

# Trends in abundance of rocky intertidal seaweeds and filter feeders across gradients of elevation, wave exposure, and ice scour in eastern Canada

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**Abstract** On NW Atlantic rocky shores, the main basal organisms in intertidal communities are seaweeds (*Ascophyllum nodosum*, *Fucus* spp. and *Chondrus crispus*) and filter feeders (barnacles, *Semibalanus balanoides*, and mussels, *Mytilus* spp.). Their ecology has been extensively studied in New England (United States), but knowledge gaps exist for northern shores, which are subjected to stronger environmental stress. Therefore, we studied the above organisms on Canadian shores. We quantified the summer abundance of these seaweeds and filter feeders across full vertical (intertidal elevation) and horizontal (wave exposure and winter ice scour) environmental gradients on the Gulf of St. Lawrence and open Atlantic coasts of Nova Scotia. At the regional scale along the open Atlantic coast, seaweeds showed similar abundances in Nova Scotia than values reported for New England. However, both filter feeders were considerably less abundant in Nova Scotia. At the local scale in Nova Scotia, intense winter ice scour (which only occurs on the Gulf of St. Lawrence coast) was associated with a very low abundance of all species except barnacles. Spatial trends in Nova Scotia were similar to patterns

known for certain species elsewhere, such as *A. nodosum* being almost restricted to sheltered habitats, regardless of elevation, and *C. crispus* being almost restricted to low elevations, regardless of exposure. Other trends were, however, characteristic of Nova Scotia, such as *C. crispus* being frequent at low elevations in exposed habitats, unlike in New England, where mussels often predominate there because of competitive advantages. In Nova Scotia, mussels were always restricted to cracks and crevices, unlike in New England, where they form extensive intertidal beds on exposed shores. The direct effects of increased environmental stress and indirect effects through altered interspecific interactions might explain the regional differences in local species distribution, which will require experimental validation.

**Keywords** Barnacles · Ice scour · Intertidal elevation · Mussels · Seaweeds · Wave exposure

## Introduction

Ecology aims to understand the distribution and abundance of organisms, properties that are determined by the complex interaction of abiotic and biotic factors (Brown et al., 1996). Rocky intertidal habitats harbour a unique diversity of marine organisms that need regular periods of emersion for

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survival. Vertical species patterns are primarily determined by the environmental gradient resulting from tide dynamics, which cause increasing emersion-related stresses (desiccation, irradiance, temperature and osmotic effects) with elevation (Raffaelli & Hawkins, 1996; Garbary, 2007). Horizontal species patterns are primarily determined by gradients in wave exposure (Denny & Wethey, 2001) and, in polar and subpolar shores, ice scour (Barnes, 1999; Gutt, 2001; Johnson, 2007). Interspecific interactions modify the fundamental niche of organisms to produce their realized niches, that is, the patterns that are observable on the shore (Menge & Branch, 2001; Bruno et al., 2003).

On NW Atlantic rocky shores, intertidal communities have frequently been investigated aiming to develop ecological theory (Menge & Branch, 2001; Bertness et al., 2004). Thus, a great deal of information exists on the distribution and abundance of their seaweeds and invertebrates. However, most studies have been conducted in New England (United States), with considerably less emphasis placed on northern shores, in Canada (Chapman & Johnson, 1990; Adey & Hayek, 2005). The thorough understanding of species distribution and abundance requires information for the full environmental range in which organisms occur (Sagarin et al., 2006; Schoch et al., 2006). Rocky shores in Atlantic Canada are subjected to harsher winters than in New England (Bertness, 2007). Therefore, the ecological patterns described for New England may not necessarily apply to Canadian shores.

The first step to understanding process is the quantitative determination of pattern (Underwood et al., 2000). We measured the abundance of all species of seaweeds and benthic invertebrates across the full vertical (elevation) and horizontal (wave/ice exposure) intertidal environmental stress gradients that are found on two ecologically distinct coasts in Nova Scotia: the Gulf of St. Lawrence coast and the open Atlantic coast (Scrosati & Heaven, 2007). The Atlantic coast of Nova Scotia depicts lower mean values of sea surface temperature and nutrient concentration than the New England coast (Petrie & Yeats, 2000; Fisheries and Oceans Canada, 2007a). The Gulf of St. Lawrence coast, in addition, freezes extensively in winter (Saucier et al., 2003), causing considerable ice scour on rocky intertidal habitats (McKindsey & Bourget, 2001; Scrosati & Heaven,

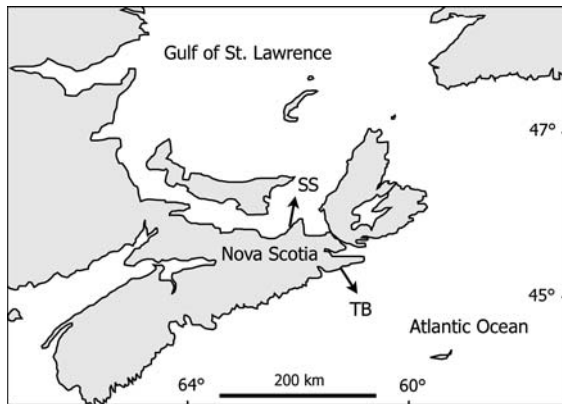
2006). Therefore, there is a gradient of increasing intertidal environmental stress from New England to Atlantic Nova Scotia to the Gulf of St. Lawrence.

Multivariate analyses have indicated that only a few basal species (sessile organisms sustaining herbivores and carnivores) explain most of the variation in community diversity across intertidal environmental gradients in Nova Scotia (Heaven, 2006). Such species are primary producers (seaweeds, *Ascophyllum nodosum* (Linnaeus) Le Jolis, *Fucus* spp. and *Chondrus crispus* Stackhouse) and filter feeders (barnacles, *Semibalanus balanoides* (Linnaeus, 1766), and mussels, *Mytilus* spp.). Due to those results and the ecological importance demonstrated experimentally for these organisms in New England (Menge & Branch, 2001; Bertness et al., 2004), in this article we focus on spatial trends in abundance of these basal species in Nova Scotia. Due to the higher environmental harshness relative to New England, we hypothesized that these species would be less abundant in Nova Scotia. Since consumers are normally more sensitive to changes in environmental stress than primary producers (Menge & Sutherland, 1987), we also hypothesized that the regional changes in abundance would be more noticeable for filter feeders than for seaweeds. In Nova Scotia, we hypothesized that abundance would be lower on the Gulf of St. Lawrence coast than on the Atlantic coast because of the intense ice scour on the Gulf coast in winter. At the local scale, we hypothesized that abundance would vary sharply across elevation and exposure gradients. Since regional environmental changes affect local environmental gradients, we also hypothesized that local abundance trends in Nova Scotia would not be entirely the same as those described for New England. Finally, we determined the relative contribution of vertical and horizontal environmental gradients to spatial abundance changes in Nova Scotia.

