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Variation in rhodolith morphology and biogenic potential of newly discovered rhodolith beds in Newfoundland and Labrador (Canada)

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Abstract

For the first time the subarctic northwestern Atlantic, we examined variation in rhodolith (*Lithothamnion glaciale*) morphology and biogenic potential in two large (>500 m^2) rhodolith beds we discovered recently between the depths of 5–25 m off St. Philip's and Holyrood, Newfoundland and Labrador. Rhodoliths at St. Philip's were >50% larger and contained 7% more internal space in deep (15–17 m) than shallow (8–10 m) water, whereas shallow rhodoliths were >180% larger at Holyrood than at St. Philip's. Rhodoliths were predominantly spheroidal and compact at St. Philip's and platy or bladed at Holyrood. Shallow rhodoliths varied in length from 41.1–114.6 mm at St. Philip's and 61.3–189.1 mm at Holyrood. Rhodolith density was similar between beds (858.1–938.9 individuals m^{-2}) although biomass was significantly higher at Holyrood than St. Philip's (25.3 versus 19.4 kg m^{-2}). There was a strong positive relationship (R2>0.93) between rhodolith volume and dry weight in both beds. Invertebrates associated with shallow rhodoliths belonging to the taxonomic groups Asteroidea, Echinoidea, Ophiuroidea, Bivalvia, Gastropoda, Polyplacophora, Crustacea, and Annelida were present at both sites, although they varied in terms of size, density, and biomass. Brittle stars (*Ophiopholis aculeata*) and chitons (*Tonicella marmorea*) accounted for at least 82% (up to 2026.7 individuals m^{-2}) of total numbers of invertebrates in each bed. Larger rhodoliths appeared to facilitate reproduction and feeding in dominant fish and invertebrate species. Differences in hydrodynamic conditions within and between beds may have contributed to these patterns.

Keywords: biodiversity; brittle stars; chitons; invertebrates; red coralline seaweeds.

Introduction

Rhodoliths are red, benthic, long-lived (often >100 years), non-geniculate coralline seaweeds (Rhodophyta, Corallinaceae) growing as free-living balls, branched twigs, or rosettes from the low intertidal zone down to depths >150 m in tropical to polar seas (see review by Foster 2001, and more recent studies by Steller et al. 2003, Gherardi 2004, Brandano et al. 2005, Konar et al. 2006, Figueiredo et al. 2007, Hinojosa-Arango et al. 2009, Sciberras et al. 2009, Riosmena-Rodriguez and Medina-Lopez 2010). Individual rhodoliths can grow from detached fragments of existing rhodoliths (in which case they are primarily made up of coralline tissues) or possess a core made of other materials (i.e., nucleated rhodoliths) when they originate from recruitment of algal spores on hard substrata (Bosellini and Ginsburg 1971, Freiwald and Henrich 1994, Basso et al. 2009, Adey and Hayek 2011). The terms "rhodolith", "rhodolite" (used in geology), and "maërl" (French name) have been used interchangeably in the literature (Foster 2001), even though these terms may refer to different structures. In the present study, we use the term "rhodolith" in reference to coatings of red coralline seaweeds (nucleated or not), in which the corallines comprise over 50% of the specimen (*sensu* Steneck 1986). We also use the term "fleshy seaweed" to refer to those seaweeds that do not incorporate calcium carbonate in their tissues.

Growth rates of rhodolith species are remarkably low (typically <1 mm y^{-1}) (Frantz and Kashgarian 2000, Blake and Maggs 2003, Bosence and Wilson 2003, Rivera et al. 2004), and there are large intra- and interspecific variation in rhodolith growth forms (e.g., foliose, fructicose, and lumpy) and shapes (e.g., spheroidal, discoidal, and ellipsoidal) (Bosence 1976, Piller and Rasser 1996, Riosmena-Rodriguez et al. 1999, Perry 2005, Basso et al. 2009). Rhodoliths can form extensive beds (aggregations) overlying calcareous sediments produced by the accumulation of eroding rhodolith fragments (Foster 2001). These beds typically occur in environments where water motion (waves and currents) or bioturbation are strong enough to move individual rhodoliths within beds, thereby preventing burial by sediments or overgrowth by other organisms, but not so high as to cause their destruction (Steller and Foster 1995, Marrack 1999, Ballantine et al. 2000, Ryan et al. 2007).

Rhodolith beds are particularly abundant in the Mediterranean Sea and along the west coast of North America (Gulf of California), the east coasts of Central (eastern Caribbean) and South America (Brazil), and Atlantic coasts of European countries, including Norway, France, Ireland, and Scotland (Bosence 1983, Foster 2001). Accordingly, most of our knowledge of the distribution, structure, and function of rhodolith beds comes from studies in these regions. One emerging consensus is that the high structural complexity of rhodolith beds allow them to support a rich diversity of

soft and hard bottom invertebrates, including polychaetes, crustaceans, asteroids, ophiuroids, echinoids, and molluscs (Bosence 1979, BIOMAERL 1999, Bordehore et al. 2003, Steller et al. 2003, Hinojosa-Arango and Riosmena-Rodriguez 2004, Figueiredo et al. 2007, Foster et al. 2007, Sciberras et al. 2009, Riosmena-Rodriguez and Medina-Lopez 2010).

Rhodolith extraction, eutrophication, mariculture, fishing, and pollution are among the major threats to European rhodolith beds (Barbera et al. 2003, Grall and Hall-Spencer 2003, Hall-Spencer et al. 2003). Challenges facing researchers studying the biology and ecology of rhodoliths and the beds they form include the following: (1) general lack of distinctive external features and the need for harmonized taxonomic criteria to differentiate rhodolith-forming algal species that often display high morphological plasticity (Steneck and Paine 1986, Steneck 1990, Braga et al. 1993, Bailey and Chapman 1998, Riosmena-Rodriguez et al. 1999, Basso et al. 2004, Adey et al. 2005, Harvey and Woelkerling 2007); (2) scarcity of data on growth rates and longevity of rhodoliths, which are difficult to assess accurately and can vary with temperature and depth (Littler et al. 1991, Frantz and Kashgarian 2000, Blake and Maggs 2003, Bosence and Wilson 2003, Rivera et al. 2004, Steller et al. 2007); and (3) considerable depths at which rhodoliths occur (Littler et al. 1991, Harris et al. 1996, Basso 1998, Brandano et al. 2005, Amado-Filho et al. 2007, Sciberras et al. 2009), complicating the collection of specimens and monitoring of beds at ecologically meaningful scales.

