediate elevations but have little influence at low elevations because of prolonged submergences due to tide dynamics. We measured the abundance of all benthic algae and invertebrates in 1033 quadrats covering the natural range of furoid canopy cover at high, middle, and low elevations in wave-sheltered rocky intertidal sites spanning 350 km of coast in Atlantic Canada. Univariate and multivariate analyses indicated that benthic species richness, diversity, and composition differed significantly between low-cover (0–40%) and high-cover (60–100%) canopy treatments at high and middle elevations but not at low elevations. At high and middle elevations, high canopy cover increased benthic richness and diversity by allowing several species to occur and enhancing the abundance of most species, compared with low canopy cover. At low elevations, species generally occurred in both canopy treatments and showed a similar abundance between them. These results reveal the ecological generality of the dependency of canopy effects on elevation, which we previously found through a manipulative experiment done at one location. Overall, we conclude that environmental stress mediates seaweed canopy effects on the structure of intertidal communities.

**KEY WORDS:** *Ascophyllum* · Canopy · Environmental stress · *Fucus* · Intertidal · Seaweed · Species diversity · Understory

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## INTRODUCTION

Rocky intertidal ecology has traditionally been important to develop ecological theory (Paine 1966, Underwood 1980, Menge & Sutherland 1987). This paper focuses on the richness, diversity, and composition of rocky intertidal communities. Richness is the number of species in a community, while diversity refers to how likely 2 randomly selected individuals

belong to different species and is based on richness and the relative abundance of species (Krebs 1999). Composition is a multivariate measure that considers the identity of species in addition to their relative abundance. These traits may exhibit different spatial patterns in nature, so they provide complementary information on community structure and functioning (Heaven & Scrosati 2008, Kraufvelin et al. 2010, Hooper et al. 2012, Cardinale et al. 2013).

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Bioengineering by canopy-forming species may influence those traits in understory communities. Such bioengineers (also known as ecosystem engineers or foundation species) can improve the abiotic conditions of understory habitats by preventing extreme levels of irradiance, temperature, or water loss from occurring. Such effects, however, are expected to be most prevalent at environmentally stressful sites, as sites from mild environments do not require such bioengineers for local conditions to be benign (He et al. 2013). Recent studies have found that canopy-forming bioengineers can enhance local species richness in stressful habitats but remain less important in milder ones (Fogel et al. 2004, Crain & Bertness 2005, Cavieres & Badano 2009, Bulleri et al. 2012) and may even have negative effects on understory organisms by competing with them for light, space, or nutrients (Bertness et al. 1999). Different bioengineer species, however, have commonly been used to test bioengineer effects on the associated species richness at different stress levels, which does not readily clarify whether abiotic stress or bioengineer differences caused the observed effects (Badano & Cavieres 2006, Lamit et al. 2011). Only a few studies used the same bioengineer species for such tests, finding that positive effects on understory richness are higher in stressful habitats than in milder ones (Arroyo et al. 2003, Wright et al. 2006, Schöb et al. 2013). Nonetheless, all of those studies evaluated bioengineer effects only on plant species richness, without considering the associated consumers, and only rarely (Cavieres & Badano 2009) were bioengineer effects on species composition tested using multivariate analyses.

In a recent study, we tested the effects of the same canopy-forming algal species on the overall (producers and consumers) species richness, diversity, and composition of understory communities along a vertical intertidal gradient (Watt & Scrosati 2013). For intertidal assemblages considered as a whole, abiotic stress increases markedly from low to high elevations due to the increasing extremes reached by temperature and desiccation towards high elevations because of tides (Raffaelli & Hawkins 1999, Menge & Branch 2001). By lying flat on the substrate during low tides, flexible seaweed canopies shade understory habitats, preventing thermal and desiccation extremes from occurring. Thus, canopies ameliorate understory conditions at high and intermediate elevations, but have little influence at low elevations because of short emersion times (Bertness et al. 1999, Watt & Scrosati 2013). Consequently, a manipulative experiment found that intertidal seaweed canopies affect under-

story species richness, diversity, and composition at high and intermediate elevations (richness and diversity being higher under canopies) but have no effects at low elevations (Watt & Scrosati 2013).

That experiment was done at a wave-sheltered location on the Atlantic coast of Canada (Watt & Scrosati 2013). While that location is representative of wave-sheltered habitats from the cold-temperate NW Atlantic coast (Adey & Hayek 2005, Longtin et al. 2009), evaluation of the same hypothesis at larger spatial scales would test the generality of the observed effects. Furthermore, that experiment measured canopy effects after 1 yr of recolonization in cleared quadrats, but full recovery of disturbed systems may take years. Although canopies were indeed found to affect understory communities differently depending on elevation, measuring the effects after longer times would test the generality of such effects. By surveying quadrats from pristine habitats spanning the natural range of canopy cover, a mensurative study would generate understory community data representing a greater time range for development, including many years for stable areas of the shore. Therefore, we tested whether seaweed canopies affect understory species richness, diversity, and composition differently across elevations through a mensurative study that collected data from pristine wave-sheltered locations at a regional scale along the coast of Atlantic Canada. We hypothesized that canopies would have significant effects on understory richness, diversity, and composition at high and intermediate elevations but little or no effects at low elevations.

