

Intertidal mussels as ecosystem engineers: their associated invertebrate biodiversity under contrasting wave exposures

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Abstract Mussels often act as ecosystem engineers in rocky intertidal habitats, favoring the occurrence of many small invertebrates by increasing habitat complexity and improving local environmental conditions. This study tests the hypothesis that invertebrate assemblages from intertidal mussel beds differ between wave-sheltered and wave-exposed habitats. To this aim, we surveyed exposed and sheltered sites spanning 350 km of coastline in Nova Scotia, Canada. We identified all invertebrates and measured their abundance in replicate quadrats that were fully covered by mussels. In total, we found 50 invertebrate taxa living in these mussel beds. Multivariate analyses revealed that the composition of invertebrate assemblages differed significantly between both habitat types. Exposed habitats supported a greater species richness, and the species that mainly explained the compositional difference between both environments were more abundant in exposed ones. Assemblages were taxonomically dominated by arthropods, annelids, and molluscs and numerically dominated by tubificid oligochaetes regardless of exposure. Our results suggest that exposed habitats may favor the occurrence of filter-feeders, such as barnacles, and sheltered habitats the occurrence of predators, such as small crabs and sea stars, in intertidal mussel beds from the NW Atlantic coast.

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Introduction

Understanding biodiversity patterns in nature is one of the main goals of ecology. The simplest biodiversity descriptor is richness, which is the number of species in a community (Krebs 1999). A more complex descriptor is composition, which is a multivariate measure that considers the identity and relative abundance of species (Heaven and Scrosati 2008). Investigating the drivers of species richness and composition is important because both properties are related to community functioning and stability (Hooper et al. 2012; Cardinale et al. 2013).

Richness and composition may be influenced by species that are able to modify local environmental conditions or that can create habitat through body structures. Such organisms are known as ecosystem engineers, bioengineers, or foundation species (Crain and Bertness 2006; Jones et al. 2010). Their ecological role is particularly relevant in stressful habitats, where bioengineers protect smaller species from the abiotic forces that would otherwise prevent many of them from occurring (Arroyo et al. 2003; Wright et al. 2006; He et al. 2013; Schöb et al. 2013; Watt and Scrosati 2013).

In intertidal habitats, stressful conditions occur when temperature, irradiance, and desiccation reach high values during low tides, which limit the physiological performance of organisms and can even cause their death if extreme values are reached (Raffaelli and Hawkins 1999). During high tides, intertidal organisms are subjected to the physical stress caused by waves, which limit maximum body size and can detach organisms if the waves are strong (Denny and Wethey 2001). In these environments, mussels often are important ecosystem engineers. By strongly attaching themselves to the substrate in

dense monolayered or multilayered beds, mussels create microhabitats among their shells that remain moist and thermally benign during low tides and offer protection against wave action during high tides (Seed 1969, 1996; Suchanek 1985). In addition, mussel beds increase habitat complexity through the aggregation of living individuals, empty shells, and byssal threads, which provide substrate for colonization and also trap sediments and organic particles that serve as food for small invertebrates (Seed 1969; Suchanek 1985; Crooks and Khim 1999; Commito and Rusignuolo 2000; Thiel and Ullrich 2002). Mussel beds also provide shelter from consumers for small organisms (Witman 1985). Therefore, although mussels may outcompete other primary-space holders such as seaweeds and other sessile invertebrates (Paine and Levin 1981; Menge and Sutherland 1987), their bioengineering properties often enhance local biodiversity by facilitating the establishment and persistence of a variety of small invertebrates (Palomo et al. 2007; Arribas et al. 2013).

Quantification of such biodiversity is important from a basic ecological standpoint but also for conservation purposes, as the protection of mussel beds would imply the protection of numerous small species that are often ignored in intertidal diversity studies (Bruno et al. 2003; Bertness 2007; Scrosati and Heaven 2007). A number of studies have investigated how diverse species assemblages are within intertidal mussel beds. About 300 species (including invertebrates, seaweeds, and small fish) were reported for intertidal mussel beds from the NE Pacific coast (Suchanek 1992), up to 92 species from the SE Pacific coast (Prado and Castilla 2006; Valdivia and Thiel 2006), 69 species from the NW Pacific coast (Tsuchiya and Nishihira 1986), 31 species from the SW Pacific coast (Palomo et al. 2007), 35 species from the southern African coast (Hammond and Griffiths 2004), up to 46 species from the SW Atlantic coast (Borthagaray and Carranza 2007; Silliman et al. 2011; Arribas et al. 2013), and up to 57 species from the NE Atlantic coast (Crowe et al. 2004; O'Connor and Crowe 2007). On the NW Atlantic coast, studies on intertidal mussels have mainly focused on their distribution, population ecology, and interspecific interactions with their consumers and competitors (Menge 1978; Hunt and Scheibling 2001; Bertness et al. 2004; Lauzon-Guay et al. 2005; Tam and Scrosati 2011, 2014). Only one study appears to have documented the fauna living in NW Atlantic intertidal mussel beds (Murray et al. 2007). That study reported only 15 species, probably as a result of the limited geographic coverage (two sites spanning 15 km) and uniformity in the surveyed habitat conditions (wave-sheltered habitats).