Over four decades have elapsed since the first published account of rhodoliths in the northwestern Atlantic (Adey 1966, Bosence 1983, Foster 2001). Yet, our knowledge of rhodoliths in this vast region is still limited to only a few studies characterizing the main species that form them (arctic: *Lithothamnion tophiforme* [Esper] Unger, subarctic: *L. glaciale* Kjellman: Adey and Adey 1973, Adey et al. 2005), general geographical concentrations (Adey and Hayek 2011), and how individual rhodoliths may be used as paleoenvironmental indicators (Halfar et al. 2000). Our recent (2007 and 2009) discovery of two shallow (5 to >25 m deep) rhodolith (*L. glaciale*) beds in Conception Bay (southeastern tip of the island of Newfoundland) presented an opportunity to provide the first integrated, quantitative analysis of rhodolith morphology, biogenic potential, and organization as beds in the subarctic northwestern Atlantic.

The current study examines variation in morphological traits of rhodoliths and associated invertebrate macrofauna within and between these two beds in Conception Bay. Specifically, we (1) determined how rhodolith size and shape changed with depth in one bed and in shallow water between beds, (2) quantified and compared the abundance of dominant invertebrate macrofauna associated with shallow rhodoliths between beds, and (3) described invertebrate- and fish-rhodolith interactions we recorded while sampling one bed. Results are interpreted in the context of current knowledge of rhodoliths and rhodolith beds in other parts of the world, with the overall objective of generating testable hypotheses on the formation and maintenance of rhodolith beds in this region.

Materials and methods

Study sites and preliminary observations

Our study was conducted during the summer of 2009 at two subtidal sites, namely, St. Philip's and Holyrood, separated by approximately 27 km within Conception Bay, Newfoundland and Labrador (Canada) (Figure 1). The seabed at each site was covered by a relatively large (>500 m^2) rhodolith bed formed around the primary productivity of the locally dominant red coralline seaweed *L. glaciale*. Each bed extended from a depth of approximately 5 m to below 25 m, which is the deepest observation point in this study. Rhodoliths below 25 m were not sampled, because our primary interest was to characterize variation in morphological traits and invertebrate macrofauna associated with the shallowest rhodoliths, while providing key information on the abundance (density and biomass) of rhodoliths in the upper portion of each bed. Rhodoliths occurred as one layer (St. Philip's) or up to three layers (Holyrood), and were more sparsely distributed at St. Philip's than Holyrood. Preliminary diver observations suggested differences in the size and shape between shallow (<10 m) and deeper (>15 m) rhodoliths at St. Philip's only (rhodoliths at Holyrood were consistently large throughout the bed); there were also differences in shallow rhodoliths between sites (Figure 2). There were no obvious differences in the density (1–4 branches cm^{-2} of rhodolith surface) and length (<1 cm) of branches (distal protuberances) between rhodoliths at the two sites. The abundance of dominant rhodolith-associated invertebrate macrofauna also appeared to vary between sites. Based on these observations, rhodoliths at St. Philip's were sampled within two depth strata, 8–10 m (shallow) and 15–17 m (deep), while those at Holyrood were sampled in the 8–10 m range. Accordingly, depth-related changes in rhodolith morphology (total volume and volume of internal space) and weight were examined with data from St. Philip's. Data from both St. Philip's and Holyrood were used to determine whether or not the shape (sphericity), morphology (total volume, and volume of internal space), and weight of shallow rhodoliths and associated macrofauna varied between sites (see details below).

Variation in rhodolith morphology and weight

To test the postulate that rhodolith morphology varied with depth, we first compared two morphological traits, namely, total volume and volume of internal space, and wet weight of shallow and deep rhodoliths at St. Philip's. On 29 June 2009, we haphazardly collected 9 and 10 rhodoliths in shallow (8–10 m) and deep (15–17 m) water, respectively, *via* SCUBA diving. We swam over the seabed within each depth stratum and stopped every 3–5 m to collect the first rhodolith that showed no sign of structural damage (no broken branches or missing portions). Rhodoliths were carefully placed in mesh bags and carried to the surface, where they were stored in rigid containers and then transported to the Ocean Sciences Center, Memorial University of Newfoundland, for analysis. Each rhodolith was examined within six days of collection