## MATERIALS AND METHODS

We surveyed 4 locations spanning 350 km along the Atlantic coast of Nova Scotia, Canada: Taylor Head (44° 48.79' N, 62° 34.26' W), Tor Bay Provincial Park (45° 10.97' N, 61° 21.31' W), an unnamed location northeast of Tor Bay Provincial Park (45° 11.11' N, 61° 20.58' W), and Godie Point (45° 36.69' N, 60° 49.19' W). Because of their geographic position, these locations covered a greater longitudinal than latitudinal span. We only sampled wave-sheltered areas of the shore, which are characterized by values of maximum water velocity between 3 and 6 m s<sup>-1</sup> (Scrosati & Heaven 2007), in contrast with values of 12 m s<sup>-1</sup> in habitats that face the open ocean directly in Nova Scotia (Hunt & Scheibling 2001). The intertidal range (vertical extent between the lowest and highest tides) is approximately 1.8 m on the studied

coast. Between 0 m (chart datum, or lowest normal tide in Canada) and 1.5 m (above chart datum), extensive canopies of furoid seaweeds occur. These canopies are dominated by *Ascophyllum nodosum* (Phaeophyceae, Fucales) and, secondarily, also include species of *Fucus* (Phaeophyceae, Fucales). The relative abundance of those canopy species is similar at the lower, middle, and upper thirds of the 0 to 1.5 m elevation range (Table 1).

For our study, we divided the intertidal range dominated by furoid canopies into 3 zones of equal vertical extent: the low (0–0.5 m), middle (0.5–1 m), and high (1–1.5 m) elevation zones. In May 2008, in each elevation zone at each location, we surveyed 20 cm × 20 cm quadrats that were established randomly along the shoreline in pristine areas of the coast. We surveyed 344 quadrats at each of the high and low intertidal zones and 345 quadrats at the middle zone, totaling 1033 quadrats for the study. For each quadrat, we measured the percent cover of all species larger than 1 mm (except epiphytes on furoid canopies) using a 20 cm × 20 cm frame divided into 100 squares with monofilament line. For each quadrat, we first measured the overall percent cover of furoid canopy by counting the number of squares where canopy cover was 50% or more. We surveyed quadrats that had either a canopy cover between 0 and 40% (hereafter low cover) or canopy cover between 60 and 100% (hereafter high cover). For each quadrat, we then measured the percent cover of each furoid algal species, after which we carefully lifted the canopy and measured the percent cover of benthic algae and invertebrates. If a species was present, but covered less than 1% of the quadrat, we recorded its cover as 0.5%. We identified species using field guides (Gibson 2003, Martínez 2003, Sept 2008) and taxonomic keys (Pollock 1998, Sears 1998). Organisms were identified to as low a taxonomic level as possible, as has previously been done in community analyses

Table 1. Composition of furoid macroalgal canopies (percent relative abundance of each species based on coverage data) at the low, middle, and high intertidal zones from wave-sheltered rocky shores in Atlantic Canada, based on data from 1033 quadrats spanning 350 km of coastline

Species	Low	Middle	High
<i>Ascophyllum nodosum</i>	59.2	72.2	71.9
<i>Fucus vesiculosus</i>	33.6	27.4	26.2
<i>Fucus distichus evanescens</i>	3.1	0.3	0
<i>Fucus serratus</i>	4.1	0.1	0
<i>Fucus spiralis</i>	0	0	1.9

that evaluate all producers and consumers (Thompson et al. 2007, Valdivia & Molis 2009, Golléty et al. 2011). We quantified species abundance as percent cover because alternative measures of abundance (e.g. density of individuals) cannot always be determined accurately for clonal species (Scrosati 2005), or, for example for biomass, would have required destructive sampling, which we avoided for conservation concerns. Additionally, abundance was measured using the same metric for all species because that is a requirement to produce diversity indices (Magurran 2004). We collected the data during low tides, excluding tide pools for consistency.

