Vol. 539: 19–31, 2015
doi: 10.3354/meps11484

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 12

Intertidal communities differ between breakwaters and natural rocky areas on ice-scoured Northwest Atlantic coasts

Jordan L. Musetta-Lambert[1,4,*], Ricardo A. Scrosati[2], Elise A. Keppel[2], Myriam A. Barbeau[3], Marc A. Skinner[1,5], Simon C. Courtenay[1,6]

[1]Fisheries and Oceans Canada at the Canadian Rivers Institute, Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, New Brunswick E3B 5A3, Canada

[2]Department of Biology, St. Francis Xavier University, 2320 Notre Dame Avenue, Antigonish, Nova Scotia B2G 2W5, Canada

[3]Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, New Brunswick E3B 5A3, Canada

[4]*Present address:* School of Environmental Sciences, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1, Canada

[5]*Present address*: Stantec Consulting Ltd, 102-40 Highfield Park Drive, Dartmouth, Nova Scotia B3A 0A3, Canada

[6]*Present address*: Department of Environment and Resource Studies, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1, Canada

ABSTRACT: This is the first study of the ecological significance of rocky breakwaters as habitat for intertidal biota in marine environments that freeze in winter. Percent cover of intertidal seaweeds and invertebrates was quantified on exposed (high wave action and winter ice scour) and sheltered sides of 18 breakwaters (>5 yr old) and compared with 18 natural rocky intertidal areas along 430 km of the southern Gulf of St. Lawrence coast (Atlantic Canada) in the summer of 2010. Sheltered areas of breakwaters differed from natural rocky shores in having lower biotic richness and total abundance. However, these indices were not significantly different between habitat types for exposed areas. Multivariate analysis revealed significant differences in community composition between breakwaters and natural rocky shores in both sheltered and exposed areas. *Ulva* spp. (*U. intestinalis* and *U. lactuca*), *Hildenbrandia rubra*, and *Mytilus edulis* (exposed areas only) were more abundant on breakwaters than on natural rocky shores, while *Semibalanus balanoides*, *Calothrix* spp., *Fucus* spp., *Chordaria flagelliformis* (exposed areas only), and *Ascophyllum nodosum* (sheltered areas only) were less abundant on breakwaters. Our study shows that breakwaters from marine shores affected by winter sea ice support substantially different biotic communities than natural rocky intertidal areas. Thus, the findings of this study provide vital information for management decisions related to habitat loss and compensation when the coastal landscape is altered through the construction of breakwaters.

KEY WORDS: Abundance · Breakwaters · Community composition · Ice scouring · Richness · Rocky intertidal · Wave exposure

INTRODUCTION

Artificial defense structures are typical features on marine coasts near human settlements, protecting industrial, commercial, and recreational activities against harsh sea conditions (Collins et al. 1994, Bacchiocchi & Airoldi 2003, Bulleri & Chapman 2010, Airoldi & Bulleri 2011). These structures are becoming increasingly abundant as human populations continue to increase in the coastal zone, where weather events become more extreme and frequent with climate change, and as sea level rises (Carter &

*Corresponding author: jmusetta@uoguelph.ca

Draper 1988, Thompson et al. 2002, Lotze et al. 2006). Therefore, it is important to understand how these human modifications alter the ecology of coastal environments to establish effective management and compensation policies (Bulleri & Airoldi 2005, Airoldi & Beck 2007, Bulleri & Chapman 2010).

Research on the ecology of intertidal artificial rocky structures, including breakwaters, is limited. Furthermore, the existing research on the quality of habitat offered by such structures is conflicting. Some studies show that they constitute acceptable habitat for local biota (Southward & Orton 1954, Thompson et al. 2002, Branch et al. 2008), while others show that they reduce habitat, alter patterns of species composition and abundance (Glasby & Connell 1999, Bulleri et al. 2005, Moschella et al. 2005, Lam et al. 2009), and promote the introduction and settlement of invasive species (Tyrrell & Byers 2007, Pister 2009). More information is available on subtidal artificial rocky structures, termed artificial reefs (Bulleri & Chapman 2004). Studies indicate that artificial reefs generally do not act as surrogates for natural rocky reefs (Connell 2001, Carvalho et al. 2013, Wetzel et al. 2014).

Breakwaters may alter the coastal environment at various spatial scales, from entire stretches of a coastline, by changing shoreline currents and dispersal of organisms (Burcharth et al. 2007), to the direct footprint of the structure displacing natural habitat or providing a new habitat type (Moschella et al. 2005, Pister 2009, Bulleri & Chapman 2010). In the present study, we investigate the habitat value of breakwaters at the footprint scale. We hereby provide the first study of the community ecology of breakwaters on the Northwest Atlantic coast. Additionally, this is the first study of the habitat value of breakwaters on marine shores that freeze in winter. Of particular importance on coasts from northern latitudes is scouring by sea ice (Bertness 2007, Gerwing et al. 2015). Intertidal ice scour occurs when pieces of sea ice move with tides, currents, waves, and winds along shorelines, damaging or removing intertidal organisms (Bergeron & Bourget 1986, Barnes 1999, Gutt 2001, Scrosati & Heaven 2006). The effects of ice scour on intertidal biota have been examined along natural rocky areas on the southern Gulf of St. Lawrence, in Atlantic Canada (Scrosati & Heaven 2006, 2007, 2008, Scrosati & Eckersley 2007, Keppel 2012). Stronger scouring on exposed areas than on sheltered areas affects intertidal community structure (Scrosati & Heaven 2007). However, ice scour has never been examined on breakwaters as a driver of community composition.

The primary objective of this study was to compare intertidal biotic communities from breakwaters and those from nearby natural rocky areas in the southern Gulf of St. Lawrence. We quantified taxa richness (algae and invertebrates), total abundance (total percent cover of all taxa), and community composition (a combined measure of taxa identity and abundance) over a large scale (430 km of shoreline) and with high replication (18 breakwaters and 18 natural rocky sites). Between both habitat types (breakwater and natural rocky area), we compared community structure separately for exposed and sheltered areas. We hypothesized that taxa richness, abundance, and composition would differ between habitat types and exposures. To better characterize key abiotic conditions in these northern environments, we also quantified the intensity of ice scour in both habitat types and exposures. This research is an essential step to determine whether breakwaters can be considered as suitable habitat for coastal algae and invertebrates, comparable to natural rocky shores. Therefore, this study provides crucial information for management decisions related to habitat loss and compensation when the coastal landscape is altered through the construction of breakwaters.