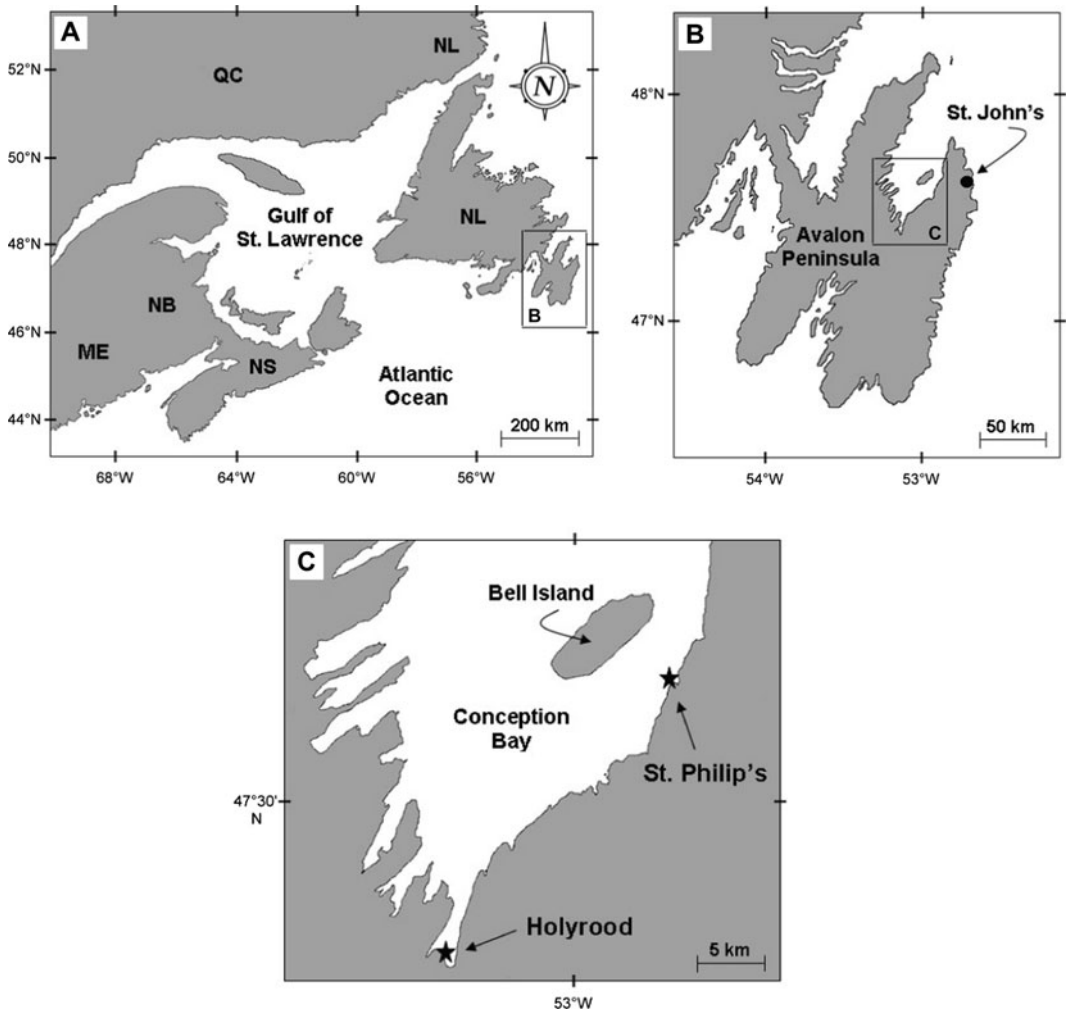

Figure 1 Maps of (A) eastern Canada, (B) the Avalon Peninsula, and (C) Conception Bay showing the location of the two study sites, St. Philip's and Holyrood [NL, Newfoundland and Labrador; QC, Québec; NB, New Brunswick; NS, Nova Scotia; ME, Maine (USA)].

in the following sequence. Using forceps, we extracted any macrofauna on the exposed surface and within accessible interstices of the rhodolith; note that macrofauna in these rhodoliths was not sampled but simply removed to allow accurate assessment of rhodolith volumes and weight. The rhodolith was then sealed with a thin pellicle of plastic, which was tightly applied to its surface with a vacuum food sealer (model VS107WM-CN; Rival; Boca Raton, Florida, USA). The rhodolith and its pellicle were immersed in a large beaker containing seawater. The difference in water volumes prior to and after immersion was used to estimate total rhodolith volume (i.e., combined volumes of rhodolith tissues and space within the rhodolith, hereafter termed the "internal space"). The pellicle was removed and its volume (measured as above) was subtracted from the estimated total rhodolith volume to provide a corrected measure of total rhodolith volume. The rhodolith (without its pellicle) was broken into pieces to allow extraction of any macrofauna within deeper interstices (down to the center of the rhodolith) that could not be removed initially. Rhodolith pieces were re-immersed in a beaker of seawater, and the difference in water volumes was used to determine the volume of rhodolith tissue alone. The volume of internal space was subsequently determined by subtracting the volume of rhodolith tissue from the corrected total rhodolith volume. Finally, the wet rhodolith was weighed on a balance (model PB-3002-S/FACT; Mettler Toledo; Greifensee, Switzerland) with a precision of ±0.01 g. To further test the postulate that rhodolith morphology varies between sites, we also compared the two morphological traits and weights explained above between shallow rhodoliths from the two sites. We used the same rhodolith collection and measurement procedures described above to assess 14 rhodoliths taken in 8–10 m of water on 24 June 2009 at the Holyrood site. Although data were available for the two depth strata at St. Philip's and the shallow depth stratum at Holyrood, we did not compare characteristics between deep rhodoliths at St. Philip's and shallow rhodoliths at Holyrood to avoid the potentially confounding effects of depth and site, which may complicate data interpretation, as well as to maintain consistency with our two main postulates.

To further investigate potential differences in the morphology of rhodoliths, we examined differences in the shape