For each quadrat, we determined richness as the number of species found therein and diversity by calculating Shannon-Wiener's index ( $H'$ ):

$$H' = -\sum p_i \log(p_i) \quad (1)$$

where  $p_i$  was the proportional abundance of species  $i$  in the quadrat, i.e. that species' percent cover divided by the sum of percent cover values for all species in the quadrat (Krebs 1999). We evaluated the effects of canopy cover and intertidal elevation on benthic species richness and diversity through separate analyses of variance (ANOVA). We considered canopy cover as a fixed factor with 2 levels (low and high), elevation as a fixed factor with 3 levels (low, middle, and high), and site as a random factor nested within the canopy cover × elevation interaction. The nested nature of the design accounted for the spatial segregation of the 3 elevation zones (Underwood 1997, Wikström & Kautsky 2007). Since both interaction terms were significant, tests of simple effects investigated canopy cover effects at each elevation zone, considering site as a nested factor within canopy cover. Richness data were normally distributed (tested with normal probability plots) and had homogenous variances (Levene's test,  $p > 0.05$ ), but diversity data failed to meet the homoscedasticity assumption ( $p < 0.05$ ), so diversity data were square-root-transformed before analyses to meet that assumption. We did these analyses with JMP 5.1 for Macintosh. We evaluated the effects of canopy cover and intertidal elevation on benthic species composition through a permutational multivariate ANOVA (PERMANOVA) based on the arrangement of factors described above. Since the interaction term was also significant, we ran multivariate tests of simple effects to evaluate canopy effects separately for each elevation zone. We also ran canonical analyses of principal coordinates (CAP; Anderson & Willis 2003) to graphically investigate canopy cover effects on benthic species composition at each elevation zone. We com-

Table 2. Abundance of benthic species (mean percent cover  $\pm$  SE) at the low, middle, and high intertidal zones of wave-sheltered rocky shores from Atlantic Canada under low (0–40%) and high (60–100%) furoid canopy cover. Mean abundance values that were lower than 0.01% are indicated as 'present'. Blanks represent 0 abundance