To understand the contribution of intertidal mussels to local biodiversity on NW Atlantic rocky shores, we carried out a larger study that surveyed sites spanning 350 km of coastline. In addition, we surveyed two contrasting types of environment that span the full range of physical stress caused by waves: exposed and sheltered habitats. On marine rocky

shores, wave action is a major factor that affects both intertidal community structure (Menge and Branch 2001; Bertness 2007; Heaven and Scrosati 2008) and mussel population structure (Alvarado and Castilla 1996; Alunno-Bruscia et al. 2000; O'Connor 2010; Tam and Scrosati 2014). Therefore, the hypothesis of the present study was that the composition of invertebrate assemblages living in intertidal mussel beds would differ significantly between exposed and sheltered habitats.

Materials and methods

We surveyed six rocky intertidal sites along the coast of Nova Scotia (Canada), three being wave-exposed and three being wave-sheltered (Fig. 1). The exposed sites face the open ocean directly, with no opposing lands being visible from the shore: Tor Bay Provincial Park (45° 10' 58.42" N, 61° 21' 11.73" W), Crystal Crescent Beach Provincial Park (44° 26' 50.54" N, 63° 37' 19.97" W), and Kejimikujik National Park (43° 49' 7.01" N, 64° 50' 5.09" W). Values of maximum water velocity (an indication of wave exposure) in exposed habitats from this coast average 8 m s⁻¹ (Scrosati and Heaven 2007), with peaks of 12 m s⁻¹ (Hunt and Scheibling 2001). The sheltered sites face land at distances between tens of meters and a few hundred meters, with no open waters visible from the shore: an unnamed site near Tor Bay Provincial Park (45° 11' 18.05" N, 61° 21' 17.47" W), an unnamed site near Bedford Basin (44° 39' 6.53" N, 63° 34' 25.43" W), and Halifax's waterfront (44° 38' 53.45" N, 63° 34' 13.09" W). Values of maximum water velocity in sheltered habitats in this region average 4 m s⁻¹ (Scrosati and Heaven 2007), with many days showing calm waters. Because of the limited water exchange with the open ocean, compared with the exposed sites, the sheltered sites may have slightly lower values of seawater salinity at times.

Two mussel species occur in rocky intertidal habitats from the NW Atlantic coast: *Mytilus edulis* Linnaeus, 1758 and *Mytilus trossulus* Gould, 1850 (Tam and Scrosati 2011). They are morphologically similar and, thus, only identifiable with accuracy using genetic analyses (Rawson and Harper 2009). The present study did not distinguish both species in the field, but changes in basic population traits along wave exposure gradients are similar for both species (Tam and Scrosati 2014). Thus, the structure of invertebrate assemblages living in mussel beds is expected to depend largely on basic mussel population traits (Suchanek 1985; Palomo et al. 2007). On wave-exposed NW Atlantic shores, mussels are small (mean length <1 cm; Tam and Scrosati 2014) as a result of size limits imposed by waves (Carrington et al. 2009), which allows the mussels to form dense populations (Fig. 2). On wave-sheltered shores, mussels attain larger sizes (up to 8 cm long; Tam and Scrosati 2014) because they can live

Fig. 1 Map showing the location of the three wave-sheltered sites (*BB* an unnamed site near Bedford Basin, *HW* Halifax's waterfront, *UT* an unnamed site near Tor Bay Provincial Park) and three wave-exposed sites (*KE* Kejimikujik National Park, *CC* Crystal Crescent Beach Provincial Park, *TB* Tor Bay Provincial Park) surveyed on the NW Atlantic coast

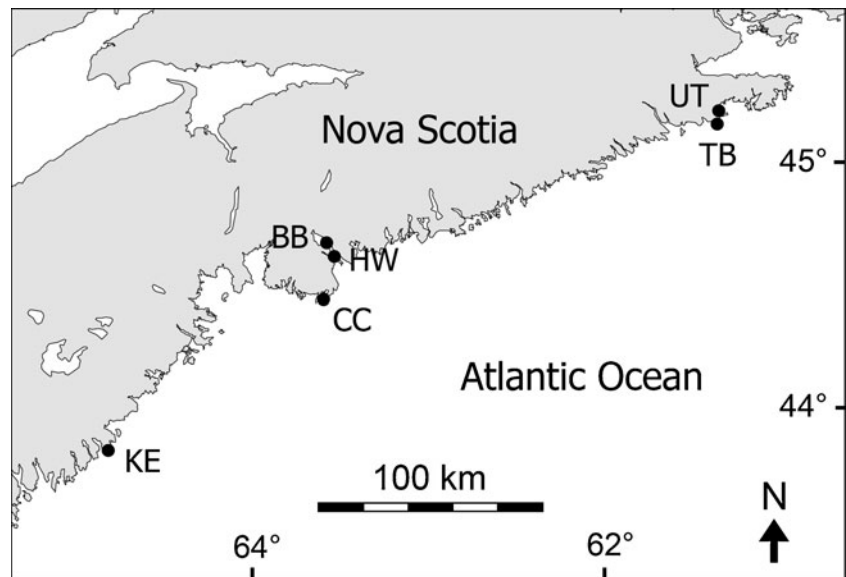


Fig. 2 Top view of intertidal mussel beds from a wave-exposed shore (upper panel) and a wave-sheltered shore (lower panel) from Nova Scotia, Canada. The inner border of the quadrat's side is 10 cm long. Photographs taken at low tide by R.A. Scrosati