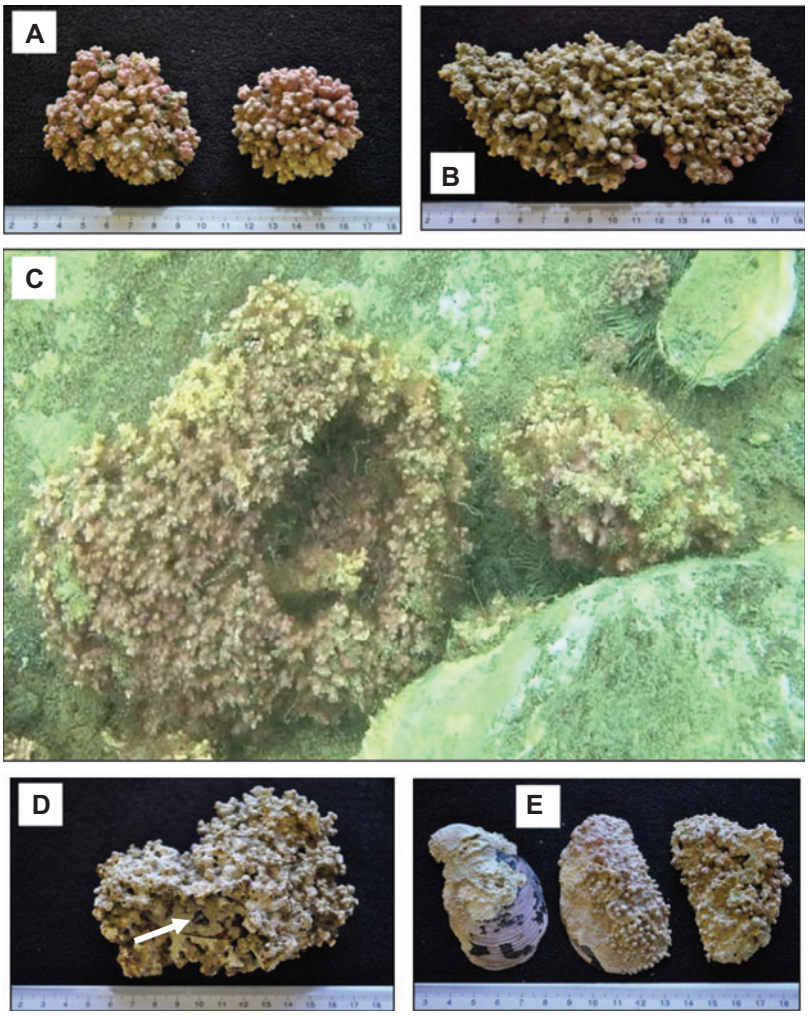

Figure 2 Difference in morphology of shallow (8–10 m deep) rhodoliths at the two study sites, St. Philip's and Holyrood (scale, when provided, is in centimeters; see Figure 1 for location of sites). Size and shape of representative rhodoliths at St. Philip's (A) and Holyrood (B). (C) Large [>15 cm] rhodolith with empty cavity at Holyrood. Note the presence of tens of brittle-star arms [mainly the daisy brittle star, *Ophiopholis aculeata*] projecting from the walls of the rhodolith and thin mat of red filamentous algae in some interstices. (D) Rhodolith with a core (arrow) of horse mussel [*Modiolus modiolus*] shell fragment at St. Philip's. (E) Empty shells of *M. modiolus* at different stages of colonization by red coralline seaweeds at Holyrood.

(degree of sphericity) of shallow rhodoliths from the two sites. Logistical considerations prevented the collection of deep rhodoliths at the St. Philip's site; hence, we were unable to examine depth-related differences in shape. With a vernier caliper (±0.1 mm), we measured the length of the longest (L), intermediate (I), and shortest (S) axes of 81 and 56 rhodoliths acquired in July 2009 at depths of 8–10 m at St. Philip's and Holyrood, respectively. The next section provides further details about the collection of those rhodoliths, which were part of a larger pool of rhodoliths used to characterize the rhodolith macrofauna. We aggregated the three linear dimensions obtained from each rhodolith using the spreadsheet TRIPLOT (http://www-staff.lboro.ac.uk/~gydjg2/downloads/tri-plot_v1-4.xls) developed by Graham and Midgley (2000) from the pioneering work by Sneed and Folk (1958). Essentially, the spreadsheet creates a triangular diagram of deviation (or similarity) in the shape of measured particles (in our case, each rhodolith) from three categories of shapes forming the apices of the triangle, namely, spheroidal, discoidal, and ellipsoidal. Accordingly, it uses the mathematical relationships S/L, I/L, and (L-I)/(L-S) to calculate deviations in sphericity between apices discoidal and spheroidal, spheroidal and ellipsoidal and discoidal and ellipsoidal, respectively. It also calculates the proportion of particles that belong to each of 10 finer shape categories ranging from "compact" to "very elongate". Finally, we measured the dry weight and volume of tissue of each rhodolith to determine the relationship between weight and volume of rhodoliths at each site. Dry weight was used as opposed to wet weight to provide standardized values that can be compared with those in other studies. Dry weight was determined after drying rhodoliths to constant weight (between 24 and 36 h) at 60°C in an oven (model Lindberg Blue M; Thermo Scientific; Asheville, NC, USA). Rhodolith

size (i.e., length of the longest axis, L) data were also used to construct size frequency distributions of shallow rhodoliths at each site.

Characterization of rhodolith macrofauna and abundance

Preliminary observations of a few rhodoliths at the St. Philip's site suggested that the abundance of brittle stars and chitons surpassed that of any other rhodolith macrofauna. To verify this pattern, we documented the abundance of other invertebrates associated with rhodoliths, and determined whether the pattern varied between sites; we then examined the composition of the invertebrate macrofauna associated with shallow rhodoliths at the two sites. In July 2009, we hand collected (*via* SCUBA diving) all rhodoliths in 9 (St. Philip's) and 10 (Holyrood) quadrats (30 cm×30 cm) placed at meter intervals along a transect line in the depth range of 8–10 m. Rhodoliths were carefully removed from the seabed, immediately placed in sealed plastic bags to keep all associated macrofauna, and carried to the surface; these were then placed in rigid containers for transportation to the Ocean Sciences Center. Rhodoliths were kept in these plastic bags within large holding tanks supplied with cold seawater pumped from Logy Bay throughout the three-week period required to process them all. Water in each bag was changed every two days. Each rhodolith was carefully inspected for invertebrate macrofauna and then broken into smaller pieces when necessary to ensure all organisms were extracted. Invertebrates were preserved in 4% formalin prepared with filtered seawater for further identification and measurement (see below). Given that most invertebrate species were found both on the periphery and within interstices of rhodoliths, they were not separated into epifaunal and cryptofaunal groups, but rather treated as a whole, which was also consistent with our main objective of examining macrofauna in general. Invertebrates were classified into the following broad taxonomic groups, because disintegration or lack of body tissues in some specimens or difficulties in identifying juvenile specimens prevented greater taxonomic resolution: Asteroidea (sea stars), Echinoidea (urchins), Ophiuroidea (brittle stars), Bivalvia (mussels and clams), Gastropoda (snails), Polyplacophora (chitons), Crustacea (decapods and amphipods), and Annelida (polychaetes). For each site, we calculated the mean size (i.e., diameter or length of the body regions, depending on the species), density, and biomass of specimens in most taxonomic groups based on data from each quadrat. The biomass of ophiuroids could not be assessed reliably due to a high proportion of individuals with one or several arms partly or entirely missing. Likewise, many polychaete worms were lacking body parts; hence, their size and biomass were not determined. We also did not collect data on epiphytic seaweeds in this study as only a small proportion (<5%) of rhodoliths had trace amounts of fleshy seaweeds, mainly filamentous red algae, on their surfaces. Encrusting invertebrates, such as sponges and bryozoans, were also present in only trace amounts on the surfaces of rhodoliths (Figure 2); hence these were not measured. Rhodolith data (number of individuals and total tissue dry weight in each quadrat) were used to estimate the abundance (i.e., density and biomass) of shallow rhodoliths at each site. Dry weight was used as opposed to wet weight to accurately determine only the weight of rhodolith tissue, thus providing standardized biomass values that can be compared with those in other studies.