	Low zone		Middle zone		High zone	
	Low cover (n = 77)	High cover (n = 267)	Low cover (n = 111)	High cover (n = 234)	Low cover (n = 234)	High cover (n = 110)
<b>Algae</b>						
<i>Bangia atropurpurea</i>	0.60 $\pm$ 0.36	0.20 $\pm$ 0.10		0.11 $\pm$ 0.09	0.01 $\pm$ 0.01	
<i>Calothrix</i> spp.	0.01 $\pm$ 0.01				Present	0.05 $\pm$ 0.05
<i>Ceramium</i> spp.	0.25 $\pm$ 0.11	0.03 $\pm$ 0.02		Present		
<i>Chaetomorpha</i> spp.	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01				
<i>Chondrus crispus</i>	17.48 $\pm$ 2.20	19.53 $\pm$ 1.69	0.53 $\pm$ 0.36	2.15 $\pm$ 0.47		0.01 $\pm$ 0.01
<i>Chordaria flagelliformis</i>	0.06 $\pm$ 0.03	0.13 $\pm$ 0.09				
<i>Cladophora rupestris</i>	0.55 $\pm$ 0.25	0.18 $\pm$ 0.04		0.12 $\pm$ 0.06		
<i>Cladophora</i> spp.	0.34 $\pm$ 0.14	0.04 $\pm$ 0.01		Present		
<i>Corallina officinalis</i>	5.12 $\pm$ 1.00	3.20 $\pm$ 0.49	0.01 $\pm$ 0.01	0.29 $\pm$ 0.09		
<i>Cystoclonium</i> spp.	0.04 $\pm$ 0.02	0.10 $\pm$ 0.06		0.02 $\pm$ 0.01		
<i>Devaleraea ramentacea</i>	0.06 $\pm$ 0.04	0.01 $\pm$ 0.01				
<i>Dumontia contorta</i>	0.56 $\pm$ 0.26	0.47 $\pm$ 0.11	0.02 $\pm$ 0.02	0.11 $\pm$ 0.03		
<i>Elachista chondrii</i>	0.01 $\pm$ 0.01	Present				
<i>Elachista</i> spp.	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02				
<i>Hildenbrandia rubra</i>	1.58 $\pm$ 0.31	3.01 $\pm$ 0.37	1.78 $\pm$ 0.40	6.85 $\pm$ 0.60	0.62 $\pm$ 0.19	6.95 $\pm$ 1.22
<i>Laminaria digitata</i>		0.07 $\pm$ 0.05				
<i>Laminaria longicuris</i>	0.05 $\pm$ 0.03	0.02 $\pm$ 0.01				
<i>Lithothamnion glaciale</i>	1.81 $\pm$ 0.72	3.38 $\pm$ 0.46	0.04 $\pm$ 0.01	2.16 $\pm$ 0.31		0.01 $\pm$ 0.01
<i>Mastocarpus stellatus</i>		0.01 $\pm$ 0.01				
<i>Palmaria palmata</i>	0.71 $\pm$ 0.56	0.09 $\pm$ 0.07				
<i>Petalonia fascia</i>	0.01 $\pm$ 0.01					
<i>Polysiphonia</i> spp.	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01				
<i>Porphyra</i> spp.		Present		Present		
<i>Ralfsia</i> spp.	0.14 $\pm$ 0.08	0.06 $\pm$ 0.02	0.34 $\pm$ 0.28	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.03 $\pm$ 0.02
<i>Rhodochorton purpureum</i>	0.36 $\pm$ 0.20	0.12 $\pm$ 0.07	0.58 $\pm$ 0.39	0.56 $\pm$ 0.30	0.06 $\pm$ 0.03	
<i>Rhodomela confervoides</i>	0.10 $\pm$ 0.08	0.08 $\pm$ 0.03				
<i>Scytosiphon</i> spp.	0.04 $\pm$ 0.03	0.08 $\pm$ 0.05				
<i>Spongomorpha aeruginosa</i>	0.03 $\pm$ 0.01	Present				
<i>Ulva intestinalis</i>				Present		
<i>Ulva lactuca</i>		0.01 $\pm$ 0.01		0.07 $\pm$ 0.04		
<b>Lichen</b>						
<i>Verrucaria maura</i>	5.22 $\pm$ 0.86	2.11 $\pm$ 0.29	8.65 $\pm$ 1.66	4.49 $\pm$ 0.67	10.56 $\pm$ 1.38	4.18 $\pm$ 0.72
<b>Invertebrates</b>						
<i>Acmaea testudinalis</i>	0.36 $\pm$ 0.04	0.30 $\pm$ 0.02	0.12 $\pm$ 0.03	0.17 $\pm$ 0.02		Present
<i>Alcyonidium</i> spp.				Present		Present
<i>Anomia simplex</i>	0.06 $\pm$ 0.02	0.14 $\pm$ 0.01		0.02 $\pm$ 0.01		
<i>Asterias vulgaris</i>	0.06 $\pm$ 0.03	0.11 $\pm$ 0.03		0.03 $\pm$ 0.02		
<i>Astyris lunata</i>		0.01 $\pm$ 0.01				
<i>Bittium alternatum</i>		Present		Present		
Bryozoa	0.06 $\pm$ 0.02	0.25 $\pm$ 0.05	0.01 $\pm$ 0.01	0.09 $\pm$ 0.02		
<i>Buccinum undatum</i>				Present		
<i>Cancer irroratus</i>		0.01 $\pm$ 0.01				
<i>Carcinus maenas</i>	0.05 $\pm$ 0.03	0.05 $\pm$ 0.02		0.09 $\pm$ 0.03		0.01 $\pm$ 0.01
<i>Clava multicornis</i>	0.01 $\pm$ 0.01	0.06 $\pm$ 0.01	Present	0.04 $\pm$ 0.01		
<i>Coryphella</i> spp.		0.01 $\pm$ 0.01				
<i>Crenella glandula</i>	0.07 $\pm$ 0.02	0.03 $\pm$ 0.01		0.02 $\pm$ 0.01	Present	0.01 $\pm$ 0.01
<i>Dynamena pumila</i>	0.21 $\pm$ 0.04	2.01 $\pm$ 0.34	0.13 $\pm$ 0.07	3.02 $\pm$ 0.48		0.01 $\pm$ 0.01
<i>Electra pilosa</i>	0.01 $\pm$ 0.01	0.06 $\pm$ 0.02		0.01 $\pm$ 0.01		
<i>Flustrellidra hispida</i>	0.09 $\pm$ 0.02	0.17 $\pm$ 0.02	0.01 $\pm$ 0.01	0.12 $\pm$ 0.02		0.01 $\pm$ 0.01
<i>Gammarus</i> (biramous uropod)	0.23 $\pm$ 0.03	0.25 $\pm$ 0.02	0.12 $\pm$ 0.02	0.17 $\pm$ 0.02	0.16 $\pm$ 0.02	0.29 $\pm$ 0.02
<i>Gammarus</i> (uniramous uropod)	0.16 $\pm$ 0.03	0.15 $\pm$ 0.01	Present	0.01 $\pm$ 0.01	Present	Present
Halacaridae		0.02 $\pm$ 0.01	Present	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01	0.05 $\pm$ 0.01
<i>Halichondria bowerbanki</i>	0.03 $\pm$ 0.03	0.08 $\pm$ 0.05				
<i>Halichondria panicea</i>	0.01 $\pm$ 0.01	0.03 $\pm$ 0.01				

(Table continued on next page)

Table 2 (continued)