longer in those physically benign habitats, which results in less packed stands compared with exposed shores (Fig. 2).

Between early September and early October 2012, at each study site we collected the mussels and the invertebrates living in the mussel matrix from 15 quadrats (10 cm × 10 cm) established at random along the middle intertidal zone. Although mussels may cover different extents of the substrate on different shores (Tam and Scrosati 2011), for consistency we only surveyed quadrats where mussel cover was 100 % (Fig. 2). The samples were transported to the laboratory in a cooler and stored in the freezer for later processing. For each quadrat, we identified all invertebrates (>0.5 mm) to the lowest possible taxonomic level under a microscope using field guides (Knopf 1981; Gibson 2003) and a taxonomic key (Pollock 1998). For each quadrat, we determined invertebrate richness as the number of invertebrate species found therein (Krebs 1999).

We tested for effects of wave exposure on invertebrate richness through a nested analysis of variance (ANOVA), considering “wave exposure” as a fixed factor (with two levels: exposed and sheltered) and “site” as a random factor (with three levels) nested within wave exposure. Before running the ANOVA, we applied a square root transformation ($X+1$) of the data to meet the homoscedasticity and normality assumptions, which we confirmed with Cochran's *C* test and normal probability plots, respectively (Underwood 1997). The ANOVA was done with SYSTAT 13 software. We tested for effects of wave exposure on the composition of invertebrate assemblages from mussel beds through a multivariate analysis of similarities (ANOSIM). We also did a nonmetric multidimensional scaling ordination (NMDS), based on Bray-Curtis similarities, to visualize the compositional differences between the two exposure levels. To identify the species that

contributed the most to the differences in composition between both exposure levels, as well as to identify the species that mainly characterized each exposure level, we performed an analysis of similarity percentages (SIMPER). We did these multivariate analyses with PRIMER 6.1.11 software, applying the log ($X+1$) transformation of the data before analyses to reduce the effect of the dominant species in the samples (Clarke and Warwick 2001).

Results

Invertebrate richness was significantly higher in mussel beds from exposed habitats than in beds from sheltered habitats ($F_{1, 4}=37.37$, $p=0.004$; Fig. 3a). Differences in invertebrate richness among sites were significant ($F_{4, 84}=4.11$, $p=0.004$), but they were not large and did not mask the fundamental difference between the two exposure levels (Fig. 3b). In total, we identified 50 invertebrate taxa (from 10 phyla), 36 of which occurred in the exposed environments against 30 that occurred in the sheltered environments. Arthropods, annelids, and molluscs were the phyla with the highest number of species, representing together almost 70 % of the total number (Table 1). Information on invertebrate abundance for each site appears in an online appendix (Appendix 1).

The composition of invertebrate assemblages differed significantly between exposed and sheltered habitats ($R=0.46$, $p<0.001$; Fig. 4). Only 32 % of the identified taxa occurred in both types of environment (Table 1). Moreover, species of Platyhelminthes occurred only in exposed habitats, while species of Bryozoa, Chordata (a tunicate), and Echinodermata (a sea star) occurred only in sheltered habitats (Table 1). The average multivariate dissimilarity between the exposure groups was 77 % (SIMPER analysis). The main species that explained the compositional differences between both environments were an unidentified species of Tubificidae (the most abundant species, although it predominated in exposed habitats) and *Semibalanus balanoides* (acorn barnacle, especially abundant in exposed habitats), followed by nematode worms, a mite species (Halacaridae), *Littorina saxatilis* (periwinkle), and *Amphiporus angulatus* (a nemertean worm), all of which were also more abundant in exposed habitats than in sheltered ones (Table 2).