Statistical analysis

We used one-tailed t-tests (two-sample assuming equal variances) to compare differences in (1) total volume, volume of internal space, and wet weight of shallow and deep rhodoliths at the St. Philip's site, and of shallow rhodoliths at the St. Philip's and Holyrood sites [June 2009 collection], and (2) dimensions (i.e., long, intermediate and short axes), dry weight, tissue volume, density, and biomass of rhodoliths collected in shallow water at the two sites [July 2009 collection]. We preferred this approach over an analysis of variance (ANOVA) given that not all comparisons were conceptually relevant, including a comparison of total volume, volume of internal space, and wet weight between deep and shallow rhodoliths at St. Philip's and Holyrood, respectively. We used simple linear regression to determine the relationship between dry weight and tissue volume of shallow rhodoliths at each site (July 2009 collection). We used a two-way ANOVA (Zar 1999) with the factors Site (St. Philip's and Holyrood) and Taxon (Ophiuroidea and Polyplacophora) to investigate differences in the proportions of brittle stars and chitons (relative to total number of invertebrate individuals) living on shallow rhodoliths within and between study sites. This analysis was treated as a particular case of the generalized linear models (Proc Genmod; McCullagh and Nelder 1989, SAS Institute Inc. 1999, Bolker et al. 2008), which assumed a binomial distribution of the response variable (i.e., the ratio of number of individuals in each species to total number of invertebrates). Thus, we did not test for normality and homoscedasticity in the data.

Where required (regression analysis), normality was verified using Shapiro-Wilk's statistic (SAS Institute Inc. 1999) and homoscedasticity by examining the graphical distribution of the residuals and by applying the Levene test (Snedecor and Cochran 1989). To detect differences among levels within a factor, we used least-square means multiple comparisons tests (LS means, SAS Institute Inc. 1999). A significance level of 0.05 was used for all statistical tests.

Results

Variation in rhodolith morphology and weight

The analysis of rhodoliths collected in shallow (8–10 m) and deep (15–17 m) water at the St. Philip's site in June 2009 confirmed the postulate that rhodolith morphology and (wet) weight varied with depth (Figure 3). Indeed, total volume and volume of internal space of deep rhodoliths were, on average, 54% and 75% larger than those of shallow rhodoliths, respectively ($t_{0.05(1),17}$=2.27, p=0.018 and $t_{0.05(1),17}$=2.53, p=0.011;

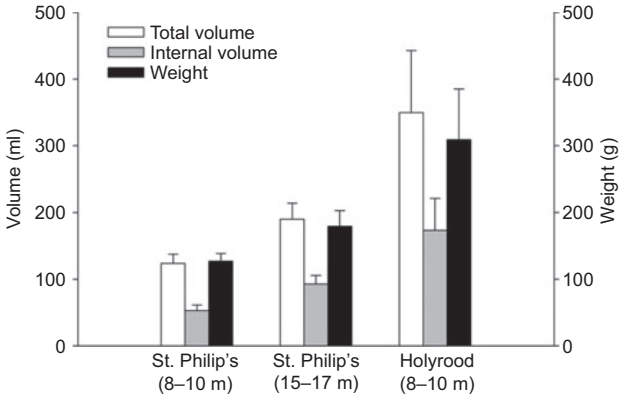

Figure 3 Mean (+SE) total volume (combined volumes of rhodolith tissue and internal space), volume of internal space, and wet weight of shallow (8–10 m deep) and deep (15–17 m) rhodoliths collected at the St. Philip's and Holyrood sites in June 2009 [n=9 (St. Philip's – shallow), 10 (St. Philip's – deep), and 14 (Holyrood – shallow)].

Figure 3). Likewise, the proportion of internal space relative to total volume was also significantly higher by 7% in deep than shallow rhodoliths ($t_{0.05(1),17}$=2.53, p=0.011; Figure 3). Although deep rhodoliths were 41% heavier (wet weight) than shallow rhodoliths ($t_{0.05(1),17}$=1.96, p=0.033; Figure 3), tissue density was similar in deep (1.85±0.04 g ml^{-1}) and shallow (1.82±0.05 g ml^{-1}) rhodoliths ($t_{0.05(1),17}$=0.56, p=0.29), suggesting that the observed changes in weight were mainly results of changes in rhodolith size (see below) rather than different tissue densities.

The comparison of rhodoliths collected in shallow (8–10 m) water at both St. Philip's and Holyrood in June 2009 also supported the postulate that rhodolith morphology and weight varied between sites. In this case, the total volume of rhodoliths at Holyrood was 182% larger than at St. Philip's ($t_{0.05(1),21}$=1.91, p=0.035; Figure 3), whereas the volume of internal space was more than twice (227%) as large at the former site ($t_{0.05(1),21}$=1.97, p=0.031; Figure 3). Moreover, the proportion of internal space relative to total volume in rhodoliths from Holyrood (48%) was 7% higher than at St. Philip's ($t_{0.05(1),21}$=1.86, p=0.038), which is consistent with the difference observed between deep and shallow rhodoliths at St. Philip's (see above). Rhodoliths at Holyrood were significantly heavier by 143% than those at St. Philip's ($t_{0.05(1),21}$=1.88, p=0.037; Figure 3), but the average tissue density (1.79±0.063 g ml^{-1}) did not differ from that of rhodoliths at St. Philip's ($t_{0.05(1),21}$=0.31, p=0.38). The latter pattern further suggested that the observed changes in rhodolith weight between sites were mainly due to changes in rhodolith size, as opposed to differences in the degree of rhodolith calcification and non-biogenic materials trapped within the rhodoliths.