MATERIALS AND METHODS

Study area

The studied region spans 430 km of the southern coast of the Gulf of St. Lawrence, a semi-enclosed body of water connecting the Atlantic Ocean with the St. Lawrence Estuary. This area is considered one of Canada's most sensitive regions to sea level rise (Shaw et al. 1998, Forbes et al. 2004), demonstrating the need for coastal protection. The coastal substrate is primarily sand, sandy gravel, mud deposits, and, to a lesser extent, exposed bedrock (Loring & Nota 1973, Wade et al. 1997, Hanson 2009). The Gulf of St. Lawrence is the southernmost limit in North America of pack ice, which can be found throughout the winter through to May (Koutitonsky & Bugden 1991, Gilbert & Pettigrew 1997, Hanson 2009). Our study sites ranged from Cap-Pelé (46° 14′ 08.37″ N, 64° 15′ 44.13″ W; Fig. 1), on the partially sheltered Northumberland Strait where wave action is moderate, to Pleasant Bay (46° 49′ 55.25″ N, 60° 47′ 52.77″ W), on the exposed northwest coast of Cape Breton Island, Nova Scotia, which is exposed to higher wave action. Average daily maximum water velocity (an estimate of wave exposure) in natural intertidal habi-

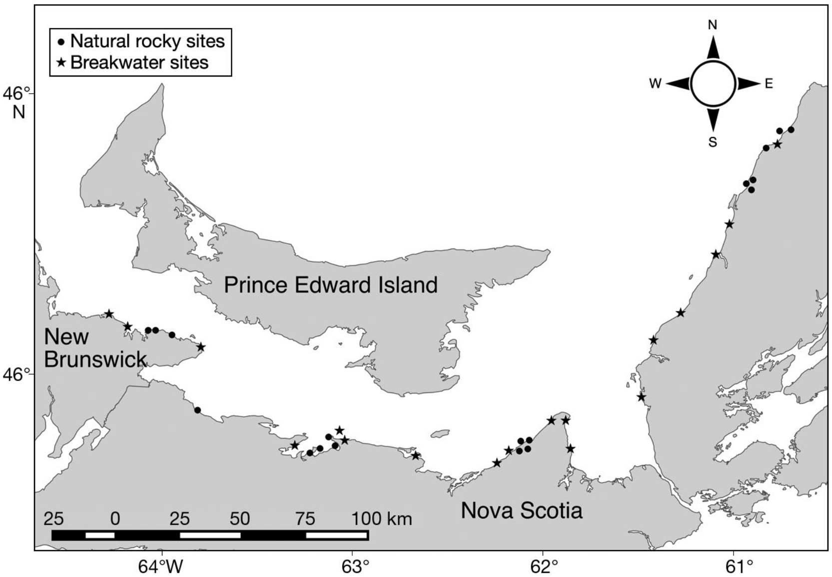

Fig. 1. Study locations of 18 breakwaters and 18 natural rocky intertidal sites sampled throughout 430 km of the southern Gulf of St. Lawrence between Cap-Pelé, New Brunswick (furthest site west), and Pleasant Bay, Nova Scotia (furthest site east)

tats ranges from 3.4 m s^{-1} in sheltered areas to 5.2 m s^{-1} in exposed areas in the Arisaig region, at the centre of our studied coastal range (Scrosati & Heaven 2007). Surface seawater temperature ranges from 15 to 20°C from late spring to fall (Hanson 2009). Winter intertidal temperature measured under the ice foot normally ranges between −2.4 and −1.1°C, without dropping below −7°C (Scrosati & Eckersley 2007). Monthly salinity averages are between 28.4 and 30.6 (Fisheries and Oceans Canada 2007).

Sampling design

Sampling occurred from July through August 2010, a time when intertidal species richness is maximal along this coast (Scrosati & Heaven 2007, Heaven & Scrosati 2008). Preliminary research indicated that taxa richness and abundance (measured as percent cover) are stable during this time of year (see the Supplement at www.int-res.com/articles/suppl/m539p019_supp.pdf). We selected 18 breakwaters and 18 natural rocky intertidal sites using an inventory compiled by Fisheries and Oceans Canada (Gulf Fisheries Centre, Moncton, NB). Breakwaters deemed suitable for sampling were constructed of natural rock material (boulders 0.5 × 0.5 m or greater in size), the most common building material for breakwaters in the southern Gulf of St. Lawrence (P. MacDonald, Fisheries and Oceans Canada, Small Craft Harbours, Antigonish, NS, pers. comm.). Other criteria for selection included that breakwaters were at least 5 yr of age, and were still partially submerged at low tide with one side facing open waters (thus sustaining high wave action) and the other side facing the shore (thus sustaining negligible wave action). The age criterion was intended to allow time for biotic communities to become established, but we neither directly tested the adequacy of this criterion nor controlled for intermittent maintenance, restructuring, or dredging. Natural rocky intertidal sites were selected to have both exposed and sheltered areas similar to breakwaters. Wave exposure and (winter) ice scour are important environmental factors influencing recruitment, size, abundance, and structure of intertidal biotic communities on this coast (Scrosati & Heaven 2007, Heaven & Scrosati 2008).

We examined the mid-intertidal zone because it is exposed for a sufficient period of time during low tides to sample and because, in this region, species richness is similar to that in the low intertidal zone (Scrosati & Heaven 2007, Scrosati et al. 2011) and higher than at the environmentally harsher high intertidal zone (Bertness 2007, Scrosati & Heaven 2007). Due to the changes in tidal amplitude along the studied coastal range, the mid-intertidal zone was at an elevation of 1.3 m (above Canadian chart datum, or lowest normal tide = 0 m) at the furthest west sites and 0.7 m at the furthest east sites (Keppel 2012). For consistency, we limited sampling to rock faces excluding tide pools and shaded crevices.