## Materials and methods

### Study sites

Our study sites were Sea Spray Shore (45° 46' N, 62° 9' W; hereafter SS), on the Gulf of St. Lawrence coast near Arisaig, and Tor Bay Provincial Park (45° 11' N, 61° 21' W; hereafter TB), on the open Atlantic



**Fig. 1** Map of Nova Scotia indicating the study sites: Tor Bay Provincial Park (TB) on the Atlantic coast, and Sea Spray Shore (SS) on the Gulf of St. Lawrence coast

coast (Fig. 1). On the basis of exploratory biological surveys done for several sites along 500 km of coastline (focusing on the basal species described below), we found that SS and TB are representative sites for the Gulf of St. Lawrence and Atlantic coasts, respectively, of Nova Scotia (Heaven, 2006). We restricted our surveys to rocky intertidal sites with stable bedrock (volcanic rock at SS and metamorphose sedimentary rock at TB). Surface seawater temperature and salinity patterns are described for both coasts elsewhere (Scrosati & Heaven, 2007).

#### Environmental gradients

We sampled the full intertidal range (vertical gradient) at each site, between 0 m in elevation (chart datum) and an upper intertidal boundary determined using ecological indicators to account for the effects of wave exposure on emersion-related physiological stresses (see details in Scrosati & Heaven, 2007). We divided the intertidal range equally in three zones (high, mid- and low zones). Wave exposure (horizontal gradient) is narrower and lower on the southern Gulf of St. Lawrence coast than on the open Atlantic coast (Fisheries and Oceans Canada, 2007b). Thus, two wave-exposure levels were selected for SS (sheltered and exposed), and three for TB (sheltered, intermediate and exposed). Values of maximum water velocity for each site are given elsewhere (Scrosati & Heaven, 2007), although it is

worth highlighting here that the exposed level at SS is more similar to the intermediate level at TB because of the above reason. Significant ice scour occurs only on the Gulf of St. Lawrence coast at our latitudes in Nova Scotia. Sea ice forms in early winter and melts in late winter and early spring (Saucier et al., 2003). Measurement of the damage caused by sea ice to metallic cages that were affixed to rocky surfaces for an entire winter at SS indicated that ice scour is strong on wave-exposed areas and milder on wave-sheltered areas (Scrosati & Heaven, 2006; see also Fig. 2 in Scrosati & Heaven, 2007). Therefore, the two levels used for wave exposure at SS also represented differences in ice scour intensity. For simplicity, the term “exposed” will refer to high levels of wave exposure and ice scour, whereas the term “sheltered” will refer to low levels of such variables for SS.

#### Species abundance

Between 8 July and 21 August 2005, we measured the abundance of *Ascophyllum nodosum* (Phaeophyceae, Fucales), *Fucus* spp. (Phaeophyceae, Fucales), *Chondrus crispus* (Rhodophyta, Gigartinales), *Semibalanus balanoides* (Crustacea, Cirripedia) and *Mytilus* spp. (Mollusca, Bivalvia) for each combination of elevation and exposure levels for SS (six combinations) and TB (nine combinations). For each elevation  $\times$  exposure combination, we determined the percent cover of each taxon for 20, 625-cm<sup>2</sup> (25 cm  $\times$  25 cm) quadrats randomly distributed across the rocky surface. We identified organisms using field guides (Gibson, 2003; Martínez, 2003) and taxonomic keys (Villalard-Bohnsack, 2003). We excluded tide pools from sampling. When percent cover was less than 1%, we recorded it as 0.5%. The accurate field identification of recruits and juveniles of the four *Fucus* species on these shores (*Fucus distichus* Linnaeus, *Fucus serratus* Linnaeus, *Fucus spiralis* Linnaeus and *Fucus vesiculosus* Linnaeus; Novaczek & McLachlan, 1989; Villalard-Bohnsack, 2003) is impossible. Thus, we grouped these species into a single “*Fucus* spp.” taxon. Two species of *Mytilus* occur in Nova Scotia (*M. edulis* Linnaeus, 1758 and *M. trossulus* Gould, 1850), but their accurate field identification is also impossible because of morphological overlaps and

occasional hybridization. Reliable identifications can only be achieved through genetic analyses in the laboratory (Moreau et al., 2005; Riginos & Cunningham, 2005), so we considered a single “*Mytilus* spp.” taxon, as done in field studies in the NW Atlantic (Hunt & Scheibling, 1998, 2001; Cusson & Bourget, 2005). A list of all the seaweeds and benthic invertebrates identified at our sites appears in a community study published elsewhere (Scrosati & Heaven, 2007).

### Data analysis

We identified trends in abundance across vertical and horizontal gradients separately for each taxon through two-way, fixed-model analysis of variance (ANOVA). Factors were elevation (3 levels) and wave/ice exposure (2 levels for SS and 3 levels for TB). To minimize departures from normality within cells (each elevation  $\times$  exposure combination) and from homogeneity of variance among cells, data were rank-transformed before analyses (Quinn & Keough, 2002). We used a conservative significance level of 0.01 for all ANOVAs. When main effects (elevation and/or exposure) were significant, we compared factor levels with Tukey HSD tests (Howell, 2002). When interaction effects (elevation  $\times$  exposure) were significant, we tested for simple effects (differences among factor levels tested separately across each level of the other factor) by performing separate one-way ANOVAs. We used the error term from each two-way ANOVA to compute the  $F$  statistic for simple effects because that error term is an adequate estimate of the error variance (Howell, 2002; Quinn & Keough, 2002). When simple effects were significant, we compared factor levels separately across each level of the other factor with Tukey HSD tests (Howell, 2002). For brevity, only the results of such Tukey HSD tests are reported (Figs. 2–6); details of all simple effects appear in Heaven (2006). To evaluate the relative contribution of each source of variation to the spatial variability in abundance for each taxon, we calculated the magnitude of effect for each factor and their interaction (Howell, 2002) after performing each two-way ANOVA.