The analysis of dimensions of rhodoliths collected in shallow (8–10 m) water at St. Philip's and Holyrood in July 2009 also supported the postulate that rhodolith shape (degree of sphericity) varied between sites. The length of long, intermediate, and short axes of rhodoliths at St. Philip's was, on average, 65% ($t_{0.05(1),17}$=6.82, p<0.001), 66% ($t_{0.05(1),17}$=6.28, p<0.001) and 81% ($t_{0.05(1),17}$=3.32, p<0.01) that of rhodoliths at Holyrood, respectively (Table 1). Thus, rhodoliths at St. Philip's were more spheroidal than those at Holyrood (Figures 2 and 4). In fact, 70% of the rhodoliths at St. Philip's were compact (all categories of compactness pooled) compared with only 46% at Holyrood, in which rhodoliths were predominantly platy or bladed (Figure 4). Rhodolith tissue weight ($t_{0.05(1),17}$=4.25, p<0.001) and volume ($t_{0.05(1),17}$=4.16, p<0.001) at Holyrood were both significantly greater (2.5-fold) than at St. Philip's (Table 1). Moreover, there was a strong positive relationship between those two parameters at each site (R^2=0.93 and 0.97 at St. Philip's and Holyrood, respectively; Figure 5). There was also a marked difference in size-frequency distributions of rhodoliths at the two sites, with >80% of the rhodoliths <80 mm in length (longest axis) at St. Philip's and >70% of the rhodoliths >80 mm at Holyrood (Figure 6). In fact, rhodolith size ranged from 41.1–114.6 mm at St. Philip's (n=81) and from 61.3–189.1 mm at Holyrood (n=56).

Table 1 Mean (and associated standard error, SE) length (mm) of long, intermediate, and short axes, dry weight (g), and tissue volume (ml) of shallow (8–10 m deep) rhodoliths collected at the St. Philip's (n=81) and Holyrood (n=56) sites in July 2009.

Parameter	Study site			
	St. Philip's		Holyrood	
	Mean	SE	Mean	SE
Axes				
Long	66.5	2.7	101.7	4.3
Intermediate	52.7	1.9	80.4	3.8
Short	37.7	1.7	46.6	2.0
Weight	57.9	8.6	149.0	18.8
Volume	36.9	6.5	90.1	10.6

The between-site difference in mean values was statistically significant for each parameter (one-tailed t-tests, α=0.05, p<0.01).

Characterization of rhodolith macrofauna and abundance

The analysis of invertebrate macrofauna associated with shallow (8–10 m deep) rhodoliths collected at St. Philip's and Holyrood in July 2009 indicated that species richness did not differ between sites and a strong numerical dominance by brittle stars [mainly the daisy brittle star, *Ophiopholis aculeata* (Linnaeus)] and chitons [mainly the mottled red chiton, *Tonicella marmorea* (Fabricius O.)] at the two sites. Brittle stars and chitons made up 82% and 94% of the total number of invertebrates at St. Philip's and Holyrood, respectively. Their proportions differed within and between sites as shown by the significant Site×Taxon interaction in the corresponding ANOVA (Table 2). Specifically, the proportion of brittle stars was significantly higher than that of chitons at both sites, although the difference was 6.5-fold higher at Holyrood than St. Philip's (Table 2, Figure 7). The proportion of brittle stars at St. Philip's averaged 46% and

