

POPULATION STRUCTURE OF THE BARNACLE, *SEMIBALANUS
BALANOIDES* (CIRRIPIEDIA, THORACICA), ACROSS INTERTIDAL
ENVIRONMENTAL STRESS GRADIENTS IN NORTHERN NOVA SCOTIA,
CANADA

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ABSTRACT

We describe spatial trends in population structure of the barnacle, *Semibalanus balanoides*, across gradients of environmental stress on the Gulf of St. Lawrence coast of Nova Scotia, Canada. In the early summer of 2006, we examined vertical gradients of intertidal elevation and horizontal gradients of exposure to wave action and winter ice scour. Recruits were considerably less abundant than adults at all sites, suggesting a high post-recruitment mortality. Although adult barnacles seemed less abundant in areas subjected to strong winter ice scour than in sheltered areas, such a trend lacked statistical support. Adult barnacles were more abundant at high elevations than at low elevations, possibly as a result of vertical differences in the intensity of competition and predation. Size structure was better developed at the high intertidal zone than at the low intertidal zone, with larger organisms occurring at high elevations. In general, it appears as though biotic interactions at the low intertidal zone may play a greater role than abiotic factors at the high intertidal zone in determining the population structure of *S. balanoides*, although field experimentation will be necessary to confirm this notion.

RESUMEN

Describimos tendencias espaciales en la estructura poblacional del balano *Semibalanus balanoides* a través de gradientes de estrés ambiental en la costa del golfo de San Lorenzo en Nova Scotia, Canadá. En el verano temprano de 2006, examinamos gradientes verticales de elevación intermareal y gradientes horizontales de exposición al oleaje y al raspado por hielo marino invernal. Los reclutas fueron considerablemente más abundantes que los adultos en todos los sitios, sugiriendo una alta mortalidad luego del reclutamiento. Aunque los balanos adultos parecían ser menos numerosos en áreas sujetas a un raspado intenso por hielo marino invernal que en áreas protegidas, tal tendencia no mostró un sustento estadístico. Los balanos adultos fueron más numerosos en el intermareal superior que en el inferior, posiblemente como resultado de diferencias verticales en la intensidad de la competencia y predación. La estructura de tamaños estuvo mejor desarrollada en

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el intermareal superior que en el inferior, con organismos más grandes ocurriendo en el alto intermareal. En general, parece que las interacciones bióticas fueran más importantes en el intermareal inferior que los factores abióticos en el intermareal superior en la determinación de la estructura poblacional de *S. balanoides*, aunque experimentos de campo serán necesarios para confirmar esta noción.

INTRODUCTION

On cold-temperate coasts in the N.W. Atlantic, barnacles are significant components of rocky intertidal communities (Bertness, 2007). The present study characterizes the population structure of the barnacle, *Semibalanus balanoides* (Linnaeus, 1766), across full intertidal gradients of environmental stress in the Gulf of St. Lawrence, Nova Scotia, Canada. This species is the predominant barnacle in rocky intertidal habitats along the Gulf of St. Lawrence (Véliz et al., 2004; Scrosati & Heaven, 2007). The distribution of this species along the Atlantic coast of North America extends from Baffin Island, Nunavut, to Cape Hatteras, South Carolina (Drouin et al., 2002).

Rocky intertidal habitats are good model systems for studying factors affecting the abundance and distribution of organisms, because they host well defined gradients of environmental stress over relatively short distances, which most other habitats do not show (Bertness & Leonard, 1997). Such gradients occur across both vertical and horizontal planes. As a result of tidal fluctuations, a vertical gradient of increasing temperature, irradiance, desiccation, and osmotic stresses with elevation occurs (Raffaelli & Hawkins, 1996; Garbary, 2007). Horizontal stress gradients include gradients in the degree of exposure to wave action (Denny & Wetthey, 2001; Scrosati & Heaven, 2007) and, on polar and subpolar shores, ice scour (Scrosati & Heaven, 2006).