Species composition was more consistent in exposed habitats than in sheltered ones, as indicated by the higher dispersion of the data shown by NMDS ordination for sheltered habitats (Fig. 4). In fact, SIMPER analysis indicated that the average similarity among quadrats from exposed habitats was 55 %, while that for sheltered habitats was only 19 %. A species of Tubificidae contributed the most to explaining within-group similarity for both exposure levels (Table 3). Sheltered habitats were secondarily characterized by

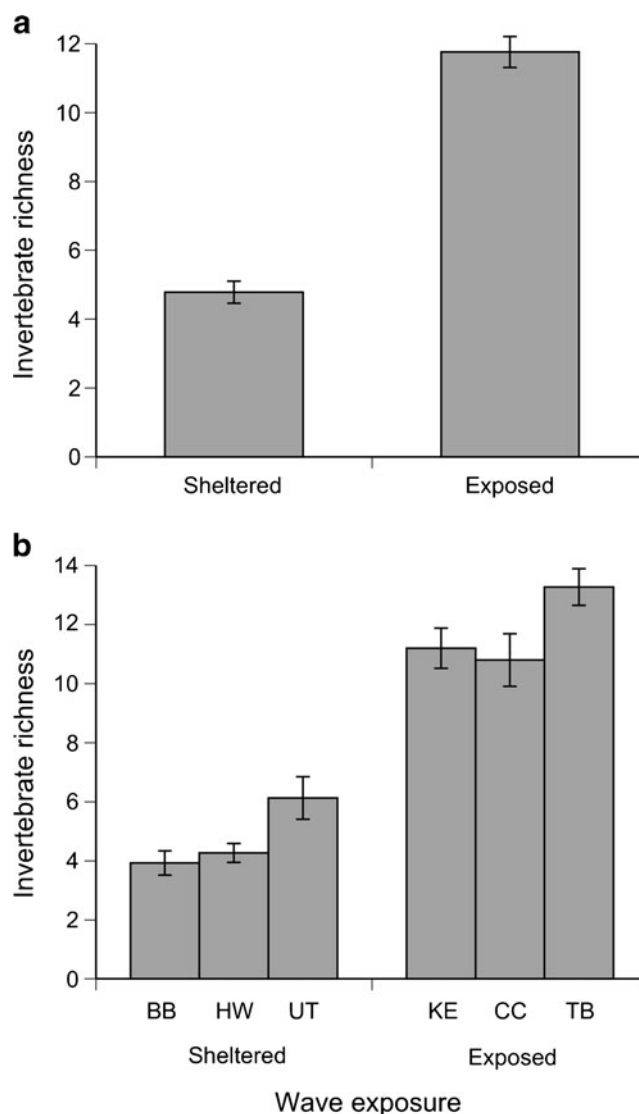


Fig. 3 Invertebrate richness in intertidal mussel beds on rocky shores from Nova Scotia, Canada: **a** mean richness (\pm SE, $n=45$) for wave-sheltered habitats and wave-exposed habitats and **b** mean richness (\pm SE, $n=15$) for each surveyed site (BB an unnamed site near Bedford Basin, HW Halifax's waterfront, UT an unnamed site near Tor Bay Provincial Park, KE Kejimikujik National Park, CC Crystal Crescent Beach Provincial Park, TB Tor Bay Provincial Park)

Littorina littorea (another periwinkle) and *Amphiporus angulatus*, while exposed habitats were secondarily characterized by *Semibalanus balanoides* (Table 3).

Discussion

This study evaluated the invertebrate biodiversity of intertidal mussel beds from NW Atlantic rocky shores. Through a larger geographic coverage and by surveying contrasting levels of wave exposure, we found invertebrate richness to be more than three times higher than reported for two intertidal sites on the Gulf of Maine (Murray et al. 2007). Such a gain is logical

Table 1 Summary of the abundance (individuals dm⁻², mean \pm SE, $n=45$) of invertebrate taxa occurring in intertidal mussel beds from wave-sheltered habitats and wave-exposed habitats on rocky shores from Nova Scotia, Canada. *Dashes* indicate absences