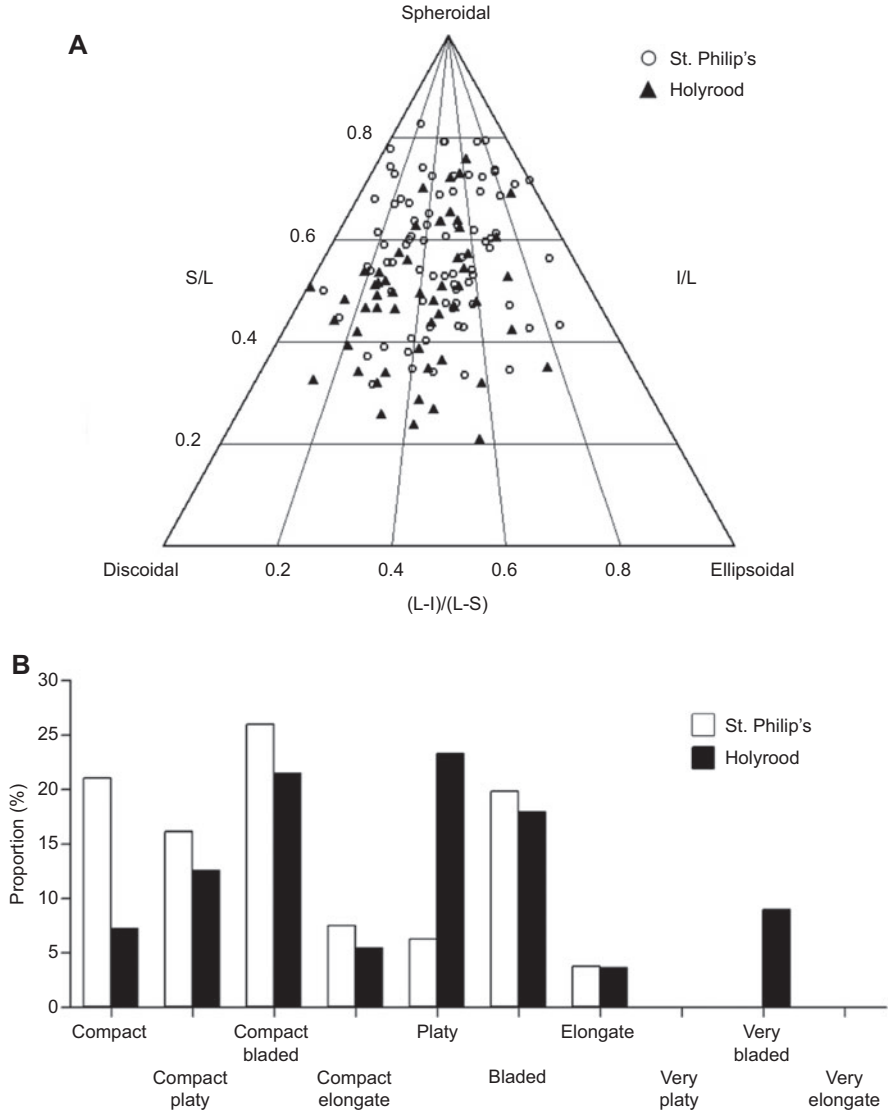

Figure 4 (A) Ternary diagram showing deviation in the shape of shallow [8–10 m deep] rhodoliths collected at the St. Philip's [n=81] and Holyrood [n=56] sites in July 2009 from three shape categories (spheroidal, discoidal, and ellispsoidal) forming the apices of the triangle. Each data point is a calculation of sphericity based on the length of longest [L], intermediate [I], and shortest [S] axes of one rhodolith. (B) Proportion of rhodoliths plotted in (A) in each of ten finer shape categories defined by Sneed and Folk (Sneed and Folk 1958) (see Materials and methods for details).

was significantly higher by 32% at Holyrood (LS means, $p<0.001$; Table 2, Figure 7). Interestingly, we observed the opposite trend for chitons, with a proportion at St. Philip's (36%) that was more than twice that at Holyrood (16%) (LS means, $p<0.001$; Table 2, Figure 7). Although brittle stars were slightly smaller in terms of disc diameter at St. Philip's (5.6±0.3 mm) than Holyrood (6.1±0.2 mm) (Table 3), this difference was (marginally) not significant ($t_{0.05(1),17}=1.68$, $p=0.055$). Brittle star density at Holyrood was remarkably high, 2026.7±151.0 individuals m^{-2}, and more than twice the observed value of 898.8±110.5 individuals m^{-2} at St. Philip's ($t_{0.05(1),17}=5.91$, $p<0.001$) (Table 3). There was no significant difference in shell length between chitons from St. Philip's (6.5±0.2 mm) and Holyrood (6.2±0.1 mm) ($t_{0.05(1),17}=1.36$, $p=0.095$) (Table 3). The similarity in mean sizes of brittle stars and chitons between sites was also reflected by similar size frequency distributions in both species (Figure 8). The density of chitons at the two sites was second only to that of brittle stars and unmatched by any other group of invertebrates (Table 3).

Although the density of urchins at St. Philip's (76.5±10.4 individuals m^{-2}) was comparable to that of bivalves and gastropods, it was more than 1.5-fold higher than at Holyrood (48.9±9.5 individuals m^{-2}) (Table 3). Urchins and chitons showed similar biomass values at St. Philip's (37.7±14.7 and 41.5±17.6 g m^{-2}, respectively; $t_{0.05(1),16}=0.17$, $p=0.43$) and Holyrood (25.8±8.4 and 16.6±4.6 g m^{-2}, respectively; $t_{0.05(1),18}=0.96$, $p=0.17$) (Table 3). Finally, the biomass values of echinoids, bivalves, gastropods, polyplacophorans, and crustaceans were generally higher (by up to three-fold) at

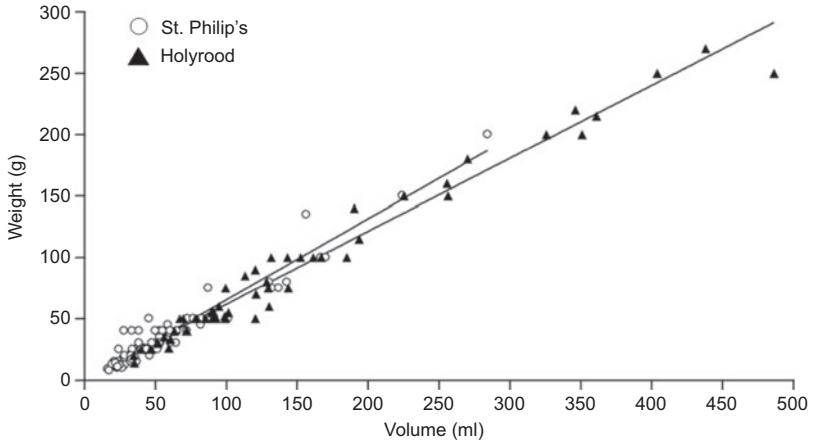

Figure 5 Relationship between dry weight and tissue volume of shallow (8–10 m deep) rhodoliths collected at the St. Philip's (n=81) and Holyrood (n=56) sites in July 2009.
The two lines are the linear fit to these data: y=0.659x-1.463 (St. Philip's; R^2=0.93, p<0.001) and y=0.594x+1.556 (Holyrood; R^2=0.97, p<0.001).

St. Philip's than Holyrood; however, such a comparison could not be made for ophiuroids and annelids due to absence of accurate biomass data (see above) (Table 3). Asteroids were the only group in which all three variables (i.e., size, density, and biomass) did not differ between the two sites (Table 3). Although rhodolith density at St. Philip's [858.1±54.1 (SE) rhodoliths m^{-2}] was similar to that at Holyrood (938.9±112.9 rhodoliths m^{-2}) ($t_{0.05(1),17}$=0.62, p=0.27), rhodolith biomass was significantly higher at Holyrood (25.3±1.3 kg rhodoliths m^{-2}) than St. Philip's (19.4±1.2 kg rhodoliths m^{-2}) ($t_{0.05(1),17}$=3.32, p=0.002).