Gradients in abiotic stress are the basis of complex species interactions in intertidal habitats. Several biotic factors are important in structuring barnacle populations. The strength of the effect of such factors depends on the local degree of environmental stress. Biotic factors affecting the population structure of *S. balanoides* include competition (Menge, 1976, 2000; Grant, 1977; Leonard, 2000; Buschbaum, 2001; Kent et al., 2003), predation (Connell, 1961; Bertness, 1989), and mutualism and commensalism (Raimondi, 1988; Bertness, 1989; Bertness et al., 1998; Barnes, 1999; Buschbaum, 2001; Holmes et al., 2005). Generally, the importance of competition in establishing population structure is minimized when predators are abundant, when physical stress is intense or frequent, and when recruitment is nominal (Bertness, 1989). Essentially, the population structure of barnacles is established in high intertidal areas by heat and desiccation stresses, and in low intertidal areas by predators and competitors (Connell, 1961). The abundant

centre hypothesis states that the highest densities of organisms of a particular species are generally found in the centre of their range, where environmental conditions are theoretically most favourable (Sagarin & Gaines, 2002).

In this paper, we characterize the population structure of *Semibalanus balanoides* across full vertical (elevation) and horizontal (wave/ice exposure) gradients of environmental stress for a shore in the southern Gulf of St. Lawrence. Specifically, we examined spatial changes in population density, mean size, and size structure. Characterizing *S. balanoides* populations across full environmental stress gradients for the first time in this region should allow for a greater understanding of the factors influencing the population structure of this species. It should also facilitate future work on intertidal community organization on the southern Gulf of St. Lawrence coast, as this barnacle is one of the most abundant benthic species on this shore (Scrosati & Heaven, 2007).

We hypothesized that the density of barnacle adults would be lower in sites heavily exposed to ice scour than in sites sheltered from ice scour, as intense ice scour should result in greater barnacle mortality (Scrosati & Heaven, 2006). Across the vertical gradient, we hypothesized that the highest density of adult barnacles would be found at the mid-intertidal zone, in accordance with the abundant centre hypothesis (Sagarin & Gaines, 2002) and the findings of Grosberg (1982) that adult intertidal barnacles were most abundant at mid elevations. We also hypothesized that the mean size of barnacles would be greatest at the low intertidal zone, where abiotic stress is relatively low and food (plankton) access relatively high, factors that together may facilitate growth. We hypothesized that size variability would be greatest at the low intertidal zone because potentially higher growth rates and greater survivorship in this region may allow for larger barnacles to exist, while recruits of similar size to those found higher up on the shore may occur simultaneously. Consequently, the size structure at the low intertidal zone would be better developed, having relatively more size classes than at higher elevations.

MATERIAL AND METHODS

We did our study at Sea Spray Shore (45°46'N 62°9'W), located near Arisaig, on the southern coast of the Gulf of St. Lawrence, Nova Scotia, Canada. This site is located in the subarctic zone, and so is exposed to great seasonal variability in abiotic conditions. In summer, seawater temperatures reached a maximum of 21°C; in winter, seawater was near the freezing point (Scrosati & Heaven, 2007). Winter temperatures are low enough to freeze the water, forming sheets of ice that lie on the surface of the seawater (Saucier et al., 2003). Such ice sheets may accumulate on the shore due to wave action, currents, and wind, and grind across

rocky intertidal habitats, causing great physical disturbance (Scrosati & Heaven, 2006). The degree of ice scour is spatially correlated with the degree of wave exposure (see fig. 2 in Scrosati & Heaven, 2007). Seawater salinity ranged between 30 and 32 ppt (Scrosati & Heaven, 2007). The predominant substrate on this rocky shore is volcanic bedrock. Maximum tidal amplitude is about 1.8 m.

We sampled the full vertical extent of the intertidal zone at each of two sites, one exposed to strong waves and winter ice scour and one sheltered from both stressors. Both sites were visually representative of typical exposed and sheltered habitats along this coast. Values of ice scour intensity appear in Scrosati & Heaven (2006), while values of maximum water velocity appear in Scrosati & Heaven (2007). At each site, we divided the intertidal zone into three equal elevation ranges (high, mid, and low intertidal zones). We delimited all sampling areas using permanent nails that were secured to the rocky substrate with marine epoxy.

We examined the population structure of *Semibalanus balanoides* across the vertical and horizontal gradients between 21 and 25 June 2006. Sampling was done during low tides to obtain accurate measurements. Three descriptors of population structure were analysed: density, mean size, and size structure. At each combination of elevation (high, mid, and low) and exposure (sheltered and exposed) levels, we measured the density of barnacles in 40 random, 5 cm × 5 cm quadrats within a 100 m stretch of representative shoreline. All living adults and recruits were counted in each quadrat. Living barnacles were considered to be those having firmly closed opercular valves at low tide. Adults were considerably larger than recruits at the time of sampling (fig. 1), thus making it easy to identify both life-history stages. To characterize barnacle mean size and size structure for each elevation × exposure combination, the basal diameter of 100 random barnacles was measured (to the nearest 1 mm) in each of 10 random, 10 cm × 10 cm quadrats.