Taxa abundance, richness, and community composition

Percent cover of invertebrates and algae on exposed and sheltered sides of breakwaters and natural rocky areas was quantified using a non-destructive approach (Scrosati 2005, Heaven & Scrosati 2008). We aligned a 50-m transect parallel to the shoreline at the mid-intertidal zone of the exposed and sheltered areas of each site. We sampled 8 random quadrats (25 × 25 cm) per transect at breakwater sites and 4 quadrats per transect at natural rocky sites. The quadrat was divided with monofilament into 100 subquadrats to facilitate measurement of percent cover. The cover of canopy-forming organisms (e.g. *Fucus* sp.) was quantified first and then moved aside to record the cover of understory taxa. Organisms were identified to genus or species level in the field or, when not possible, were taken for laboratory identification using guides and taxonomic keys (Gosner 1978, Pollock 1998, Villalard-Bohnsack 2003). Genus-level identification was used solely for wave-damaged and unidentifiable species. If a species was present in less than 1% of the quadrat, it was given a value of 0.5% cover (Scrosati & Heaven 2007).

We calculated taxa richness, total abundance, and community composition for each quadrat. Richness was measured as the total number of taxa identified in the quadrat. Total abundance was measured as the sum of the percent cover values of all taxa in the quadrat (so the total percent cover could be over 100%). Community composition is a combined multivariate measure identifying taxa and their abundance in a quadrat. Percent cover was chosen to quantify abundance because it is a non-destructive, efficient *in situ* measure and because other common measures (such as density) cannot be quantified reliably in the field for clonal organisms (Scrosati 2005).

Ice scour

Ice scour was measured at exposed and sheltered areas for a subset of breakwaters and natural rocky sites. Stainless steel rods measuring 0.32 cm in diameter and 8 cm in length were inserted 3 cm into holes drilled into the rock at the sampling sites, leaving 5 cm of the rods protruding from the rock. Rods were installed in triplicate at exposed and sheltered areas of 9 breakwaters and 9 natural rocky sites, and secured into the rock with marine epoxy (Z-Spar, Carboline Company) from late November to early December 2010, before ice formed. After ice melt in April 2011, the severity of ice scour was measured as the angle to which the rod was bent from its original perpendicular orientation to the rock face (Scrosati & Heaven 2006, Keppel 2012).

Data analysis

Univariate analyses were completed using SYSTAT 11.0 (Systat Software). We used a significance level of $\alpha = 0.05$ for most analyses. Taxa richness, total abundance, and ice scour were each analyzed using a mixed-model ANOVA with habitat type (2 levels: breakwater and natural rocky substrate) and exposure (2 levels: exposed and sheltered) as fixed factors. Site, nested in habitat type, was a random factor with 18 levels (18 breakwaters and 18 natural areas) for the biotic analyses and 9 levels for the ice scour analysis. Quadrat (n = 4–8) was the lowest unit of replication (i.e. the residual). Appropriate denominators for the *F*-ratios were determined as in Underwood (1997). The data were examined for the assumption of normality of residuals with probability plots, and the assumption was met. The assumption of homogeneity of variance was met for total abundance data (Cochran's test), but not for taxa richness data until we applied a $\log_{10}$(datum + 1) transformation. Ice scour data demonstrated heteroscedasticity, even after transformation. Since this data set had a reasonable replication (n = 9 sites), we proceeded with the ANOVA and interpreted results with caution ($\alpha = 0.01$ level), due to increased risk of type I error (Underwood 1997). Fixed main effects and their interactions were judged significant if $p < 0.05$ even when effects containing the random factor site were significant (as per Quinn & Keough 2002); any test for fixed main effects and interactions are actually testing for a significant effect over and above the variation due to both the residual and interaction terms involving the random factor. Tukey's honestly significant difference tests were used for pairwise comparisons between habitat type–exposure combinations for taxa richness, total abundance, and ice scour data.

Multivariate analyses to investigate community composition were conducted using PRIMER v6 (PRIMER-E) software with the PERMANOVA (PRIMER-E) add-on (Anderson 2001, 2005, Clarke & Gorley 2006). A fourth-root transformation was applied to abundance data (percent cover) to downweigh the influence of highly abundant taxa and allow rare taxa to contribute more to detected patterns (Clarke & Warwick 2001). The Bray-Curtis coefficient was used to construct the resemblance matrix. We used a mixed-model permutational ANOVA (PERMANOVA) design (same linear model as for the univariate analyses) to investigate differences in community composition between the natural rocky shores and breakwaters on exposed and sheltered sides. Significant fixed-factor interactions (habitat type × exposure) were investigated using post hoc pairwise comparisons. We used non-metric multidimensional scaling (nMDS) plots to visualize differences in community composition between breakwaters and natural rocky shores in exposed and sheltered areas separately; community data per quadrat were averaged for each site, and overlaid vectors were used to show Pearson correlations between taxa and nMDS axes. The taxa contributing most to differences between breakwater and natural rocky shores within exposed areas and within sheltered areas were identified by similarity percentage (SIMPER) analyses (Clarke & Warwick 2001).

RESULTS

Taxa abundance and richness

Abundances (percent cover) of a total of 62 taxa (31 algae and 31 invertebrates) were recorded during the sampling period from June to August 2010. Only 14 of the 28 invertebrate taxa and 15 of 24 algal taxa found on natural rocky shores were also found on breakwaters (Tables 1 & 2), although breakwaters also had 3 invertebrate taxa and 7 algal taxa not found at the natural rocky sites.

Richness differed more between sheltered and exposed areas of natural rocky shores than on breakwaters (Table 3, Fig. 2). Richness was significantly lower in sheltered and exposed areas of breakwaters than in sheltered areas of natural rocky shores (Table 3). Total abundance was significantly lower in sheltered and exposed areas of breakwaters than in sheltered areas of natural rocky shores (Table 3, Fig. 2). No significant differences were detected between exposed areas of breakwaters and natural rocky shores for either richness or abundance (Table 3). Richness and abundance did not differ between sheltered and exposed areas of breakwaters, but showed a marginal indication of being higher in sheltered than exposed areas of natural rocky shores (Table 3).