Taxon	Sheltered	Exposed
Annelida		
<i>Cirratulus cirratus</i> (Müller)	-	0.02 \pm 0.02
<i>Eulalia viridis</i> (Linnaeus)	0.02 \pm 0.02	0.16 \pm 0.07
<i>Fabricia sabella</i> (Ehrenberg)	-	0.02 \pm 0.02
<i>Lepidonotus squamatus</i> (Linnaeus)	-	0.02 \pm 0.02
<i>Nereis</i> sp.	-	0.02 \pm 0.02
<i>Phyllodoce</i> sp.	-	0.07 \pm 0.04
Spionidae	0.11 \pm 0.11	-
<i>Spirorbis</i> sp.	0.67 \pm 0.58	-
Tubificidae (one species)	39.80 \pm 10.44	84.27 \pm 7.75
Arthropoda		
<i>Apohyale prevostii</i> (Milne-Edwards)	0.24 \pm 0.10	1.53 \pm 0.44
<i>Caprella linearis</i> (Linnaeus)	0.02 \pm 0.02	-
<i>Carcinus maenas</i> (Linnaeus)	0.24 \pm 0.07	-
<i>Cerapus tubularis</i> Say	0.02 \pm 0.02	0.02 \pm 0.02
Chironomidae (larvae)	-	2.78 \pm 0.60
Copepoda	0.16 \pm 0.11	0.47 \pm 0.19
<i>Gammarus finmarchicus</i> Dahl	0.38 \pm 0.17	-
Halacaridae (species 1)	-	6.24 \pm 2.51
Halacaridae (species 2)	0.82 \pm 0.29	2.58 \pm 0.38
<i>Jaera marina</i> (Fabricius)	-	0.33 \pm 0.11
<i>Semibalanus balanoides</i> (Linnaeus)	0.27 \pm 0.11	19.82 \pm 3.37
<i>Unciola serrata</i> Shoemaker	-	0.09 \pm 0.05
Bryozoa		
<i>Cryptosula pallasiana</i> (Moll)	0.02 \pm 0.02	-
<i>Electra</i> sp.	0.02 \pm 0.02	-
Chordata		
<i>Botryllus schlosseri</i> (Pallas)	0.71 \pm 0.39	-
Cnidaria		
<i>Dynamena pumila</i> (Linnaeus)	0.18 \pm 0.06	0.18 \pm 0.07
Hexacorallia (species 1)	0.07 \pm 0.05	-
Hexacorallia (species 2)	-	0.02 \pm 0.02
<i>Laomedea</i> sp.	-	0.04 \pm 0.03
<i>Sertularia cupressina</i> Linnaeus	-	0.02 \pm 0.02
Echinodermata		
<i>Asterias rubens</i> Linnaeus	0.07 \pm 0.04	-
Mollusca		
<i>Anomia simplex</i> d'Orbigny	1.00 \pm 0.72	0.04 \pm 0.03
<i>Crepidula fornicata</i> (Linnaeus)	0.22 \pm 0.16	-
<i>Crepidula convexa</i> Say	0.09 \pm 0.05	-
<i>Hiattella arctica</i> (Linnaeus)	0.09 \pm 0.05	0.47 \pm 0.15
<i>Lasaea adansonii</i> (Gmelin)	-	4.00 \pm 1.51
<i>Littorina littorea</i> (Linnaeus)	1.42 \pm 0.34	0.04 \pm 0.03
<i>Littorina obtusata</i> (Linnaeus)	0.02 \pm 0.02	2.78 \pm 0.54
<i>Littorina saxatilis</i> (Olivier)	-	4.96 \pm 0.66
<i>Nucella lapillus</i> (Linnaeus)	-	2.18 \pm 0.47

Table 1 (continued)

Taxon	Sheltered	Exposed
<i>Odostomia</i> sp.	0.09 \pm 0.04	-
<i>Onoba aculeus</i> (Gould)	0.16 \pm 0.06	0.07 \pm 0.04
Opisthobranchia	0.02 \pm 0.02	-
<i>Testudinalia testudinalis</i> (Müller)	1.13 \pm 0.37	0.29 \pm 0.17
Nematoda	4.78 \pm 2.53	6.73 \pm 1.72
Nemertea		
<i>Amphiporus angulatus</i> (Müller)	2.69 \pm 0.54	4.00 \pm 0.66
<i>Tetrastemma candidum</i> (Müller)	-	0.31 \pm 0.13
Unidentified species	-	0.24 \pm 0.08
Platyhelminthes		
<i>Coronadena mutabilis</i> (Verrill)	-	0.04 \pm 0.04
<i>Foviella affinis</i> (Ørsted)	-	0.31 \pm 0.12
<i>Monoophorum</i> sp.	-	0.07 \pm 0.05

because surveys often find more species when the sampled area increases (up to a point depending on regional richness) and because more species normally occur in environmentally diverse areas (Scheiner et al. 2011). Thus, the richness within NW Atlantic mussel beds is comparable to that reported for other temperate systems, such as the NW Pacific coast (Tsuchiya and Nishihira 1986), the SW Pacific coast (Palomo et al. 2007), the southern African coast (Hammond and Griffiths 2004), the SW Atlantic coast (Borthagaray and Carranza 2007; Silliman et al. 2011; Arribas et al. 2013), the

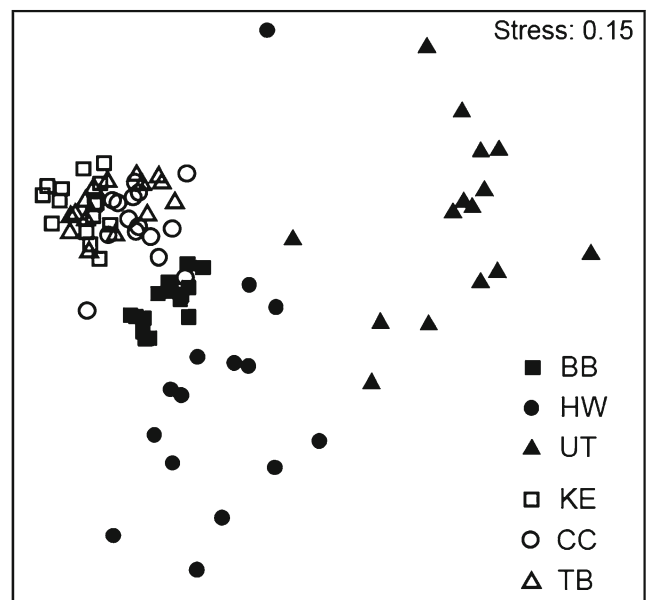
**Fig. 4** Nonmetric multidimensional scaling (NMDS) ordination summarizing the difference in species composition of invertebrate assemblages from intertidal mussel beds between wave-sheltered sites (BB an unnamed site near Bedford Basin, HW Halifax's waterfront, UT an unnamed site near Tor Bay Provincial Park) and wave-exposed sites (KE Kejimikujik National Park, CC Crystal Crescent Beach Provincial Park, TB Tor Bay Provincial Park) from rocky shores in Nova Scotia, Canada