## Results

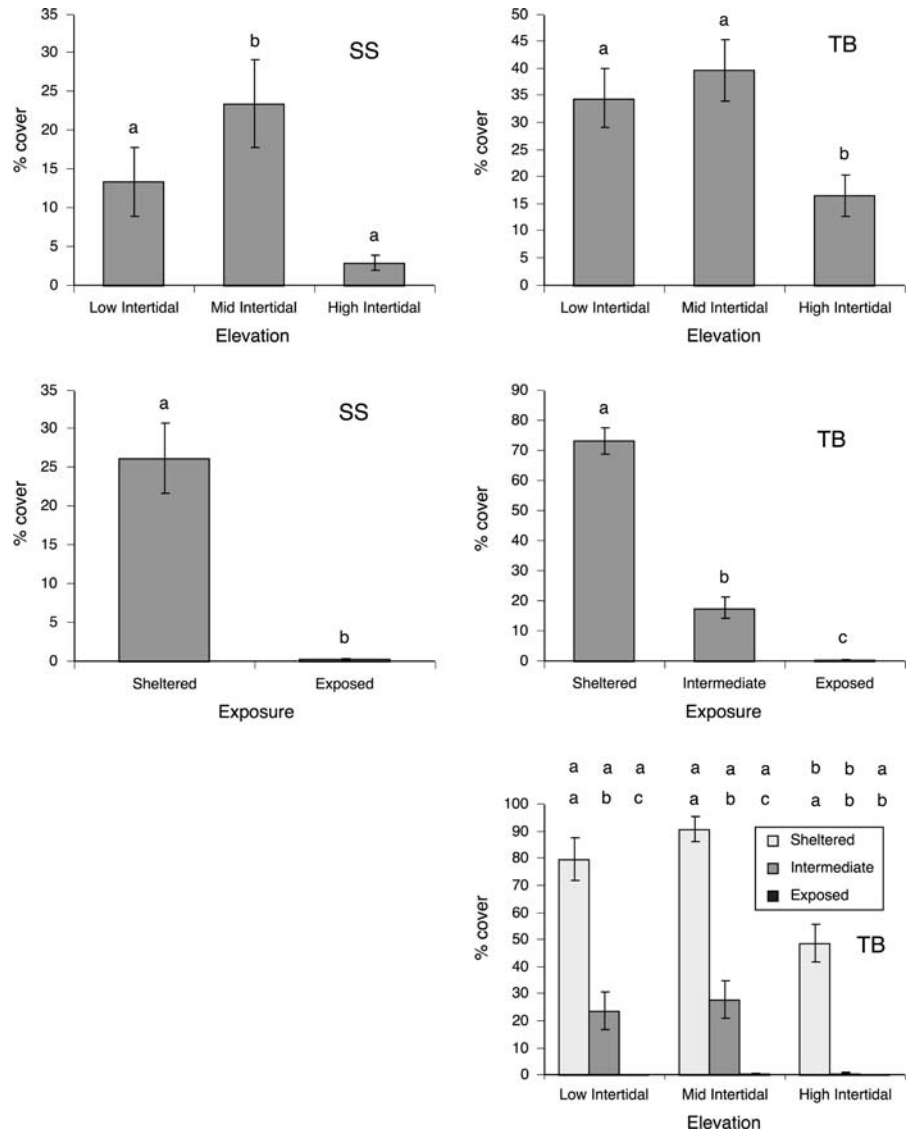
### *Ascophyllum nodosum*

At SS, *Ascophyllum nodosum* varied in abundance across the elevation ( $F_{2, 114} = 8.5$ ,  $P < 0.001$ ) and exposure ( $F_{1, 114} = 101$ ,  $P < 0.001$ ) gradients, while the elevation  $\times$  exposure interaction was not significant ( $F_{2, 114} = 3.6$ ,  $P < 0.03$ ) at the significance level considered in this study ( $\alpha = 0.01$ ). Thalli were almost absent in exposed shore areas, but occurred abundantly in sheltered areas (>25% cover on average; Fig. 2). In sheltered areas, thalli were more abundant towards lower elevations, peaking at the mid-intertidal zone (Fig. 2). For SS, the magnitude of effect was 42% for exposure and 6% for elevation. At TB, *Ascophyllum nodosum* varied in abundance across the elevation ( $F_{2, 171} = 23.4$ ,  $P < 0.001$ ) and exposure ( $F_{2, 171} = 290.2$ ,  $P < 0.001$ ) gradients, and the interaction term was significant ( $F_{4, 171} = 5.5$ ,  $P < 0.001$ ). Thalli were almost absent in exposed areas, increasing in abundance towards the sheltered areas (reaching >70% cover on average; Fig. 2). In sheltered and intermediate-exposure areas, thalli were more abundant at mid- and low elevations (Fig. 2). For TB, the magnitude of effect was 70% for exposure, 6% for elevation and 2% for the exposure  $\times$  elevation interaction.

### *Fucus* spp.

At SS, *Fucus* spp. varied in abundance across the elevation ( $F_{2, 114} = 40.7$ ,  $P < 0.001$ ) and exposure ( $F_{1, 114} = 64.8$ ,  $P < 0.001$ ) gradients, and the interaction term was significant ( $F_{2, 114} = 6.7$ ,  $P = 0.002$ ). Abundance was very low in exposed areas and higher in sheltered areas (>40% cover on average; Fig. 3). Across elevation in sheltered areas, abundance was highest at the mid- and low intertidal zones (Fig. 3). For SS, the magnitude of effect was 23% for exposure, 29% for elevation and 4% for the exposure  $\times$  elevation interaction. At TB, *Fucus* spp. varied in abundance across the elevation ( $F_{2, 171} = 7$ ,  $P = 0.001$ ) and exposure ( $F_{2, 171} = 7.6$ ,  $P = 0.001$ ) gradients, and the interaction term was significant ( $F_{4, 171} = 17.2$ ,  $P < 0.001$ ). Abundance