For each elevation × exposure combination, we calculated the mean density of barnacle adults and recruits, and the corresponding 95% confidence intervals. A significant difference in density between two given treatments occurred when their 95% confidence intervals did not overlap (Sokal & Rohlf, 1995). Mean barnacle size was calculated for each quadrat. Mean size was then calculated for each elevation × exposure combination, along with the corresponding 95% confidence intervals, using the 10 means calculated for each elevation × exposure combination. Significant differences in mean size between treatments occurred when two given 95% confidence intervals did not overlap. Size was used because it provides a better analysis of occupied space than age (Svensson et al., 2004). Jenkins et al. (2001) noted that it can be very difficult to separate individuals into age categories beyond simple categories of adults and recruits, because generations tend to overlap and growth rates of individual barnacles may vary. To calculate size structure, all measured barnacles in each quadrat were assigned to 1-mm size

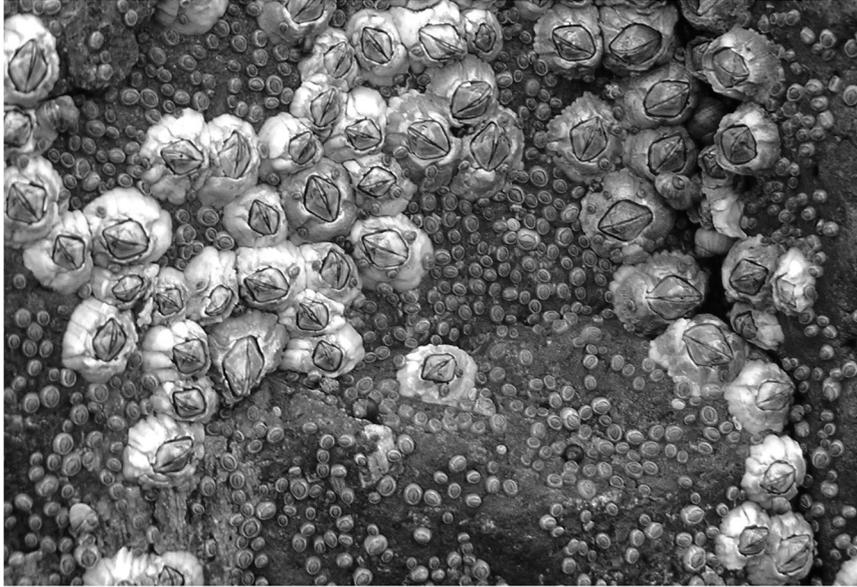


Fig. 1. View of adult and recruit *Semibalanus balanoides* (L., 1766) at Sea Spray Shore. [Photo by Ricardo Scrosati.]

classes based on basal diameter. The absolute frequency of barnacles fitting into each size class, and then the relative frequency, was calculated for each quadrat. The average relative frequency of barnacles belonging to each size class, and the corresponding 95% confidence intervals, were calculated for each combination of exposure and elevation. All calculations were done using Microsoft Excel 2004 for Macintosh.

RESULTS

Adults occurred in significantly ($p < 0.05$) lower densities than recruits at all combinations of exposure and elevation (fig. 2). In both sheltered and exposed sites, adults occurred in significantly lower densities at the low intertidal zone than at the high intertidal zone; values were intermediate at the mid intertidal zone (fig. 2A). At each elevation, the density of adults was statistically similar between sheltered and exposed sites (fig. 2A).

The density of recruits in the sheltered site was significantly lower at the low intertidal zone than at the high and mid intertidal zones. In the exposed site, recruit density was greatest at the mid intertidal zone, significantly lower at the low intertidal zone, and lowest at the high intertidal zone (fig. 2B). Recruit density was similar between exposed and sheltered shores at the high intertidal zone, and