Table 1. Abundance (mean percent cover ± SE) and presence (P: number of the 18 sites at which a taxon occurred) of invertebrate taxa across the southern Gulf of St. Lawrence on sheltered and exposed areas of breakwaters (n = 144 quadrats) and natural rocky intertidal areas (n = 72 quadrats) in summer 2010. Blank spaces represent zero abundance

Taxon	Breakwaters				Natural rocky shores			
	Sheltered		Exposed		Sheltered		Exposed	
	P	Abundance	P	Abundance	P	Abundance	P	Abundance
Acmaea testudinalis					2	0.01 ± 0.01		
Asterias vulgaris	2	0.04 ± 0.02	3	0.06 ± 0.04	3	0.26 ± 0.1	2	0.04 ± 0.02
Buccinum undatum					3	0.05 ± 0.02		
Calliopius laeviusculus					1	0.01 ± 0.01		
Cancer irroratus					2	0.06 ± 0.04		
Carcinus maenas					1	0.01 ± 0.01		
Clava multicornis					2	0.02 ± 0.01		
Crassostrea virginica	3	0.12 ± 0.07	2	0.03 ± 0.02	3	0.17 ± 0.09		
Crucibulum striatum			1	0.01 ± 0.01				
Dynamena pumila	2	0.02 ± 0.02	2	0.01 ± 0.01	8	2.47 ± 0.84	2	0.32 ± 0.28
Electra pilosa	2	0.01 ± 0.01	1	0.01 ± 0.01	3	0.34 ± 0.17	1	0.01 ± 0.01
Gammarellus angulosus	4	0.02 ± 0.01	3	0.02 ± 0.01	5	0.10 ± 0.02	3	0.08 ± 0.02
Gammarus annulatus	1	0.01 ± 0.01			1	0.01 ± 0.01		
Gammarus finmarchicus					6	0.09 ± 0.02	1	0.01 ± 0.01
Gammarus oceanicus	1	0.01 ± 0.01						
Hyale nilssoni	1	0.01 ± 0.01			2	0.01 ± 0.01		
Hyale plumulosa					1	0.01 ± 0.01		
Jaera marina	1	0.01 ± 0.01			6	0.07 ± 0.02		
Littorina littorea	14	0.90 ± 0.10	17	0.62 ± 0.07	18	0.55 ± 0.06	16	0.30 ± 0.04
Littorina obtusata	3	0.04 ± 0.01	5	0.24 ± 0.01	13	0.60 ± 0.08	14	0.12 ± 0.04
Littorina saxatilis	4	0.03 ± 0.01	3	0.07 ± 0.04	13	0.19 ± 0.03	11	0.19 ± 0.02
Membranipora spp.							4	0.11 ± 0.05
Mytilus edulis	2	0.01 ± 0.01	9	4.68 ± 1.08	14	1.98 ± 0.67	11	0.62 ± 0.35
Neomolgus littoralis	2	0.01 ± 0.01			3	0.06 ± 0.02		
Nucella lapillus					4	0.44 ± 0.21	1	0.01 ± 0.01
Obelia spp.					3	0.21 ± 0.14		
Semibalanus balanoides	16	14.49 ± 1.47	12	19.48 ± 2.30	18	29.36 ± 2.70	18	35.90 ± 3.81
Spirorbis spirorbis					1	0.01 ± 0.01		
Uhlorchestia uhleri					1	0.01 ± 0.01		
Urticina felina					1	0.01 ± 0.01		
Worm #1			1	0.01 ± 0.01				

Table 2. Abundance (mean percent cover ± SE) and presence (P: number of the 18 sites at which a taxon occurred) of algal taxa across the southern Gulf of St. Lawrence on sheltered and exposed areas of breakwaters (n = 144 quadrats) and natural rocky intertidal areas (n = 72 quadrats) in summer 2010. Blank spaces represent zero abundance. Categories left at genus level (*Ceramium* spp., *Fucus* spp., *Polysiphonia* spp.) are the total mean abundance of the component categories below them

Taxon	Breakwaters				Natural rocky shores			
	Sheltered		Exposed		Sheltered		Exposed	
	P	Abundance	P	Abundance	P	Abundance	P	Abundance
Ascophyllum nodosum	5	1.89 ± 0.85	1	4.37 ± 1.58	10	24.13 ± 4.27	4	0.10 ± 0.05
Blidingia minima					1	0.01 ± 0.01		
Calothrix spp.	1	2.77 ± 1.11	1	0.11 ± 0.09	8	4.10 ± 1.01	8	9.69 ± 2.37
Ceramium spp.	1	0.01 ± 0.01	3	0.20 ± 0.10	2	0.22 ± 0.14	3	0.34 ± 0.15
Ceramium cimbricum	1	0.01 ± 0.01	1	0.01 ± 0.01				
Ceramium nodulosum			1	0.17 ± 0.07				
Ceramium (unknown)			1	0.02 ± 0.02	2	0.22 ± 0.14	3	0.34 ± 0.15
Chondrus crispus	3	0.32 ± 0.21	5	0.22 ± 0.09	10	2.55 ± 1.10	8	0.28 ± 0.08
Chorda filum	1	2.24 ± 0.90						
Chordaria flagelliformis			3	0.18 ± 0.10			8	6.31 ± 2.41
Cladophora rupestris	2	0.10 ± 0.05	1	0.10 ± 0.06	1	0.01 ± 0.01	3	0.07 ± 0.03
Cladophora sericea	2	0.01 ± 0.01	5	0.07 ± 0.02	3	0.03 ± 0.01	3	0.12 ± 0.04
Corallina officinalis					1	0.01 ± 0.01		
Crust indet. 1	4	1.05 ± 0.54	6	3.65 ± 1.14				
Dictyosiphon macounii					1	0.21 ± 0.12	1	0.07 ± 0.05
Elachista fucicola	4	0.89 ± 0.28	7	2.17 ± 0.92	8	1.14 ± 0.40	7	0.20 ± 0.07
Fucus spp.	16	11.07 ± 2.62	14	6.58 ± 2.36	17	26.01 ± 7.02	15	7.65 ± 2.28
Fucus serratus			3	1.61 ± 0.64	7	6.01 ± 2.10	1	3.81 ± 1.97
Fucus spiralis	5	2.48 ± 0.96	3	0.40 ± 0.20	5	5.58 ± 1.82		
Fucus vesiculosus	8	7.84 ± 1.49	6	3.19 ± 1.02	8	13.91 ± 2.77	1	2.57 ± 1.30
Fucus (unknown)	13	0.75 ± 0.17	14	1.38 ± 0.49	6	0.51 ± 0.33	13	1.27 ± 0.39
Crust indet. 2					2	0.01 ± 0.01	2	0.13 ± 0.07
Halisarca spp.					1	0.08 ± 0.06	2	0.12 ± 0.08
Halothrix spp.			1	0.01 ± 0.01				
Hildenbrandia rubra	14	4.31 ± 0.85	15	4.43 ± 0.65	9	1.77 ± 0.41	4	1.97 ± 0.56
Petalonia fascia			1	0.01 ± 0.01				
Petalonia zosterifolia	3	0.15 ± 0.12	2	0.08 ± 0.06			1	0.01 ± 0.01
Polyides rotundus			1	0.33 ± 0.20				
Polysiphonia spp.	5	1.09 ± 0.53	2	0.26 ± 0.12	2	0.15 ± 0.12	2	0.06 ± 0.04
Polysiphonia elongata					2	0.14 ± 0.11	2	0.06 ± 0.04
Polysiphonia (unknown)	5	1.09 ± 0.53	2	0.26 ± 0.12	1	0.01 ± 0.01		
Porphyra spp.	1	0.43 ± 0.22	4	0.97 ± 0.35				
Saccorhiza dermatodea							7	1.42 ± 0.42
Scytosiphon spp.			1	0.03 ± 0.02				
Sphacelaria cirrosa					3	0.13 ± 0.09	1	0.01 ± 0.01
Ulva intestinalis	9	7.48 ± 1.72	12	5.85 ± 1.31	1	0.01 ± 0.01	1	0.01 ± 0.01
Ulva lactuca	5	0.40 ± 0.21	8	6.39 ± 1.83				