**Fig. 2** Abundance (mean % cover  $\pm$  SE) of *Ascophyllum nodosum* across elevation and exposure gradients at Sea Spray Shore (SS) and Tor Bay Provincial Park (TB). The four upper graphs show main effects; significant differences between factor levels are indicated by different letters. The lower graph shows simple effects (only for TB, because the interaction term was not significant for SS); the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row of letters compares means for exposure levels separately for each elevation (significant differences between means are indicated by different letters). We used a significance level of  $\alpha = 0.01$



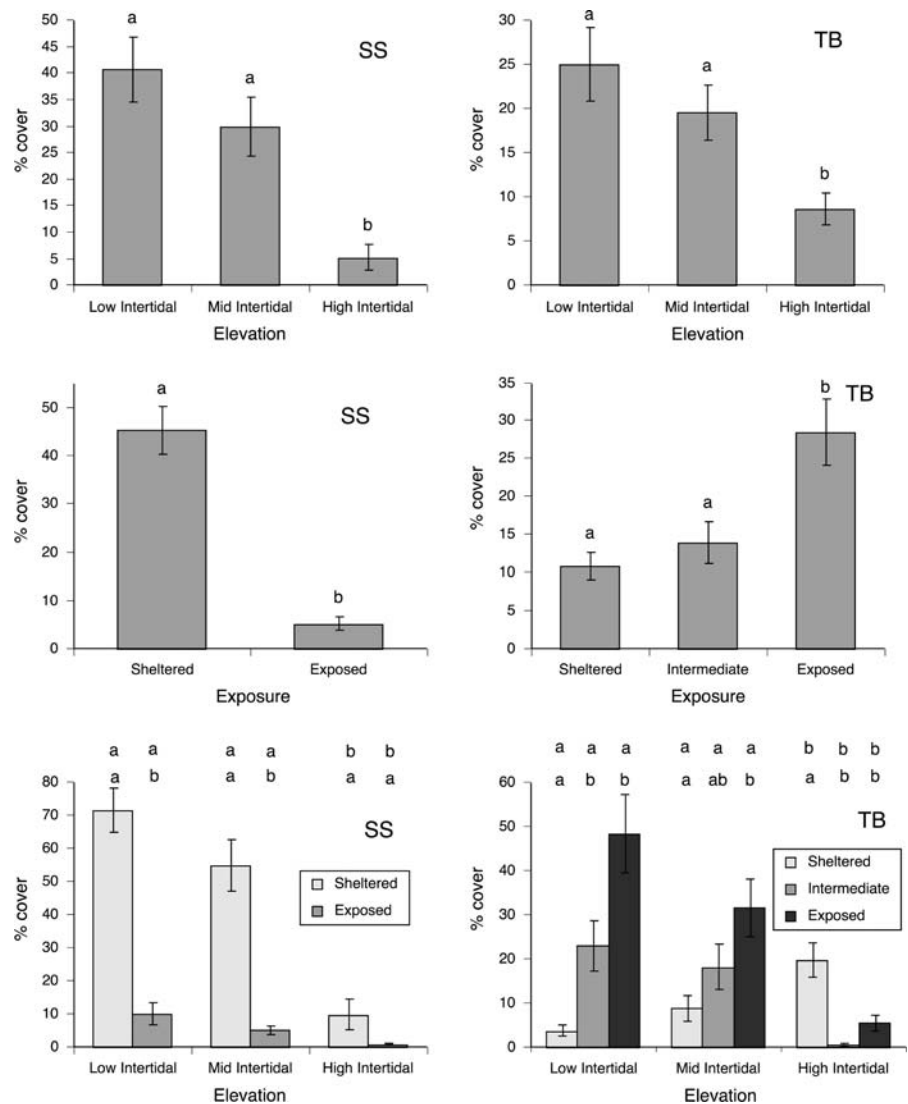
was higher in exposed areas (>25% cover on average) than in more sheltered areas (Fig. 3). The significance in the interaction term was evident in that abundance decreased with elevation in exposed areas but increased with elevation in sheltered areas (Fig. 3). For TB, the magnitude of effect was 5% for exposure, 5% for elevation and 24% for the exposure  $\times$  elevation interaction.

*Chondrus crispus*

*Chondrus crispus* only varied in abundance across the elevation gradient (SS:  $F_{2, 114} = 105.8, P < 0.001$ ;

TB:  $F_{2, 171} = 198.3, P < 0.001$ ). Abundance was statistically unaffected by exposure (SS:  $F_{1, 114} = 3.6, P = 0.06$ ; TB:  $F_{2, 171} = 1.6, P = 0.203$ ) or by the elevation  $\times$  exposure interaction (SS:  $F_{2, 114} = 1.7, P = 0.196$ ; TB:  $F_{4, 171} = 0.9, P = 0.449$ ). On both coasts, thalli were absent at the high intertidal zone, rare at the mid-intertidal zone, and abundant at the low zone (>14% cover at SS and >30% cover at TB, on average; Fig. 4). No significant differences in abundance occurred across the exposure gradient at the low intertidal zone. The magnitude of effect for elevation was 63% at SS and 69% at TB.

**Fig. 3** Abundance (mean % cover  $\pm$  SE) of *Fucus* spp. across elevation and exposure gradients at Sea Spray Shore (SS) and Tor Bay Provincial Park (TB). The four upper graphs show main effects; significant differences between factor levels are indicated by different letters. The two lower graphs show simple effects; the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row of letters compares means for exposure levels separately for each elevation (significant differences between means are indicated by different letters). We used a significance level of  $\alpha = 0.01$