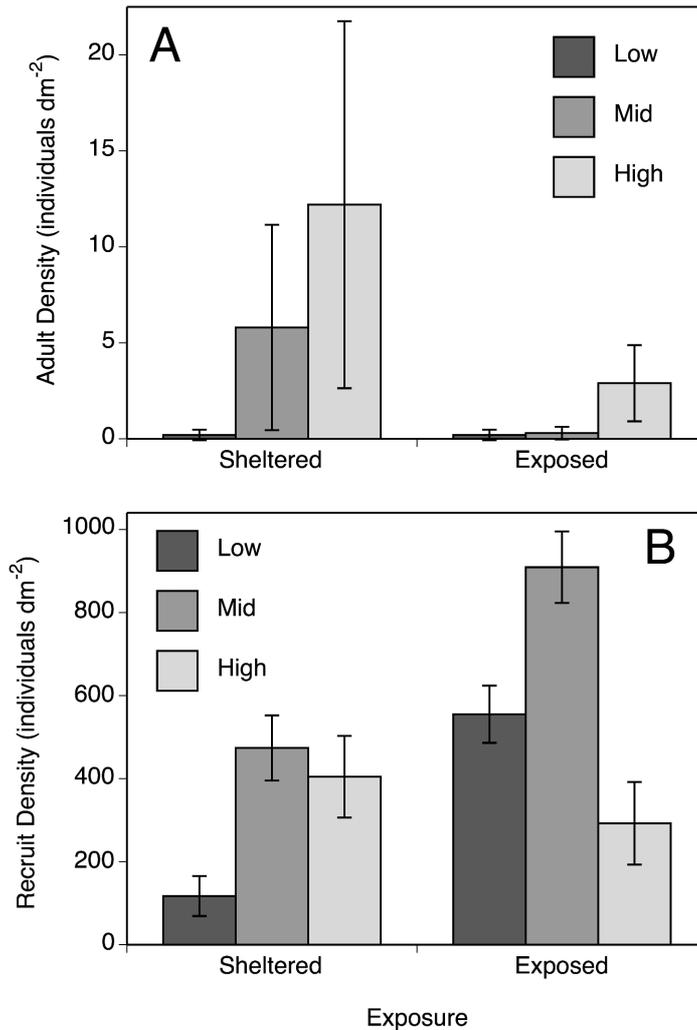


Fig. 2. Density of: A, adult; and B, recruit *Semibalanus balanoides* (L., 1766) on sheltered and exposed areas at Sea Spray Shore in June 2006 at the low, mid, and high intertidal zones. Values represent mean density (individuals · dm⁻²) ± 95% confidence intervals.

significantly higher in the exposed site than in the sheltered site at the mid and low intertidal zones (fig. 2B).

There was no significant difference in mean size of barnacles at high and mid intertidal elevations between exposed and sheltered shores. At the low intertidal zone, barnacle mean size was significantly higher in the exposed site than in the sheltered site (fig. 3). On both the exposed and sheltered shores, there was no difference in mean size of barnacles across elevations (fig. 3).

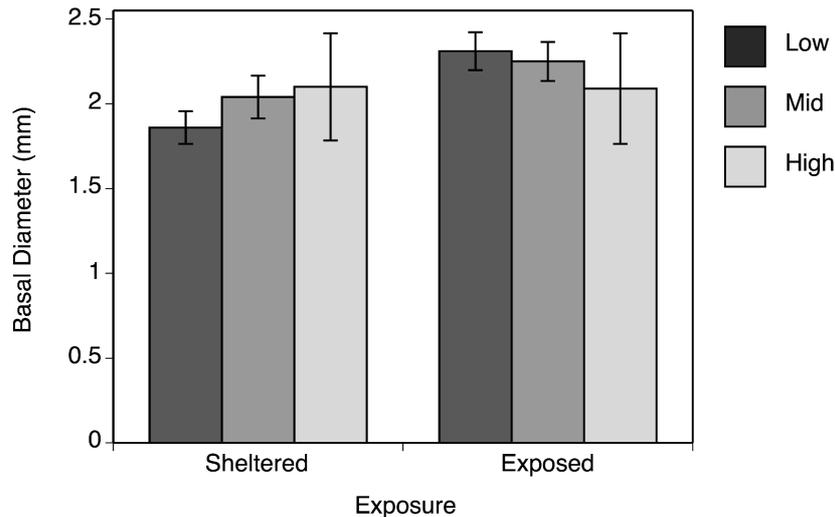


Fig. 3. Size of *Semibalanus balanoides* (L., 1766) on sheltered and exposed areas at Sea Spray Shore in June 2006 at the low, mid, and high intertidal zones. Values represent mean basal diameter (mm) \pm 95% confidence intervals.

The size structure was best developed at the high intertidal zone at each exposure, with nine size classes in the sheltered site and eight size classes in the exposed site. The low intertidal zone had fewer size classes. Size class 2 was generally the most abundant class at each combination of exposure and elevation, while larger size classes were always low in relative abundance (fig. 4).