	Low zone		Middle zone		High zone	
	Low cover (n = 77)	High cover (n = 267)	Low cover (n = 111)	High cover (n = 234)	Low cover (n = 234)	High cover (n = 110)
<b>Invertebrates</b>						
<i>Halisarca</i> spp.	0.01 ± 0.01	0.07 ± 0.04		0.01 ± 0.01		
<i>Halocladus variabilis</i>		0.01 ± 0.01	Present	Present		0.01 ± 0.01
<i>Harmothoe imbricata</i>		Present		Present		
<i>Hiatella arctica</i>	0.02 ± 0.01	0.01 ± 0.01				
<i>Idotea balthica</i>	0.03 ± 0.01	0.03 ± 0.01		0.01 ± 0.01		
<i>Idotea phosphorea</i>	0.01 ± 0.01	0.01 ± 0.01				
<i>Jaera marina</i>	0.10 ± 0.02	0.12 ± 0.01	0.01 ± 0.01	0.05 ± 0.01		0.03 ± 0.01
<i>Lacuna vincta</i>	0.32 ± 0.03	0.31 ± 0.02	0.02 ± 0.01	0.09 ± 0.01		
<i>Leptasterias tenera</i>	0.01 ± 0.01	0.01 ± 0.01		Present		
<i>Leucosolenia botryoides</i>	0.06 ± 0.02	0.04 ± 0.01	Present	0.01 ± 0.01		
<i>Littorina littorea</i>	1.77 ± 0.25	1.05 ± 0.07	0.67 ± 0.11	1.03 ± 0.08	0.25 ± 0.04	0.46 ± 0.06
<i>Littorina obtusata</i>	0.09 ± 0.02	0.24 ± 0.02	0.23 ± 0.05	0.37 ± 0.02	0.10 ± 0.01	0.36 ± 0.02
<i>Littorina saxatilis</i>	0.01 ± 0.01		0.17 ± 0.02	0.01 ± 0.01	0.37 ± 0.02	0.15 ± 0.02
<i>Margarites costalis</i>	0.07 ± 0.02	0.11 ± 0.01	Present	0.03 ± 0.01		
<i>Membranipora</i> spp.	0.12 ± 0.02	0.19 ± 0.02	Present	0.03 ± 0.01		
<i>Mytilus</i> spp.	0.22 ± 0.03	0.26 ± 0.02	0.09 ± 0.02	0.48 ± 0.13	0.07 ± 0.01	0.27 ± 0.03
Nematoda	0.15 ± 0.03	0.15 ± 0.01		0.05 ± 0.01	Present	0.02 ± 0.01
Nemertea	0.04 ± 0.02	0.01 ± 0.01	Present	0.01 ± 0.01		Present
<i>Nereis</i> spp.		Present		0.01 ± 0.01		
<i>Nucella lapillus</i>	0.09 ± 0.03	0.26 ± 0.04	0.18 ± 0.05	0.25 ± 0.03	Present	0.05 ± 0.02
<i>Obelia</i> spp.	0.14 ± 0.04	0.28 ± 0.03	0.04 ± 0.01	0.46 ± 0.06		0.04 ± 0.02
Oligochaeta	0.09 ± 0.02	0.05 ± 0.01	0.03 ± 0.01	0.11 ± 0.01	0.01 ± 0.01	0.11 ± 0.02
<i>Ophiopholis aculeata</i>		Present				
<i>Semibalanus balanoides</i>	0.69 ± 0.14	1.11 ± 0.15	6.31 ± 1.56	6.50 ± 0.87	2.96 ± 0.46	6.75 ± 1.42
<i>Spirorbis borealis</i>	0.03 ± 0.01	0.01 ± 0.01		Present		
<i>Spirorbis spirorbis</i>	0.23 ± 0.03	0.21 ± 0.02		0.02 ± 0.01	0.02 ± 0.02	
<i>Strongylocentrotus droebachiensis</i>		0.01 ± 0.01				
<i>Tonicella rubra</i>	0.01 ± 0.01	Present				
<i>Urticina felina</i>	0.02 ± 0.01	0.01 ± 0.01		0.01 ± 0.01		
<i>Urosalpinx cinerea</i>	0.01 ± 0.01	0.02 ± 0.01		0.01 ± 0.01		

pared quadrats by calculating Bray-Curtis distances using fourth-root-transformed abundance data. We did these analyses with PERMANOVA+ for PRIMER 6.1.11 (Clarke & Warwick 2001).