Community composition

Community composition varied significantly with habitat type and exposure (Table 4). The communities in all 4 combinations of those 2 factors differed significantly from each other (Table 4, vectors in Fig. 3).

Of the 8 species contributing 4.5% or more to the difference between breakwater and natural rocky communities, 5 were common to both exposed and sheltered areas (Table 5). *Semibalanus balanoides*, *Calothrix* spp., and *Fucus* spp. were all less abundant in both exposed and sheltered areas of breakwaters than in natural rocky shores, whereas *Hildenbrandia rubra* and *Ulva intestinalis* were more abundant on breakwaters than on natural rocky shores. Other species contributing at least 4.5% to the difference in exposed communities were *Chordaria flagelliformis* (less abundant on breakwaters) and *Mytilus edulis* (more abundant on breakwaters). In sheltered areas, *Ascophyllum nodosum* was also influential in discriminating breakwater from natural rocky shore communities and was much less abundant on breakwaters.

Table 3. Mixed-model ANOVA results evaluating the effect of habitat type (natural vs. breakwater) and exposure (exposed vs. sheltered) on taxa richness (number of taxa quadrat^{-1}, transformed using $\log_{10}$[datum + 1]) and total abundance (total percent cover per quadrat) for 18 breakwater and 18 natural rocky intertidal sampling sites throughout the southern Gulf of St. Lawrence. Sites were sampled throughout July and August 2010. p-values for Tukey's honestly significant difference pairwise comparisons related to the goals of our study are included. BE: breakwater exposed; BS: breakwater sheltered; NE: natural exposed; NS: natural sheltered

Source of variation	df	MS	*F*	p	BE, NE	BE, BS	NE, NS	BS, NS
Richness								
Type	1	6.671	19.96	<0.001				
Exposure	1	0.400	1.85	0.183				
Type × Exposure	1	1.485	6.87	0.013	0.205	0.714	0.074	<0.001
Site(Type)	34	0.334	17.36	<0.001				
Exposure × Site(Type)	34	0.216	11.23	<0.001				
Error	360	0.019						
Abundance								
Type	1	67438	5.04	0.031				
Exposure	1	9886	1.73	0.198				
Type × Exposure	1	43368	7.57	0.009	0.963	0.603	0.080	0.001
Site(Type)	34	13394	16.86	<0.001				
Exposure × Site(Type)	34	5732	7.22	<0.001				
Error	360	794						

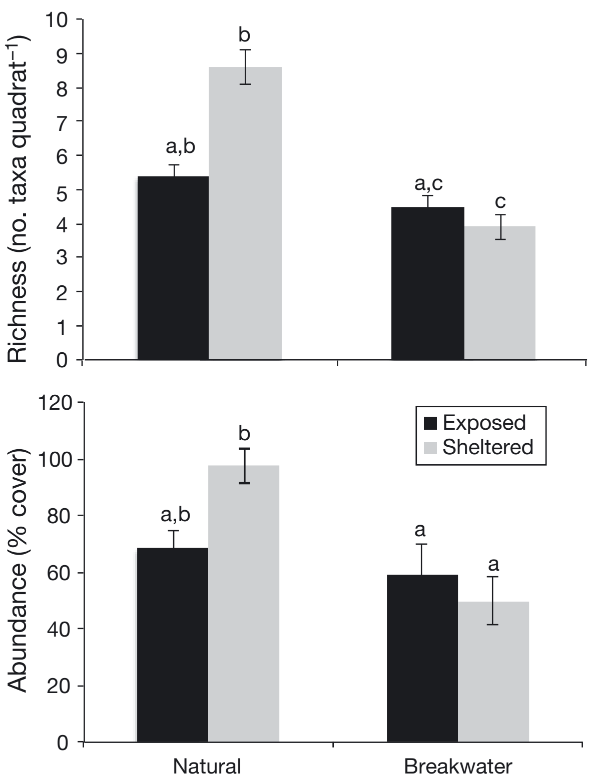

Fig. 2. Mean taxa richness (upper panel) and abundance (percent cover pooling over taxa; lower panel) on exposed and sheltered sides of 18 breakwaters and 18 natural rocky shores in the southern Gulf of St. Lawrence in summer 2010. Error bars are 1 SE; n = 144 quadrats per exposure for breakwaters, and n = 72 quadrats per exposure for natural sites. Richness means and standard errors are calculated from untransformed data. Treatments sharing the same letter above the corresponding bars are not statistically different based on Tukey's honestly significant difference tests

Ice scour

Ice scour, inferred from overwinter deformation of steel rods installed along breakwaters and natural rocky shores, was significantly stronger on the exposed than the sheltered sides of both breakwaters and natural rocky shores ($F_{1,16}$ = 150.04, p < 0.001; Fig. 4). There was no difference in ice scour intensity between breakwaters and natural rocky shores when pooling data from exposed and sheltered habitats (habitat type: $F_{1,16}$ = 1.06, p = 0.319; habitat type × exposure interaction: $F_{1,16}$ = 0.003, p = 0.957).