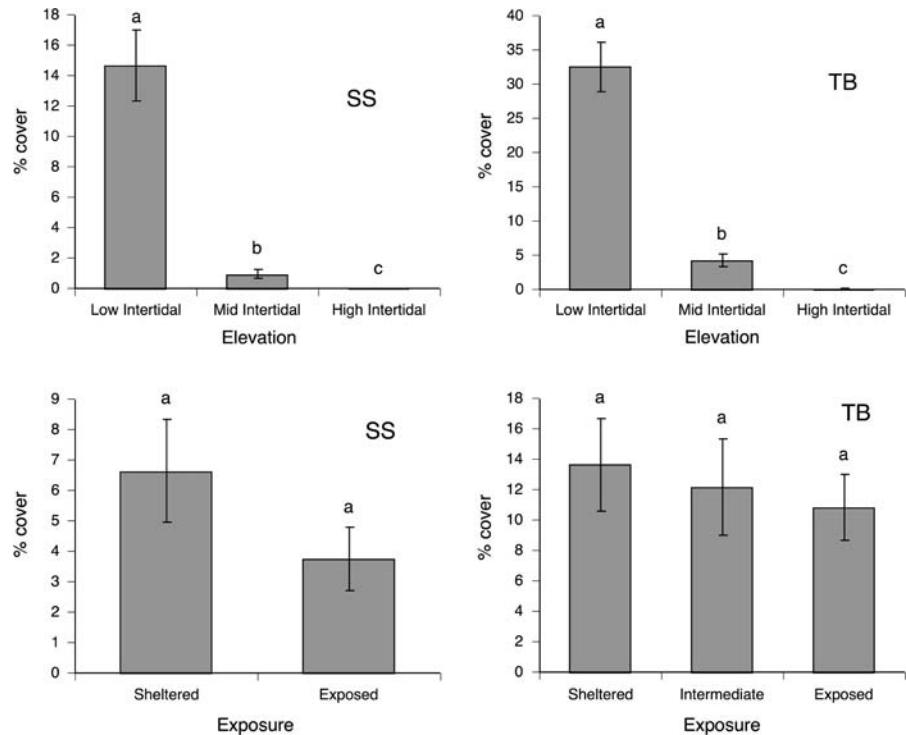


### *Semibalanus balanoides*

The most prominent feature for *Semibalanus balanoides* was the large difference in abundance between the Gulf of St. Lawrence coast and the Atlantic coast. Mean cover for elevation  $\times$  exposure combinations ranged between 30 and 80% for SS, but were always less than 4% at TB (Fig. 5). A high proportion of barnacle cover at SS was made up by recruits, however, adults being less common. At SS, *Semibalanus balanoides* only varied in abundance across the elevation gradient ( $F_{2, 114} = 6.3$ ,  $P = 0.003$ ), exposure having no significant effect ( $F_{1, 114} = 2.6$ ,  $P = 0.113$ ); the interaction term was significant

( $F_{2, 114} = 9$ ,  $P < 0.001$ ). Abundance was similar between exposed and sheltered areas (Fig. 5). Across the elevation gradient, abundance was highest at the mid-intertidal zone. At mid- and low elevations, abundance was higher in exposed areas, while, at high elevations, abundance was higher in sheltered areas (Fig. 5). For SS, the magnitude of effect was 7% for elevation and 11% for the exposure  $\times$  elevation interaction. At TB, *Semibalanus balanoides* varied in abundance across the elevation ( $F_{2, 171} = 44.6$ ,  $P < 0.001$ ) and exposure ( $F_{2, 171} = 7.1$ ,  $P = 0.001$ ) gradients, and the interaction term was significant ( $F_{4, 171} = 6.6$ ,  $P < 0.001$ ). Abundance generally increased from the low to the high intertidal

**Fig. 4** Abundance (mean % cover  $\pm$  SE) of *Chondrus crispus* across elevation and exposure gradients at Sea Spray Shore (SS) and Tor Bay Provincial Park (TB). The four graphs show main effects; significant differences between factor levels are indicated by different letters. We used a significance level of  $\alpha = 0.01$



zone (Fig. 5). Across the exposure gradient, abundance was lower in exposed areas (Fig. 5). For TB, the magnitude of effect was 4% for exposure, 29% for elevation and 7% for the exposure  $\times$  elevation interaction.

#### *Mytilus* spp.

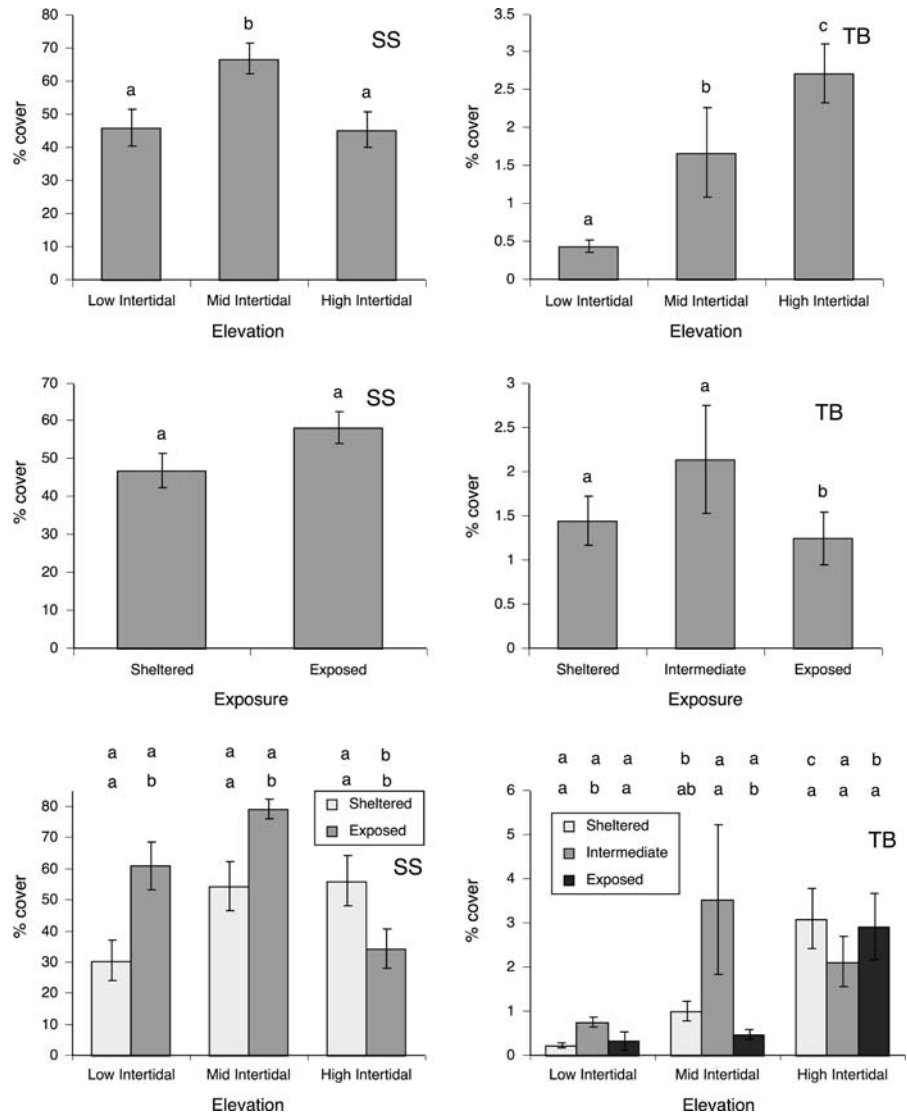
Mussels occurred in low abundance (always <7% average cover), being more abundant at SS than at TB by one order of magnitude (Fig. 6). Organisms were mostly concentrated in crevices and cracks, however, showing high densities in such microhabitats, apparently displacing all other primary-space holders there. At SS, *Mytilus* spp. varied in abundance across the elevation ( $F_{2, 114} = 15.6$ ,  $P < 0.001$ ) and exposure ( $F_{1, 114} = 7.3$ ,  $P = 0.008$ ) gradients, while the interaction term was not significant ( $F_{2, 114} = 2.7$ ,  $P = 0.072$ ). Mussel cover was higher in exposed than in sheltered areas, while, across elevation, cover peaked at the mid-intertidal zone (Fig. 6). For SS, the magnitude of effect was 4% for exposure and 18% for elevation. At TB, *Mytilus* spp. only showed a significant elevation  $\times$  exposure interaction