Table 2 Summary of SIMPER results, indicating the mean abundance (individuals dm⁻², $n=45$) of discriminating invertebrate taxa in both exposure groups, their contribution (%) to the dissimilarity between groups, and the cumulative total (%) of contributions (80 % cut-off)

Taxon	Mean abundance		Contribution	Cumulative
	Sheltered	Exposed		
Tubificidae	39.80	84.27	50.90	50.90
<i>Semibalanus balanoides</i>	0.27	19.82	13.64	64.54
Nematoda	4.78	6.73	6.01	70.56
Halacaridae (species 1)	0.00	6.24	3.66	74.21
<i>Littorina saxatilis</i>	0.00	4.96	3.65	77.86
<i>Amphiporus angulatus</i>	2.69	4.00	2.93	80.79

NE Atlantic coast (Crowe et al. 2004; O'Connor and Crowe 2007), and the SE Pacific coast (Prado and Castilla 2006; Valdivia and Thiel 2006). The richness reported for NE Pacific intertidal mussel beds (*Mytilus californianus*) was approximately six times higher (Suchanek 1992). This could be the result of *M. californianus* commonly reaching large sizes (>27 cm in length) and occurring in thick multilayered stands, which generate abundant surfaces for colonization and diverse microsites that shelter small organisms from abiotic stress and consumers (Suchanek 1985). Another contributing factor could be the higher invertebrate richness occurring on NE Pacific shores (Kozloff 1996) than on NW Atlantic shores (Pollock 1998). In addition, Suchanek (1992) also reported seaweeds (virtually absent in our mussel stands) and small fish (not found during our samplings).

Our study also revealed that the composition of invertebrate assemblages from mussel beds differs between exposed and sheltered shores. Community structure is determined by species responses to the environment and by interspecific interactions, including indirect interactions that are often impossible to predict without experimentation (Menge 1995). At present, there is a good mechanistic understanding on how

Table 3 Summary of SIMPER results, indicating the mean abundance (individuals dm⁻², $n=45$) of typifying species in both exposure groups, their contribution (%) to within-group similarity, and the cumulative total (%) of contributions (80 % cut-off)

	Mean abundance	Contribution	Cumulative
Sheltered			
Tubificidae	39.80	62.59	62.59
<i>Littorina littorea</i>	1.42	11.44	74.03
<i>Amphiporus angulatus</i>	2.69	7.97	82.00
Exposed			
Tubificidae	84.27	73.33	73.33
<i>Semibalanus balanoides</i>	19.82	10.86	84.19

intertidal communities that include mussel beds are structured on NW Atlantic rocky shores (Menge and Sutherland 1987; Hunt and Scheibling 2001; Bertness et al. 2004; Cusson and Bourget 2005). However, the processes that structure invertebrate assemblages within mussel beds are largely unknown. Thus, attempting to explain the observed compositional differences between exposed and sheltered habitats must remain speculative.

Invertebrate assemblages from the two habitat types differed in two main aspects. On the one hand, invertebrate richness was higher in exposed habitats than in sheltered ones and, on the other hand, the species that mainly explained the compositional differences were more abundant in exposed habitats. Ecological theory predicts that predation should prevail as a factor structuring communities in benign environments (Menge and Sutherland 1987; Bruno et al. 2003; Scrosati et al. 2011). Exposed mussel beds experience strong wave forces just outside of the mussel matrix (Zardi et al. 2006) and, in addition, include smaller spaces among the mussels than sheltered beds because mussels from exposed habitats are small (Tam and Scrosati 2014). Those properties should make predator activity difficult in exposed mussel beds. In fact, important predators known for NW Atlantic rocky shores (green crabs, *Carcinus maenas*, and sea stars, *Asterias rubens*; Wong et al. 2005) occurred only in sheltered mussel beds. Thus, predators could contribute to limiting invertebrate richness and abundance within sheltered mussel beds.