## RESULTS

We found 82 species, including 30 seaweeds, 51 invertebrates, and 1 lichen (Table 2). The ANOVA for species richness revealed significant main effects of canopy cover ( $F_{1,18} = 326.26$ ,  $p < 0.001$ ) and intertidal elevation ( $F_{2,18} = 701.67$ ,  $p < 0.001$ ) and a significant interaction between these factors ( $F_{2,18} = 47.36$ ,  $p < 0.001$ ). Site effects were also significant ( $F_{18,1009} = 7.59$ ,  $p < 0.001$ ), but this result has no importance for our tests of interest (evaluating canopy cover effects at different elevations). Tests of simple effects found that canopy cover had a significant effect on species richness at the high ( $F_{1,6} = 179.68$ ,  $p < 0.001$ ) and mid-

dle ( $F_{1,6} = 314.47$ ,  $p < 0.001$ ) intertidal zones (richness being higher under high canopy cover) but no significant effect at the low zone ( $F_{1,6} = 3.27$ ,  $p = 0.070$ ; Fig. 1A). The ANOVA for species diversity also revealed significant effects of canopy cover ( $F_{1,18} = 358.82$ ,  $p < 0.001$ ), intertidal elevation ( $F_{2,18} = 561.07$ ,  $p < 0.001$ ), and site ( $F_{18,1009} = 6.75$ ,  $p < 0.001$ ) and a significant interaction between canopy cover and elevation ( $F_{2,18} = 65.52$ ,  $p < 0.001$ ). Tests of simple effects showed that canopy cover had a significant effect on diversity at the high ( $F_{1,6} = 179.25$ ,  $p < 0.001$ ) and middle ( $F_{1,6} = 334.93$ ,  $p < 0.001$ ) intertidal zones (diversity being higher under high canopy cover) but no significant effect at the low zone ( $F_{1,6} = 3.15$ ,  $p = 0.080$ ; Fig. 1B).

The PERMANOVA revealed that canopy cover ( $F_{1,18} = 7.98$ ,  $p < 0.001$ ), intertidal elevation ( $F_{2,18} = 16.30$ ,  $p < 0.001$ ), and site ( $F_{18,1009} = 12.26$ ,  $p < 0.001$ ) significantly affected the species composition of benthic communities. The interaction between canopy

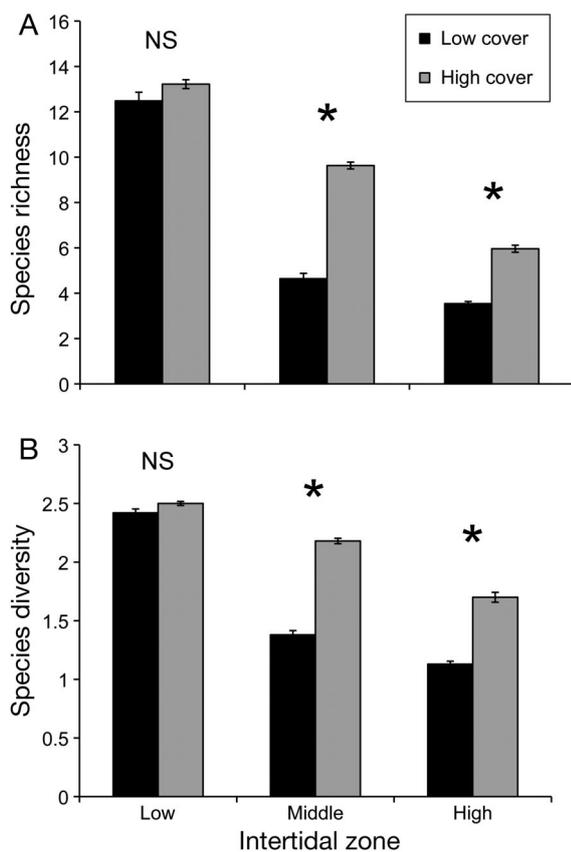


Fig. 1. Mean  $\pm$  SE benthic species (A) richness and (B) diversity found through a mensurative experiment under low (0–40%;  $n = 77, 111, 234$  at the low, middle, and high intertidal zones, respectively) and high (60–100%;  $n = 267, 234, 110$  at the low, middle, and high intertidal zones, respectively) fucoid canopy cover on the Atlantic coast of Canada. NS: no significant difference between both treatments; asterisk indicates a significant difference ( $p < 0.05$ )

cover and elevation was also significant ( $F_{2,18} = 1.85$ ,  $p = 0.030$ ), so we evaluated canopy effects for each elevation zone. Those analyses revealed that canopy cover significantly affected benthic species composition at the high ( $F_{1,6} = 3.79$ ,  $p = 0.030$ ; Fig. 2A) and middle ( $F_{1,6} = 5.66$ ,  $p = 0.004$ ; Fig. 2B) intertidal zones, but not at the low zone ( $F_{1,6} = 0.54$ ,  $p = 0.750$ ; Fig. 2C).