( $F_{4, 171} = 8.6$ ,  $P < 0.001$ ). Elevation ( $F_{2, 171} = 0.5$ ,  $P = 0.622$ ) and exposure ( $F_{2, 171} = 0.7$ ,  $P = 0.496$ ) had no significant effect on mussel abundance. Significant differences between some elevation  $\times$  exposure combinations were detected (Fig. 6), but the very low abundances (average cover was always <1.2%) rendered such comparisons not particularly meaningful. For TB, the magnitude of effect was 15% for the exposure  $\times$  elevation interaction.

#### Discussion

We found quantitative support for most of our hypotheses. Filter feeders occurred in lower abundances in Nova Scotia than farther south, in New England, but the seaweeds apparently did not differ much, at least when the open Atlantic coast of Nova Scotia and New England (published data; see below) were compared. Abundance was considerably lower on the Gulf of St. Lawrence coast for all taxa, particularly in shore areas subjected to intense ice scour every winter. At the local scale on both studied coasts in Nova Scotia, abundance varied greatly

**Fig. 5** Abundance (mean % cover  $\pm$  SE) of *Semibalanus balanoides* across elevation and exposure gradients at Sea Spray Shore (SS) and Tor Bay Provincial Park (TB). The four upper graphs show main effects; significant differences between factor levels are indicated by different letters. The two lower graphs show simple effects; the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row of letters compares means for exposure levels separately for each elevation (significant differences between means are indicated by different letters). We used a significance level of  $\alpha = 0.01$

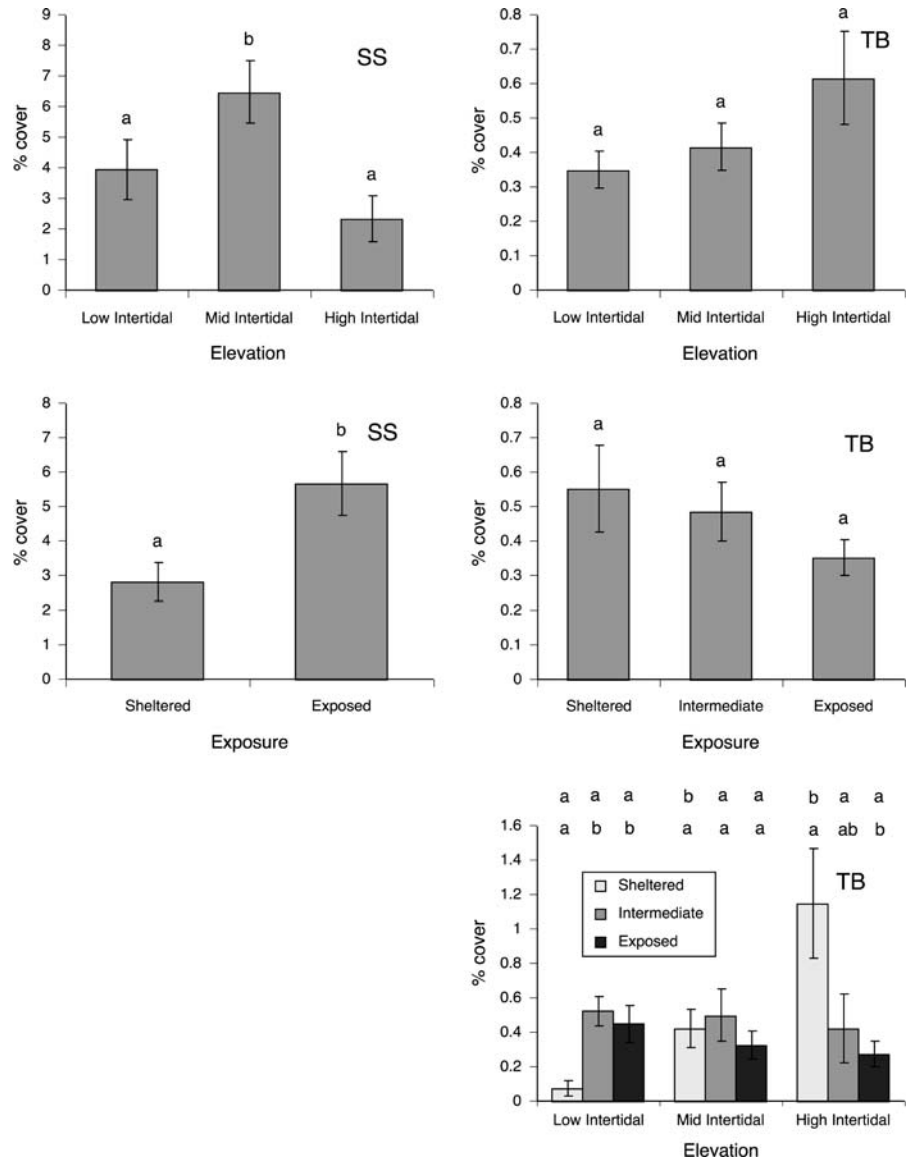


between extremes across elevation and exposure gradients. A taxon-specific discussion is offered below, aiming to improve the knowledge base on the distribution and abundance of these important basal organisms on NW Atlantic rocky shores.