Another plausible explanation, which could be true simultaneously with the previous one, relates to the delivery of food and larvae by water. On exposed shores, waves often enhance the influx of plankton and particulate organic matter (food for filter-feeders) and the supply of larvae to intertidal habitats (Gaines and Bertness 1993; Leonard et al. 1998; Raffaelli and Hawkins 1999; Bertness et al. 2006). Thus, both processes could favor many invertebrates in exposed mussel beds (particularly filter-feeders) by increasing their recruitment and enhancing their food supply. In fact, barnacles (*Semibalanus balanoides*) were among the most abundant species in exposed mussel beds, but were rare on sheltered ones (possibly also limited by predation there, as discussed above). In sheltered habitats, lower rates of food and larval supply (because of the limited water motion) and the high filtering capacity of large mussels (which would further reduce invertebrate larval influx; Riisgård 2001) could contribute to limiting invertebrate richness and abundance. Species that undergo direct development, instead of pelagic larval stages, could be less dependent on water flow to thrive in mussel beds (Commito and Boncavage 1989). That could be the case for the only species of tubificid oligochaete found in our surveys, which was, in fact, the most abundant species in both habitat types. Another species with direct development, *Crepidula fornicata*, was found in sheltered mussel beds

but not in exposed ones. Field experiments will be necessary to test the above potential explanations for the contrasting invertebrate assemblages found in exposed and sheltered shores.

It is also worth noting that, although both habitat types differed clearly in invertebrate composition, more variation existed among sheltered sites than among exposed sites. This difference could be due to local influences. Our exposed habitats are relatively pristine as a result of limited human impacts because of the high wave action and rough nature of the sites and because of the homogenizing effects of the ocean, since all sites fully face open waters. In contrast, the sheltered habitats exhibited a greater biological heterogeneity, which could have resulted from some areas being under a higher human influence (Halifax's waterfront, adjacent to the city of Halifax) than others (the habitats near Tor Bay Provincial Park, which are relatively pristine). Thus, it would seem in principle easier to predict invertebrate composition in exposed mussel beds than in beds from sheltered environments, for which extra information (e.g., pollutants, suspended sediments, salinity [Crowe et al. 2004]) could be needed to make more reliable predictions.

Overall, our study supports the notion that intertidal mussels are important ecosystem engineers that sustain a rich diversity of invertebrates. The loss of ecosystem engineers due to anthropogenic impacts is of concern because of the negative cascading effects on the species that such organisms support (Coleman and Williams 2002), which is particularly true in the case of intertidal mussel beds (Harley 2011). Thus, conservation efforts often focus on preserving ecosystem engineers (Hastings et al. 2007), which should include mussels. Conversely, when non-native mussels invade and spread in new regions, their ecological effects could be larger than anticipated because of their bioengineering capacity (Crooks 2002), which highlights the importance of studying how mussel beds affect local biodiversity. Finally, given that climate change is increasing levels of wave action globally (Young et al. 2011), our study offers baseline information to anticipate the possible effects of increases in wave action on invertebrate biodiversity sustained by mussel populations. For these reasons, future research should unravel the mechanisms through which different invertebrate assemblages originate and persist in mussel beds differing in wave exposure.

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Appendix 1. Abundance (individuals dm⁻², mean \pm SE, n = 15 quadrats) of invertebrate taxa occurring in intertidal mussel beds from wave-sheltered sites (BB: an unnamed site near Bedford Basin, HW: Halifax's waterfront, and UT: an unnamed site near Tor Bay Provincial Park) and wave-exposed sites (KE: Kejimikujik National Park, CC: Crystal Crescent Beach Provincial Park, and TB: Tor Bay Provincial Park) on rocky shores from Nova Scotia, Canada. Dashes indicate absences.

	BB	HW	UT	KE	CC	TB
Annelida						
<i>Cirratulus cirratus</i> (Müller)	-	-	-	-	0.07 \pm 0.07	-
<i>Eulalia viridis</i> (Linnaeus)	0.07 \pm 0.07	-	-	-	0.13 \pm 0.13	0.33 \pm 0.16
<i>Fabricia sabella</i> (Ehrenberg)	-	-	-	0.07 \pm 0.07	-	-
<i>Lepidonotus squamatus</i> (Linnaeus)	-	-	-	-	-	0.07 \pm 0.07
<i>Nereis</i> sp.	-	-	-	-	-	0.07 \pm 0.07
<i>Phyllodoce</i> sp.	-	-	-	-	0.07 \pm 0.07	0.13 \pm 0.09
Spionidae	-	-	0.33 \pm 0.33	-	-	-
<i>Spirorbis</i> sp.	-	-	2.00 \pm 1.72	-	-	-
Tubificidae (one species)	4.87 \pm 1.20	111.40 \pm 21.67	3.13 \pm 2.65	69.07 \pm 9.04	87.73 \pm 8.25	96.00 \pm 19.72
Arthropoda						
<i>Apohyale prevostii</i> (Milne-Edwards)	-	0.73 \pm 0.25	-	0.27 \pm 0.15	0.60 \pm 0.24	3.73 \pm 1.09
<i>Caprella linearis</i> (Linnaeus)	-	-	0.07 \pm 0.07	-	-	-
<i>Carcinus maenas</i> (Linnaeus)	0.67 \pm 0.16	0.07 \pm 0.07	-	-	-	-
<i>Cerapus tubularis</i> Say	-	0.07 \pm 0.07	-	-	0.07 \pm 0.07	-
Chironomidae (larvae)	-	-	-	2.20 \pm 0.66	1.33 \pm 0.45	4.80 \pm 1.51
Copepoda	0.40 \pm 0.34	-	0.07 \pm 0.07	0.13 \pm 0.09	1.07 \pm 0.52	0.20 \pm 0.11
<i>Gammarus finmarchicus</i> Dahl	-	-	1.13 \pm 0.46	-	-	-
Halacaridae (species 1)	0.60 \pm 0.19	1.87 \pm 0.79	-	3.33 \pm 0.67	1.33 \pm 0.35	3.07 \pm 0.81
Halacaridae (species 2)	-	-	-	2.80 \pm 1.07	0.80 \pm 0.54	15.13 \pm 7.02