At the high and middle intertidal zones, species composition differed between both canopy treatments mainly because of the absence of many species in the low-cover treatment (Table 2). Only 40% of the algae and 57% of the invertebrates found under high canopy cover also occurred under low cover at the high zone, while only 47% of the algae and 56% of the invertebrates found under high canopy cover also occurred under low cover at the middle zone. Conversely, only 2 algae and 1 invertebrate occurred only under low canopy cover at the

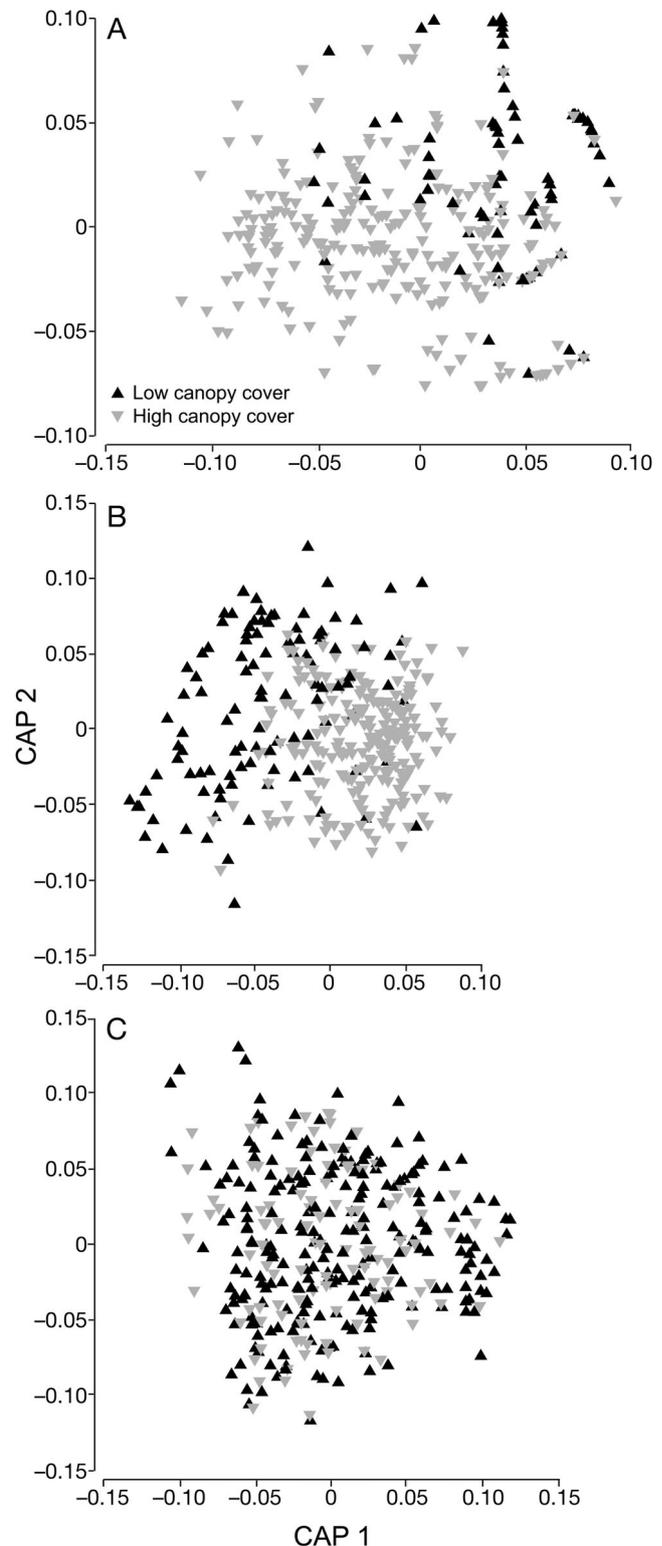


Fig. 2. Canonical analyses of principal coordinates (CAP) showing the effects of fucoid canopy cover (low cover, 0–40%, vs. high cover, 60–100%) on benthic species composition at (A) high, (B) middle, and (C) low elevations in wave-sheltered rocky intertidal habitats from Atlantic Canada. Each triangle represents a single quadrat

high zone, while no species occurred only under low cover at the middle zone. Among the species that occurred in both canopy treatments in both zones, most species were more abundant under high canopy cover; the lichen *Verrucaria maura* was the clearest representative of the few species that were more abundant under low cover. At the low intertidal zone, species typically (78% of them) occurred in both canopy treatments and generally differed little in abundance between the treatments (Table 2).

## DISCUSSION

A manipulative experiment done at a wave-sheltered location on the NW Atlantic coast recently found that furoid canopies affect the richness, diversity, and composition of intertidal communities at high and middle elevations (richness and diversity being positively affected by canopies), with no effects occurring at low elevations (Watt & Scrosati 2013). By surveying 4 sites spanning 350 km and using a sample size almost 10 times higher, our mensurative study has revealed the ecological generality of the dependency of such canopy effects on elevation.