DISCUSSION

The occurrence of adult barnacles in much lower densities than recruits at all combinations of exposure and elevation suggests that high post-recruitment mortality rates occur throughout the entire shore. High mortality is indeed a characteristic of *Semibalanus balanoides* populations, especially at early stages of development (Jenkins et al., 2001). The recruitment period for this species is limited to a few months on the N.W. Atlantic coast in winter or spring, usually earlier in the year in southern locations (Bousfield, 1954; Minchinton & Scheibling, 1991; Pineda et al., 2006). Then, it is possible that abiotic factors (e.g., heat and desiccation stress in summer and ice scour in winter) and biotic factors (e.g., predation) may considerably reduce the original number of settlers to the density levels finally seen for adults.

At each elevation, the density of adult barnacles was similar between sheltered and exposed shores, contradicting our hypothesis that the more intense ice scour occurring on exposed shores (Scrosati & Heaven, 2006) would result in lower adult

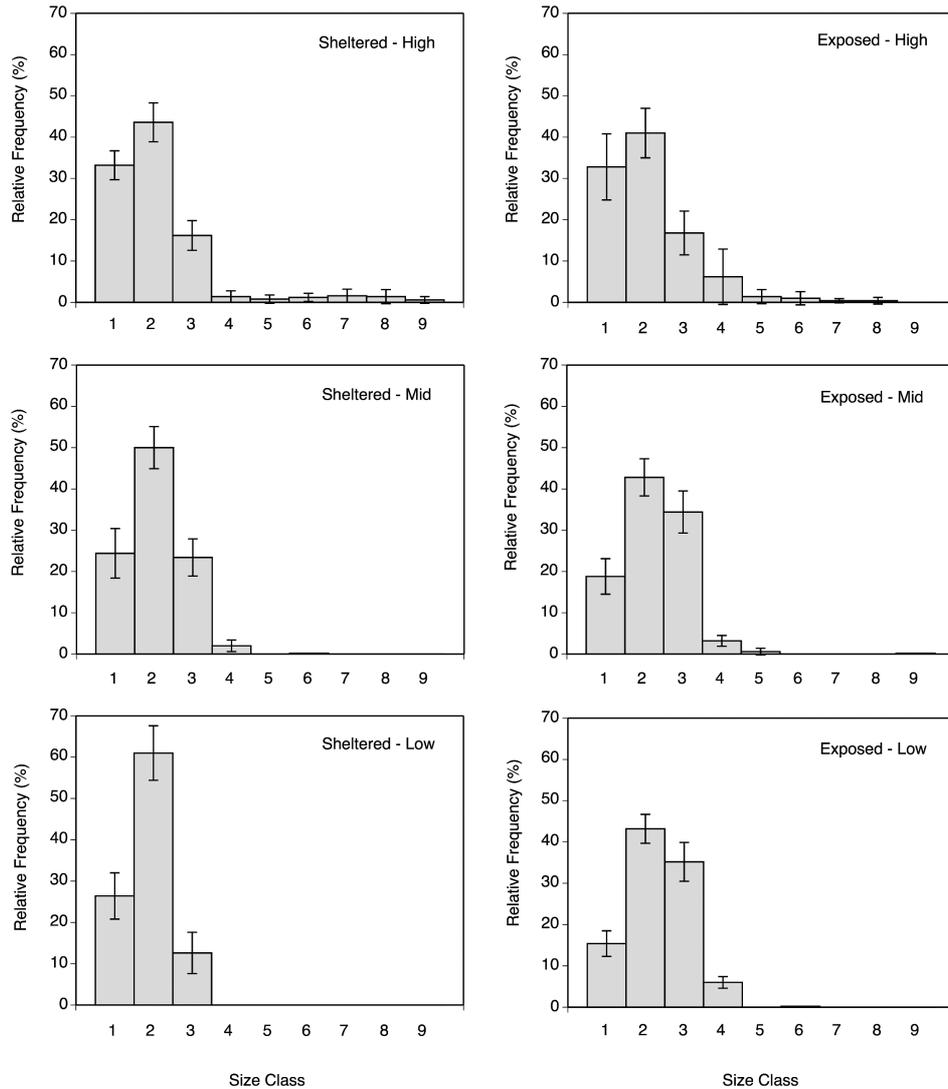


Fig. 4. Size structure of *Semibalanus balanoides* (L., 1766) on sheltered and exposed areas at Sea Spray Shore in June 2006 at the low, mid, and high intertidal zones. Values represent mean relative frequency (%) of size classes (0-1, 1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, and 8-9 mm in basal diameter) \pm 95% confidence intervals.

densities. However, it should be noted that mean adult densities were higher at high and mid elevations in the sheltered site; the high data variability found for the sheltered site seems to explain the lack of statistical differences between sites. The use of a larger size of sampling unit (quadrat) might contribute to reducing such levels of variability and show the expected differences in density between

exposures. We can only regard differences in adult density between exposure levels as apparent for the moment.