DISCUSSION

The primary question posed in our study was whether established, rubble-mound breakwaters support the same biotic communities as nearby natural rocky shores, and, therefore, constitute similar coastal habitat, within the southern Gulf of St. Lawrence. Our results indicate that the answer to this question is no. Richness, abundance, and community composition of biota on 18 established breakwaters differed significantly from values on nearby rocky intertidal shores during summer. Specifically, taxa richness and overall abundance of biota were lower on breakwaters than on natural rocky shores in sheltered areas (but not exposed areas), and community composition differed between the 2 habitat types in both sheltered and exposed areas. This is the first report on habitat quality of breakwaters in the Northwest Atlantic and, perhaps more importantly, for coastal waters that are ice-bound in winter. The results are broadly consistent with what has been reported elsewhere in the world (Bacchiocchi &

Table 4. PERMANOVA results evaluating the effect of habitat type (natural vs. breakwater) and exposure (exposed vs. sheltered) on the community composition (Bray-Curtis similarity of 4th-root transformed taxa abundances per quadrat) of 18 breakwaters and 18 natural rocky sites throughout the southern Gulf of St. Lawrence. Sites were sampled throughout July and August 2010. p-values for pairwise comparisons related to the goals of our study are included. BE: breakwater exposed; BS: breakwater sheltered; NE: natural exposed; NS: natural sheltered

Source of variation	df	MS	Pseudo *F*-ratio	p	BE, NE	BE, BS	NE, NS	BS, NS
Community composition								
Type	1	75145	6.40	0.001				
Exposure	1	23870	2.97	0.007				
Type × Exposure	1	22514	2.81	0.007	0.002	0.018	0.001	0.001
Site(Type)	34	13091	14.84	0.001				
Exposure × Site(Type)	34	8918	10.11	0.001				
Error	360	882						

Airoldi 2003, Bulleri & Chapman 2004, Moschella et al. 2005, Gacia et al. 2007).

The comparison of exposed versus sheltered sides of the habitats was a secondary goal in our study, because previous research in the southern Gulf of St. Lawrence had already shown lower taxa richness in exposed than in sheltered areas of natural rocky shores (Scrosati & Heaven 2007). We observed a trend in this direction for both richness and total abundance on natural rocky shores; however, perhaps because of the broader geographic scope and consequent increased inter-site variation in our study compared to that of Scrosati &

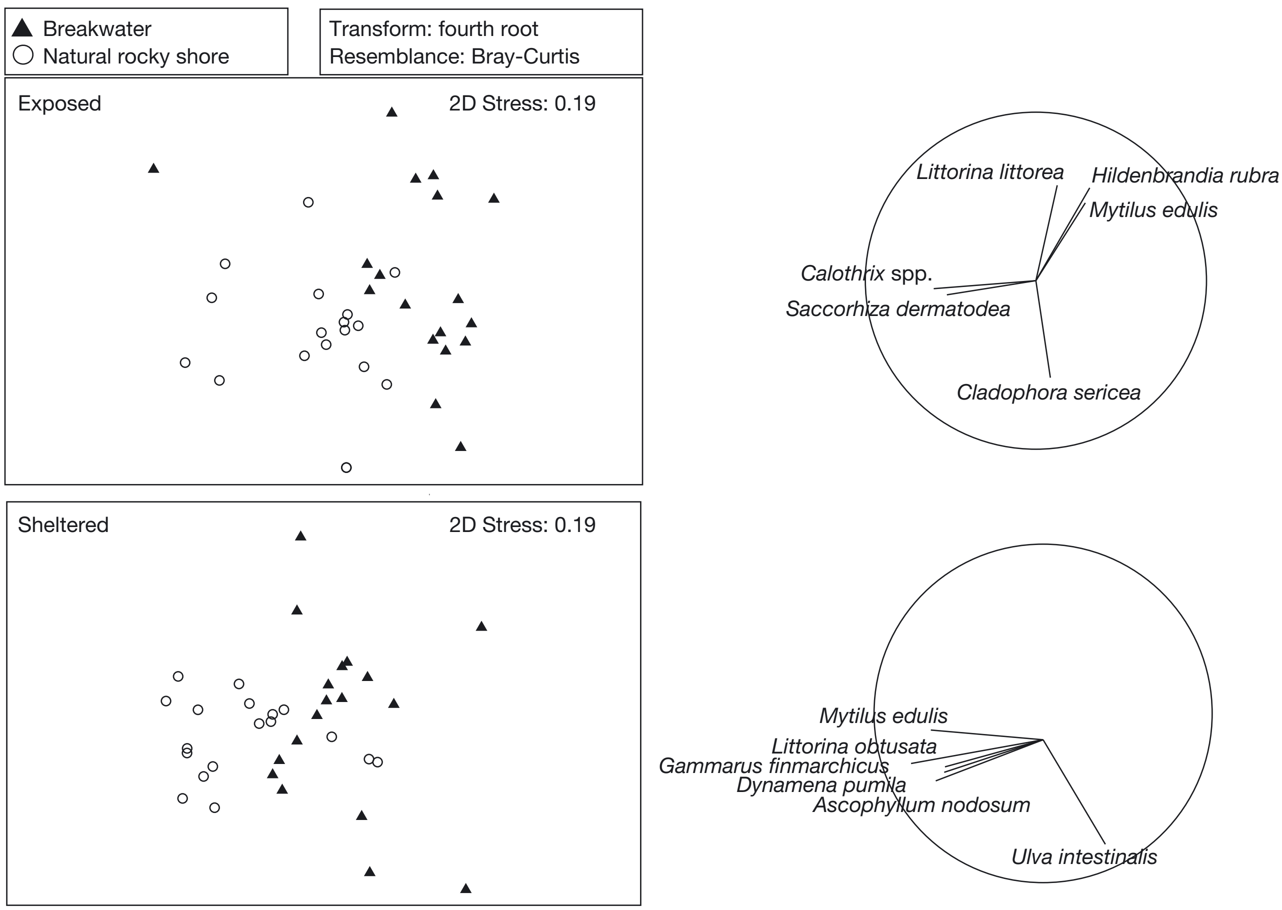

Fig. 3. Two-dimensional non-metric multidimensional scaling (nMDS) ordination plots depicting differences in community composition between breakwaters (n = 18 sites) and natural rocky shore sites (n = 18 sites; 17 of 18 visible due to 2 overlapping sites) at exposed areas and sheltered areas separately, in the southern Gulf of St. Lawrence in summer 2010. Each symbol represents a site. Vectors adjacent to each nMDS plot show Pearson correlation coefficients (r) between each taxon and the nMDS axes, depicting the direction of increased abundance across the nMDS graph. The circle indicates the maximum vector length ($r = 1$, when parallel to one nMDS axis); only taxa with a correlation of $r \geq 0.6$ with at least one nMDS axis are shown