*Ascophyllum nodosum* was virtually absent in exposed areas but abundant in sheltered areas both at SS and TB, which coincides with previous findings on NW (Kingsbury, 1976; Menge, 1976; Novaczek & McLachlan, 1989; Adey & Hayek, 2005) and also NE (Cervin & Åberg, 1997) Atlantic rocky shores. This pattern suggests that *A. nodosum* is sensitive to exposure to waves (Cousens, 1985) and ice scour (Mathieson et al., 1982; Åberg, 1992). Adey and

Hayek (2005) attributed the lower *A. nodosum* abundance in Newfoundland than in the Gulf of Maine to latitudinal differences in ice scour. Also, high losses of *A. nodosum* biomass occurred in Sweden in years with intense ice scour (Åberg 1992). Regarding wave exposure, the inability of *A. nodosum* zygotes to firmly attach to wave-exposed surfaces (Vadas et al., 1990) might explain its virtual absence on exposed shores. The predominance of *A. nodosum* on New England sheltered shores is attributed to the competitive release from mussels, which are naturally dominant organisms controlled by whelks (*Nucella lapillus*) and sea stars (*Asterias* spp.) under low wave exposure (Lubchenco & Menge, 1978; Bertness

**Fig. 6** Abundance (mean % cover  $\pm$  SE) of *Mytilus* spp. across elevation and exposure gradients at Sea Spray Shore (SS) and Tor Bay Provincial Park (TB). The four upper graphs show main effects; significant differences between factor levels are indicated by different letters. The lower graph shows simple effects (only for TB, because the interaction term was not significant for SS); the upper row of letters compares means for elevation levels separately for each exposure level, while the lower row of letters compares means for exposure levels separately for each elevation (significant differences between means are indicated by different letters). We used a significance level of  $\alpha = 0.01$



et al., 2004). Whether the *Ascophyllum–Mytilus*–predators interaction plays the same role in sheltered habitats in Nova Scotia is unknown. Mussels were in low abundance (mostly restricted to crevices) on our shores, suggesting abiotic limitation; on the other hand, whelks and sea stars were rare at our sites (Scrosati & Heaven, 2007), suggesting a weak predation control. Experiments on the possible latitudinal variation in the intensity of this trophic cascade are necessary. When viewed at the regional scale along the open Atlantic coast, the abundance of *Ascophyllum nodosum* at TB was similar to that

reported in New England (Keser & Larson, 1984; Lubchenco, 1986; Petraitis & Methratta, 2006). This suggests that the latitudinal environmental gradient (e.g., temperature and nutrients; Petrie & Yeats, 2000; Fisheries and Oceans Canada, 2007a) does not strongly affect this species along this regional range of the coast.

The broad spatial range of *Fucus* spp. at SS and TB agrees with previous findings that *Fucus* is generally present across all exposures on rocky shores in the NW (Menge, 1976; Novaczek & McLachlan, 1989; Adey & Hayek, 2005; Coyer

et al., 2006) and NE (Coyer et al., 2006) Atlantic. At SS and TB, the species of *Fucus* can only be identified in the field using adult specimens. On the basis of only such observations, *Fucus serratus* occurred almost exclusively at the low intertidal zone on sheltered areas at SS, *F. spiralis* occurred almost only at the high intertidal zone on exposed areas at TB, and *F. vesiculosus* was common throughout vertical and horizontal gradients on both coasts, while patterns for *F. distichus* were less evident due to morphological overlaps. Thus, the widespread occurrence of the genus *Fucus* across almost all environmental conditions (except on exposed areas at SS, which undergo strong ice scour in winter) seems to be explained by the sum of the ecological niches of its different species. When viewed at the regional scale along the open Atlantic coast, particularly comparing TB with New England (Lubchenco, 1986), no obvious trend in *Fucus* abundance is apparent.

*Chondrus crispus* occurred almost exclusively at the low intertidal zone at SS and TB, irrespective of exposure, which coincides with findings for NW (Mathieson & Prince, 1973; Menge, 1976; Lubchenco, 1980; Novaczek & McLachlan, 1989; Worm & Chapman, 1998; Adey & Hayek, 2005) and NE (Cervin & Åberg, 1997) Atlantic rocky shores. Along the open Atlantic coast, differences in local distribution between Nova Scotia and New England seem to exist, however. In New England, mussels have been reported to predominate over *C. crispus* at low elevations in wave-exposed habitats (Lubchenco & Menge, 1978; Menge, 1983), although this is not true everywhere in that region (R. Scrosati, pers. obs. at Pemaquid Point, southern Maine, in 2007). At TB, mussels were rare in exposed habitats and *C. crispus* did not differ in abundance between exposures. Apparently, mussels are less important for community organization on our shores. The intertidal *C. crispus* thalli at SS and TB are the highest organisms of this species on the shore, as *C. crispus* also grows at the subtidal zone (Taylor & Chen, 1994), the upper distribution limit apparently being determined by desiccation stress at low tides (Lubchenco, 1980).