The density of adult barnacles decreased towards lower elevations on both sheltered and exposed shores. This contradicts the abundant centre hypothesis, which suggests that the greatest density of adult barnacles should be observed at the centre of their distribution range, where habitat is theoretically optimal (Sagarin & Gaines, 2002). Our results also disagree with those of Grosberg (1982), which showed that adult barnacles were most abundant in mid intertidal regions, and with those of Berger et al. (2006), which showed that barnacle survivorship decreases with increasing elevation. The trend that we observed may have occurred because of the magnitude of the biotic interactions at the low intertidal zone relative to that of abiotic factors at the high intertidal zone. Predators (whelks and sea stars) and competitors (mussels and furoid seaweeds) are more abundant in low intertidal areas than in high intertidal areas at Sea Spray Shore (Scrosati & Heaven, 2007). Both predation and competition may result in increased mortality of *Semibalanus balanoides* at low elevations (Connell, 1961; Menge, 1976, 2000; Grant, 1977; Bergeron & Bourget, 1986; Bertness, 1989; Bertness et al., 1999; Minchinton & Scheibling, 1991; Holmes et al., 2005). At high elevations, barnacle survival is usually limited by abiotic factors such as heat and desiccation (Connell, 1961; Leonard et al., 1999; Miron et al., 1999; Menge, 2000). However, Bertness et al. (1999) found, through experimental manipulation, that at sites north of Cape Cod, U.S.A., shading and group benefits did not enhance survival of *S. balanoides* in high intertidal zones. Presumably, abiotic stress during the ice-free season in northern Nova Scotia is not so harsh because temperatures do not rise high enough. This might explain the higher density of adults at the high intertidal than at the low intertidal zone. Thus, at Sea Spray Shore, biotic interactions at the low intertidal zone could be more important than abiotic factors in upper intertidal zones in structuring barnacle populations. Future experimentation is necessary to test this hypothesis.

For *Semibalanus balanoides*, recruits may occur in lower densities at high, relative to lower, elevations because of reduced immersion time necessary for larval settlement (Minchinton & Scheibling, 1991), reduced food availability for settlers (Miron et al., 1999), or increased heat and desiccation stress (Connell, 1961; Leonard et al., 1999; Menge, 2000; Berger et al., 2006). Since we found such a vertical pattern at the exposed site, but not at the sheltered site, it is evident that other factors may influence barnacle recruitment across vertical intertidal gradients. Recruit density was similar between exposures at the high intertidal zone, but increased with exposure at the mid and low intertidal zones. Such a difference might be explained by the much higher abundance of furoid seaweeds in sheltered habitats than in exposed habitats (Scrosati & Heaven, 2007), which may

decrease barnacle larval settlement or increase the mortality of settlers through whiplash effects (Menge, 1976; Jenkins & Hawkins, 2003). The lack of differences in recruit density between exposed and sheltered areas at the high intertidal zone may be explained, in turn, by the scarcity of furoid seaweeds in such habitats (Scrosati & Heaven, 2007). Bulldozing of newly settled barnacles by grazing periwinkles may also contribute to early mortality of recruits in sheltered, low intertidal zones (Holmes et al., 2005). Field experiments are required to test these potential explanations.

The great similarity in mean size of *Semibalanus balanoides* across elevations and exposures may indicate that there is no optimal size that is physiologically best suited for one particular habitat. The only noteworthy difference occurred between exposure levels at the low intertidal zone, which is explained by the higher relative density of recruits, compared with adult density, in exposed than in sheltered areas at that elevation. As a result of the spatial trends in adult and recruit density, size structure was better developed at high intertidal elevations than at lower elevations. Svensson et al. (2004) studied populations of *S. balanoides* in western Europe and classified barnacles into three size classes, and their results resemble those in our study.

In summary, our work has provided a detailed description of spatial population trends for barnacles across vertical and horizontal intertidal stress gradients in northern Nova Scotia. The description of pattern is an essential first step into the understanding of a particular system (Underwood et al., 2000). Future experimentation through field manipulations will be required to test the possible factors, as discussed above, that may generate the observed patterns.

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