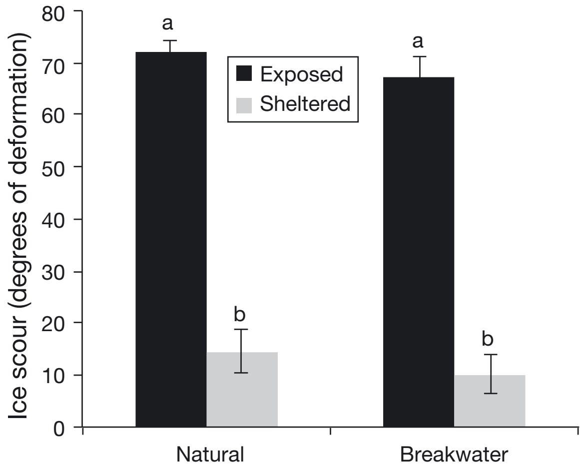

Fig. 4. Ice scour intensity (mean ± SE; n = 27 rods per habitat type × exposure combination). Treatments sharing the same letter above the corresponding bars are not statistically different ($p < 0.05$) based on Tukey's honestly significant difference tests

Heaven (2007), these differences were not statistically significant in our study. Nevertheless, our multivariate results corroborate those of Heaven & Scrosati (2008), who reported a significant difference in the biotic communities found on exposed and sheltered sides of natural rocky shores in this part of the world.

Physical environmental stress influences the intertidal community composition of natural rocky shores (Bertness 2007, Scrosati & Heaven 2007) and breakwaters (Southward & Orton 1954, Moschella et al. 2005). We found winter ice scour to be stronger on exposed than sheltered sides of breakwaters and natural rocky sites, which is consistent with a previous report for natural rocky shores (Scrosati & Heaven 2006). As well, it is likely that exposed areas of breakwaters and natural rocky shores experience higher physical stress during the ice-free period due to higher wave action. We did not measure wave action in our study, but Scrosati & Heaven (2007) found higher maximum water velocity on exposed than sheltered sides of a natural rocky shore in the Arisaig region of Nova Scotia (approximately at the centre of our studied coastal range).

Interestingly, breakwaters showed no indication of higher taxa richness or total abundance in sheltered than exposed areas, suggesting similarly strong, though different, stresses on the sheltered sides. Human activities create a major source of disturbance for breakwaters not found in natural intertidal areas. Sheltered areas of breakwaters may be subjected to increased turbidity (Bulleri & Chapman 2004, 2010, Clynick 2006, Vaselli et al. 2008) and reduced water circulation (Zyserman et al. 2005). Reduced water circulation can decrease richness and abundance of organisms by limiting dispersal (Underwood & Jernakoff 1984, Bulleri & Chapman 2004, Scrosati & Heaven 2007, Vaselli et al. 2008), altering settlement patterns (Abelson & Denny 1997, Martins et al. 2009), and increasing siltation and entrapment of pollutants, potentially increasing mortality rates (McQuaid & Lindsay 2000, Moschella et al. 2005, Gacia et al. 2007). For example, we observed seafood processing plants near 12 of our 18 breakwaters, and fishing vessels were moored within all of them.

Multivariate analyses detected differences in community structure between breakwaters and natural rocky shores not reflected in taxa richness and overall abundance. These differences were largely driven by *Semibalanus balanoides*, a common acorn barnacle, accounting for 38 and 25% of the difference between habitat types in exposed and sheltered areas, respectively, and found in higher abundance at natural sites. Barnacles were absent from some breakwaters, especially in their exposed areas, and, where barnacles were present, their average abundance was lower than on natural rocky shores. In the southern Gulf of St. Lawrence, winter ice scour results in annual die-off of barnacles not sheltered in crevices when ice scour is strong (Belt et al. 2009). Spring recruitment of barnacles is normally high and allows barnacle populations to recover (MacPherson et al. 2008, Ellrich et al. 2015). Thus, it would be profitable to evaluate whether barnacle recruitment differs between breakwaters and natural rocky areas. Differences could result from poor water circulation around breakwaters resulting in reduced larval dispersal and recruitment (Mullineaux & Butman 1991, Abelson & Denny 1997, Martins et al. 2009), reduced availability of suspended food particles, or smothering by deposited sediments (Bertness 2007, Lee & Li 2013).

Mussels (*Mytilus* spp.) were a minor contributor to community dissimilarity between breakwaters and natural rocky shores (Table 5), but interestingly they were found in only 2 of 18 sheltered breakwater areas compared to 14 of 18 sheltered natural rocky areas. Furthermore, average mussel abundance was very low in sheltered breakwater areas relative to exposed areas of breakwaters and exposed and sheltered areas of natural rocky shores. This finding was unexpected and is incongruent with findings from other parts of the world that mussels typically form smaller populations in exposed areas compared to sheltered areas of breakwaters (Bulleri & Airoldi 2005). The relative absence of *Mytilus* spp. in shel-

Table 5. SIMPER results for taxon abundance sampled throughout the southern Gulf of St. Lawrence. Average abundance (presented as untransformed data) of the most influential taxa causing dissimilarities between breakwaters and natural rocky shores, taxon-specific contribution (%), and the resulting cumulative contributions with a cut-off of ~90% are included. Average community dissimilarity between habitat types for each exposure level is indicated