<i>Jaera marina</i> (Fabricius)	-	-	-	0.13 ± 0.09	0.13 ± 0.09	0.73 ± 0.28
<i>Semibalanus balanoides</i> (Linnaeus)	0.67 ± 0.29	0.07 ± 0.07	0.07 ± 0.07	41.80 ± 6.67	3.67 ± 1.34	14.00 ± 2.31
<i>Unciola serrata</i> Shoemaker	-	-	-	-	-	0.27 ± 0.15
Bryozoa						
<i>Cryptosula pallasiana</i> (Moll)	0.07 ± 0.07	-	-	-	-	-
<i>Electra</i> sp.	-	-	0.07 ± 0.07	-	-	-
Chordata						
<i>Botryllus schlosseri</i> (Pallas)	-	-	2.13 ± 1.11	-	-	-
Cnidaria						
<i>Dynamena pumila</i> (Linnaeus)	-	0.13 ± 0.09	0.40 ± 0.13	0.07 ± 0.07	0.13 ± 0.09	0.33 ± 0.19
Hexacorallia (species 1)	-	0.20 ± 0.14	-	-	-	-
Hexacorallia (species 2)	-	-	-	-	-	0.07 ± 0.07
<i>Laomedea</i> sp.	-	-	-	0.07 ± 0.07	0.07 ± 0.07	-
<i>Sertularia cupressina</i> Linnaeus	-	-	-	-	0.07 ± 0.07	-
Echinodermata						
<i>Asterias rubens</i> Linnaeus	0.20 ± 0.11	-	-	-	-	-
Mollusca						
<i>Anomia simplex</i> d'Orbigny	-	-	3.00 ± 2.11	-	-	0.13 ± 0.09
<i>Crepidula fornicata</i> (Linnaeus)	-	-	0.67 ± 0.46	-	-	-
<i>Crepidula convexa</i> Say	-	-	0.27 ± 0.15	-	-	-
<i>Hiatella arctica</i> (Linnaeus)	0.07 ± 0.07	-	0.20 ± 0.14	-	0.40 ± 0.24	1.00 ± 0.37
<i>Lasaea adansonii</i> (Gmelin)	-	-	-	2.60 ± 0.70	1.07 ± 0.33	8.33 ± 4.33
<i>Littorina littorea</i> (Linnaeus)	0.47 ± 0.27	-	3.80 ± 0.63	0.13 ± 0.09	-	-
<i>Littorina obtusata</i> (Linnaeus)	-	0.07 ± 0.07	-	6.53 ± 1.05	1.13 ± 0.36	0.67 ± 0.21
<i>Littorina saxatilis</i> (Olivi)	-	-	-	7.80 ± 1.55	3.53 ± 0.79	3.53 ± 0.47
<i>Nucella lapillus</i> (Linnaeus)	-	-	-	0.53 ± 0.22	5.33 ± 0.93	0.67 ± 0.27
<i>Odostomia</i> sp.	-	-	0.27 ± 0.12	-	-	-
<i>Onoba aculeus</i> (Gould)	-	0.13 ± 0.09	0.33 ± 0.16	0.13 ± 0.09	-	0.07 ± 0.07
Opisthobranchia	0.07 ± 0.07	-	-	-	-	-

<i>Testudinalia testudinalis</i> (Müller)	-	-	3.40 ± 0.88	-	-	0.87 ± 0.49
Nematoda	4.27 ± 2.79	8.93 ± 7.09	1.13 ± 0.31	1.53 ± 0.91	14.13 ± 4.28	4.53 ± 1.62
Nemertea						
<i>Amphiporus angulatus</i> (Müller)	2.13 ± 0.84	5.67 ± 0.98	0.27 ± 0.12	2.80 ± 1.00	2.67 ± 0.68	6.53 ± 1.40
<i>Tetrastemma candidum</i> (Müller)	-	-	-	0.93 ± 0.36	-	-
Unidentified species	-	-	-	-	0.53 ± 0.19	0.20 ± 0.11
Platyhelminthes						
<i>Coronadena mutabilis</i> (Verrill)	-	-	-	-	-	0.13 ± 0.13
<i>Foviella affinis</i> (Ørsted)	-	-	-	0.67 ± 0.33	0.13 ± 0.09	0.13 ± 0.09
<i>Monoophorum</i> sp.	-	-	-	0.14 ± 0.20	-	-