Community structure varies across environments often because of performance changes in species and changes in interspecific interactions (Menge 1995). Information on interspecific interactions under furoid canopies is currently limited to a few species (Jenkins et al. 1999, Cervin et al. 2004). However, species composition apparently changed between our 2 canopy treatments at high and middle elevations mainly because of changes in species performance. Furoid canopies limit thermal extremes and variability in understory habitats during low tides at high and middle elevations but have almost neutral effects at low elevations (Watt & Scrosati 2013). Similarly, furoid canopies become increasingly important in limiting low-tide desiccation of understory organisms towards high elevations (Bertness et al. 1999). Algal canopies also decrease irradiance stress in understory habitats at high elevations, which are not protected by a water column as often as low elevations (Scrosati & DeWreede 1998). At the high and middle elevations that we surveyed, habitats with a low canopy cover had fewer species than habitats with a high cover, and the species that did occur in both treatments were generally less abundant under a low canopy cover. Thus, canopies seem to enhance the performance of most understory algae and invertebrates in stressful environments, greatly influencing benthic community structure.

Our findings are important not only to understand furoid canopy effects on intertidal communities but also to learn the effects of canopy-forming bioengineers in general. Studies in marine and terrestrial systems have found that canopy-forming bioengineers increase plant species richness in stressful habitats, but remain less important in benign habitats, sometimes showing no effects there (Arroyo et al. 2003, Fogel et al. 2004, Crain & Bertness 2005, Wright et al. 2006, Cavieres & Badano 2009, Schöb et al. 2013). The experiment with furoid canopies (Watt & Scrosati 2013) and the present regional-scale study provide a similar conclusion for overall (producers and consumers) species richness, diversity, and composition, using the same bioengineers for tests. Thus, the notion that canopy-forming bioengineers structure understory species assemblages mainly in stressful environments is strengthened.

It is worth noting that, under physiologically benign conditions, some studies have found that canopies can negatively affect species performance and diversity, primarily through abrasion and competition for space and light (Bertness et al. 1999, Bruno et al. 2003). As described above, at the most benign habitats that we surveyed (low intertidal elevations), our study did not detect any negative effects at the community level, only neutral effects, which relates well to the virtual absence of thermal influences of canopies at such elevations because of long submergence times (Watt & Scrosati 2013). Although intertidal furoid canopies may abrade the substrate during high tides (Beermann et al. 2013), abrasion seems not to have been particularly important in our wave-sheltered habitats. Likewise, pre-emptive competition for space seems not to be a prevalent phenomenon for the furoid algae from our coast, because *Ascophyllum nodosum* and *Fucus* spp. have small holdfasts that leave large extents of the substrate (normally >90%) available for other species to occupy. On shores subjected to higher degrees of wave exposure, furoid canopies might have negative influences on benthic species richness at low elevations through whiplash effects. Thus, it would be interesting to repeat our experiments across gradients of wave action to investigate how furoid canopies affect understory assemblages at higher levels of physical stress.

Our mensurative study found more benthic species (82 versus 38) than the manipulative experiment that we reported previously (Watt & Scrosati 2013). In part, this increment may have resulted from the larger number of quadrats used in our study (1033 versus 120), greater number of sites, and our larger

geographic coverage. For a variety of reasons, field surveys normally find more species as the sampled area increases, up to a certain point depending on regional species richness (Scheiner et al. 2011). In addition, that increment may have occurred because our mensurative study surveyed pristine habitats, as opposed to the quadrats in the manipulative experiment, which were cleared from all organisms (except furoid canopies) to create the treatments and were monitored after only 1 yr of recolonization. Counts of air bladders in intact fronds of *Ascophyllum nodosum* (an indication of age; Eckersley & Garbary 2007) suggest that such fronds may reach 8 yr of age in our sampled locations. Older thalli likely occur too, as *A. nodosum* holdfasts live longer and broken fronds (which exhibit fewer air bladders) can also survive for several years if they remain attached to holdfasts (Åberg 1992). Therefore, although some of the quadrats that we sampled may have been naturally disturbed shortly before measurements, our mensurative study surveyed understory communities that had developed for years, which allowed them to incorporate several species not found through the experiment.

Ecological research is most productive when manipulative experiments are combined with mensurative studies that expand the spatial scale of evaluation of what can reasonably be tested through experiments (Agrawal et al. 2007, Sagarin & Pauchard 2010). Besides its contribution to advancing bioengineer ecological theory, the present study offers a successful example where the conclusions from a local-scale experiment can be extrapolated to regional scales through a mensurative approach.

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