	Abundance (% cover)			
	Breakwater	Natural	Individual contribution (%)	Cumulative contribution (%)
Exposed areas				
Semibalanus balanoides	19.48	35.90	37.64	37.64
Calothrix spp.	0.11	9.69	11.02	48.66
Fucus spp.	6.58	7.65	10.51	59.17
Chordaria flagelliformis	0.18	6.31	6.62	65.79
Hildenbrandia rubra	4.43	1.97	5.50	71.29
Mytilus edulis	4.68	0.62	5.18	76.46
Ulva intestinalis	5.85	0.01	4.50	80.97
Ulva lactuca	6.39	0.00	3.69	84.66
Dark green crust	3.65	0.00	3.54	88.19
Ascophyllum nodosum	4.37	0.10	2.85	91.05
	Average dissimilarity = 82.82%			
Sheltered areas				
Semibalanus balanoides	14.49	29.36	24.62	24.62
Fucus spp.	11.07	26.01	22.68	47.3
Ascophyllum nodosum	1.89	24.13	19.59	66.88
Calothrix spp.	2.77	4.1	7.41	74.29
Ulva intestinalis	7.48	0.01	5.78	80.07
Hildenbrandia rubra	4.31	1.77	4.78	84.86
Chondrus crispus	0.32	2.55	2.32	87.17
Dynamena pumila	0.02	2.47	1.91	89.08
Mytilus edulis	0.01	1.98	1.57	90.65
	Average dissimilarity = 79.90%			

tered areas of breakwaters in our study may be the result of human interventions to restructure and reinforce breakwaters. Such maintenance activities have been reported to have negative impacts on organism settlement and survival in the intertidal zone (Bacchiocchi & Airoldi 2003, Moschella et al. 2005). Airoldi & Bulleri (2011) found that regular repair of damaged breakwaters caused a decrease in cover of several dominant intertidal bivalve species, including mussels *Mytilus galloprovincialis* and oysters *Ostrea edulis*, as well as an increase in opportunistic ephemeral algae. In addition, 2 studies have shown that sheltered areas of artificial rocky structures lack bivalve species found on exposed sides and have speculated that this is due to suffocation of their filtration system from deposition of fine sediments (Dare 1976, Gacia et al. 2007). Similarly to Gacia et al. (2007) and Vaselli et al. (2008), we observed a thin (<0.5 cm) layer of fine sediment covering the sheltered regions at a number of the breakwaters. High sedimentation rates can cause a lower richness and favor opportunistic and invasive algae (Vaselli et al. 2008, Mineur et al. 2012). Tracking and observing maintenance activities on artificial rocky structures and relating these activities to survival of biota and resulting community structure would thus be an important next step in this research.

The common brown algae *Fucus* spp. and *Chordaria flagelliformis* and the cyanobacteria *Calothrix* spp. were found in lower abundances on breakwaters than on natural rocky intertidal areas. *Chordaria flagelliformis* is a characteristic species of exposed rocky regions of the southern Gulf of St. Lawrence (Heaven & Scrosati 2008). The relative paucity of these species on exposed sides of breakwaters may hint at greater, undetected forces of ice scour and wave exposure on breakwaters than on natural rocky shores due to the abrupt topographic change between the sea bottom and breakwater surface, limiting wave dissipation found at more gradual shorelines (Putman & Johson 1949). *Fucus* spp. is an important canopy-forming bioengineer in stressful mid-intertidal regions, having strong effects on species richness and community resilience by alleviating desiccation and thermal stress in understory habitats (Bruno et al. 2003, Watt & Scrosati 2013). Abundance of fish and crustaceans has been observed to depend on such bioengineers for survival in relation to predation and abiotic stresses (Relini et al. 1994, Pickering & Whitmarsh 1997). Reduced abundance of canopy-forming species on sheltered areas of breakwaters may be due to higher turbidity and limited light availability, and result in decreased survival of invertebrates and algae reliant on this habitat feature (Jenkins et al. 2004, Watt & Scrosati 2013).

The green algae *Ulva intestinalis* and *U. lactuca* were much more abundant on breakwaters than on natural rocky shores, being most abundant in sheltered regions of breakwaters, which is consistent with findings for other closely related ephemeral macroalgae (Airoldi & Bulleri 2011). Bacchiocchi & Airoldi (2003) found that *Ulva* spp. are among the earliest colonizers of artificial rocky structures. *Ulva intestinalis* also predominates when localized eutrophication occurs (Raffaelli & Hawkins 1996), indicating that sheltered regions may suffer from nitrogen and phosphorus influxes from commercial activities (i.e. fishing vessel output, fish processing plants, sewage, river runoff from agricultural land), which can be intensified by poor hydrological circulation inside breakwaters (Airoldi & Bulleri 2011).

In conclusion, our study is the first to examine the intertidal communities occurring on breakwaters in the Northwest Atlantic in areas that freeze over throughout the winter. Results of this large-scale study demonstrate that, while rubble-mound breakwaters constructed in the southern Gulf of St. Lawrence do provide habitat for algae and invertebrates that would not be found on soft or sand substrates where such breakwaters are often built, they support communities that are qualitatively and quantitatively different from those on local natural rocky shores. As well, breakwaters may create potential 'stepping stones' for non-indigenous and invader species that replace species found in communities on natural rocky shores (Vaselli et al. 2008). These results constitute the necessary first information for project proponents and resource managers on the impacts of breakwater construction on species and habitats that support commercial, recreational, or aboriginal fisheries in Canada (DFO 2013, Kenchington et al. 2013). In addition to the next steps discussed above to understand the mechanisms of breakwater colonization, work is urgently needed and presently underway to examine the degree to which breakwaters constitute habitat for commercially important fisheries species, such as the American lobster *Homarus americanus*.

Acknowledgements. We are grateful for the funding and logistic support provided by Small Craft Harbours, Oceans and Science Branch and Habitat Divisions of the Gulf Region Department of Fisheries and Oceans (DFO), Canada, by DFO's National Centre of Aquatic Habitat Research (CAHR), and by the Canadian Rivers Institute (CRI). Additional funding came from grants awarded to R.A.S. by the Canada Research Chairs (CRC) program and the Natural Sciences and Engineering Research Council (NSERC Discovery Grant). We also acknowledge support from the University of New Brunswick's Department of Biology and St. Francis Xavier University's Department of Biology. This manuscript was improved by the constructive suggestions of three anonymous reviewers.

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Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

Submitted: February 3, 2015; Accepted: September 15, 2015
Proofs received from author(s): November 9, 2015