*Semibalanus balanoides* had a higher cover on the Gulf of St. Lawrence coast than on the Atlantic coast of Nova Scotia by one order of magnitude. In fact, barnacles had the highest cover among all benthic

species identified anywhere at SS (Scrosati & Heaven, 2007). However, at SS most of barnacle cover was made up by recruits, which occur extensively on the shore in spring (about 300–600 recruits  $\text{dm}^{-2}$ ; R. Scrosati, unpublished data). The intense ice scour occurring in winter at SS (Scrosati & Heaven, 2006) removes many organisms from the substrate, leaving adults in low densities shortly after ice melts (about 5–100 adults  $\text{dm}^{-2}$ ; R. Scrosati, unpublished data). At TB, both adults and recruits showed much lower densities. What factors could explain such a difference between both coasts? In ice-exposed areas at SS, barnacles could gain a competitive advantage because of their hard shell and small size, which would allow them to survive winter ice scour better than most other species, in crevices if scour is too strong. At TB, without significant ice scour, competitors (Menge, 1976; Peterson, 1979) and predators (Gosselin & Bourget, 1989; Minchinton & Scheibling, 1993) would regulate barnacle populations. In sheltered areas at SS, however, seaweed cover was similar than in sheltered areas at TB, but barnacle recruits were very abundant at SS and rare at TB. Thus, factors affecting pre-recruit stages (Minchinton & Scheibling, 1991) might also explain the difference in abundance between the Gulf of St. Lawrence and Atlantic coasts. Perhaps the higher concentration of chlorophyll *a* (proxy for phytoplankton abundance) in the southern Gulf of St. Lawrence (National Aeronautics and Space Administration, 2007) may favour barnacle larval development and survival and, ultimately, benthic abundance on that coast. Along the open Atlantic coast, *Semibalanus balanoides* was less abundant at TB than in New England (Keser & Larson, 1984; Bertness, 1989; Adey & Hayek, 2005). For example, Menge (1976) reported a mean barnacle cover >85% on a sheltered New England shore. Also, dense stands of hummocking barnacles are common in New England (Grant, 1977; Bertness et al., 1998), but not at TB. Bertness (2007) suggested that oligotrophic waters at northern latitudes might be responsible for the low barnacle abundance via a reduced availability of phytoplankton. Coastal chlorophyll *a* concentration decreases from New England to Nova Scotia (National Aeronautics and Space Administration, 2007), which may indicate a decreasing food availability for barnacle larvae (Pineda et al., 2006) and adults with latitude.

Mussels (*Mytilus* spp.) had a considerably lower cover than barnacles in Nova Scotia. Mussel cover

was always lower than 10% at SS and 2% at TB. In New England, mussels usually show a much higher cover (Lubchenco & Menge, 1978; Bertness et al., 2002), such as 40–90% at the mid-intertidal zone on an exposed shore (Menge, 1976). South of TB in Nova Scotia (near Halifax), mussels show intermediate values of cover (Hunt & Scheibling, 2001). The oligotrophic nature of coastal waters in Nova Scotia has been suggested as a possible explanation for the low mussel abundance via food (plankton) limitation (Chapman & Johnson, 1990; Bertness, 2007). However, mussels form dense aggregations in crevices at SS and at TB (a pattern also reported for other Gulf of St. Lawrence sites; McKindsey & Bourget, 2001), suggesting that food limitation might not be the primary cause of their habitat-wide low abundance. In fact, despite the decreasing trend in chlorophyll *a* concentration in coastal waters from New England to Nova Scotia (National Aeronautics and Space Administration, 2007), zooplankton biomass generally increases from south to north in this latitudinal range (Harrison et al., 2006). The low mussel cover in Nova Scotia might result primarily from winter ice scour (only due to ice-foot breakage on open Atlantic shores) on emergent rocky surfaces outside of crevices (Bertness, 2007). Another physical factor possibly explaining latitudinal differences in mussel abundance is wave action through an increased intensity and frequency of winter storms at higher latitudes (Hunt & Scheibling, 2001). Population limitation by predators (whelks; Hunt & Scheibling, 1998) may also be a contributing factor, although the low whelk abundance on our shores (Scrosati & Heaven, 2007) suggests that whelk predation would play a secondary role there. At the local scale, across the elevation gradient at SS, the increase in *Mytilus* spp. abundance from the low to the mid-intertidal zone coincides with an increase in the abundance of *Ascophyllum nodosum*, suggesting that *A. nodosum* may ameliorate habitat conditions, as found for New England (Bertness & Leonard, 1997; Bertness et al., 1999). Across the exposure gradient at SS, the higher abundance of *Mytilus* spp. in exposed habitats coincides with a decrease in *A. nodosum* and *Fucus* abundance. Such a contrasting pattern of abundance between mussels and fucoids has also been reported for New England, where mussels predominate in high-flow areas and fucoids in sheltered areas (Bertness et al., 2004). In wave-exposed areas, increased

oxygenation and food (plankton) provision rates and decreased consumer pressure due to hydrodynamic forces might explain mussel predominance.

The relative contribution of the vertical (elevation) and horizontal (wave/ice exposure) gradients to the spatial variation in abundance differed among taxa. The most evident case was given by the seaweeds. For *Ascophyllum nodosum*, exposure had an overwhelmingly larger effect on abundance than elevation on both coasts. *Chondrus crispus* represented the opposite case, as thalli were almost restricted to the low intertidal zone, irrespective of exposure. The species of *Fucus*, when considered together, represented an intermediate case, as elevation and exposure contributed similarly. The two filter feeders also differed in this respect. Elevation explained a higher proportion of the spatial variability in abundance than exposure for *Semibalanus balanoides* on both coasts, but neither factor explained much of the variability for *Mytilus* spp., the interaction between both factors being relatively more important. For the Gulf of St. Lawrence and open Atlantic coasts of Nova Scotia, elevation explains a larger proportion of the spatial variation in species richness (total number of species in the community) than exposure (Scrosati & Heaven, 2007). This suggests that life at the intertidal zone is generally more sensitive to environmental changes across elevation than across exposure gradients, elevation being especially important at local spatial scales (Harley & Helmuth, 2003). However, it is clear that, when viewed at the species or genus level, organisms show a higher variety of spatial patterns (see also Schoch et al., 2006).

In summary, our study in Nova Scotia has identified similarities and differences in the abundance of intertidal basal species relative to southern shores. In extreme environments, such as strongly ice-scoured habitats, species abundance was low (except for barnacles when recruits were included). In more benign environments, seaweed abundance was apparently as high as in New England, but filter-feeder abundance was generally lower than in New England. Future experimental work should elucidate the causal mechanisms behind these patterns. Changes in the degree of environmental stress and coastal nutrient concentration (which affects planktonic food supply for filter feeders) appear to be primary factors. With the expected changes in species distribution resulting from climatic and

oceanographic changes (Sagarin et al., 1999; Parmesan & Yohe, 2003; Helmuth et al., 2005), the information generated by our study offers a baseline on which to monitor future ecological change on NW Atlantic rocky shores.

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