Complementary observations

We witnessed several invertebrate- and fish-rhodolith interactions during one dive in July 2009 at the Holyrood site. While we were filming rhodoliths, a cunner, *Tautogolabrus adspersus* (Walbaum), (~20 cm long) came within a few tens of centimeters of our camera before swimming in large circles at various depths around an aggregate of rhodoliths (Figure 9). This behavior prompted us to examine a few rhodoliths more closely. We noted that 30%–35% of the largest rhodoliths had cores of fragmented or intact shells of the horse mussel, *Modiolus modiolus* (Linnaeus), while another 20%–25% contained empty cavities (Figures 2 and 9). The central cavities of <10% of the rhodoliths contained at least one live green sea urchin, *Strongylocentrotus droebachiensis* (O.F. Müller), that was sometimes too large to move out of the rhodolith, while the cavities of <5% of the rhodoliths were filled with fish eggs (Figure 9). There were also numerous empty mussel shells scattered on the seabed that were variably encrusted with the red coralline seaweed *L. glaciale* (Figure 2). These observations suggested that the morphology of some larger rhodoliths may facilitate reproduction and feeding in dominant fish and invertebrate species, while providing the opportunity to propose a successional sequence for the formation and maintenance of larger rhodoliths (see below).

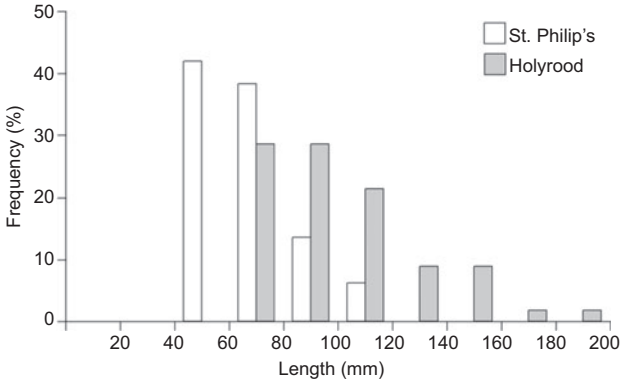

Figure 6 Frequency distributions of length (longest axis) of shallow (8–10 m deep) rhodoliths collected at the St. Philip's (n=81) and Holyrood (n=56) sites in July 2009.

Discussion

This study provides the first integrated, quantitative analysis of rhodolith (*L. glaciale*) morphology, biogenic potential, and organization as beds in subarctic ecosystems of the northwestern Atlantic using two beds we recently (2007 and 2009)

Table 2 Summary of two-way ANOVA (generalized linear model) examining the effect of site (St. Philip's and Holyrood) and Taxon [Ophiuroidea (brittle stars) and Polyplacophora (chitons)] on the proportion of individuals relative to the total number of invertebrates on shallow (8–10 m deep) rhodoliths collected in July 2009.

Source of variation	df	χ^2	p
Site	1	8.01	0.0046
Taxon	1	1001.78	<0.0001
Site×Taxon	1	663.86	<0.0001

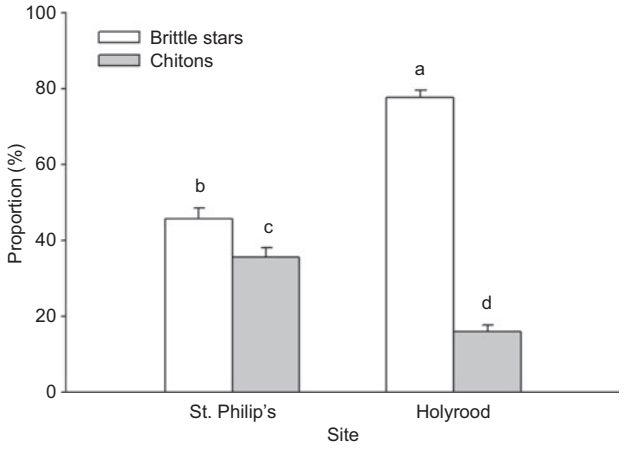

Figure 7 Mean (+SE) proportion of brittle stars (mainly the daisy brittle star, *Ophiopholis aculeata*) and chitons (mainly the mottled red chiton, *Tonicella marmorea*) relative to total number of invertebrates on shallow (8–10 m deep) rhodoliths collected at the St. Philip's and Holyrood sites in July 2009. Values not sharing the same letter are significantly different [LS means, $p<0.05$; n=9 (St. Philip's) and 10 (Holyrood)].

discovered in Conception Bay, Newfoundland and Labrador. In the current study, we show that (1) rhodolith size and shape varied with depth within one rhodolith bed and between beds at a given depth, (2) brittle stars and chitons were the two numerically dominant rhodolith-associated groups of invertebrates, and (3) invertebrate richness did not differ between beds, though the relative abundance of invertebrates in most taxa varied markedly.

Variation in rhodolith morphology

Our findings that rhodoliths at St. Philip's were more than 50% larger (total volume) in deep (15–17 m) than in shallow (8–10 m) water, and that the proportion of internal space relative to total volume (i.e., the actual amount of space within rhodoliths that can be used by invertebrates) was 7% higher (a significant difference) in deep than shallower rhodoliths are consistent with that of Amado-Filho et al. (2007), who found that rhodolith size increased from shallow to deeper zones in Espirito Santo State (Brazil). Perhaps the most plausible cause of the observed difference in rhodolith size at St. Philip's was a change in hydrodynamic conditions between the two depth strata. Although we did not measure wave energy and tidal currents at our study sites, we suggest that shallow rhodoliths experienced more wave-induced turbulence than their deeper counterparts; hence, these were more likely to be overturned or moved across the bed. Such movement could result in greater abrasion or breakage of rhodoliths, thus imposing greater limitation on the maximum achievable size of shallow water rhodoliths. This suggestion is supported by a study on the relationship between water motion and rhodolith movement in three subtidal rhodolith beds off the southwestern coast of the Gulf of California showing that (1) rhodoliths in shallow [4.5 m deep], wave-dominated beds moved more frequently due to wind-generated waves than deeper [12 m] rhodoliths; and (2) spherical, densely branched rhodoliths were more abundant in shallow than deeper water, where irregularly-shaped rhodoliths with low branch density dominated and water motion was low (Marrack 1999). The strong positive relationship between rhodolith volume and dry weight at both sites further indicated that rhodolith weight alone can be used as a reliable predictor of the amount of space available for recruitment of other organisms despite changes in rhodolith shape (see below).

Several studies have suggested that rhodolith shape (e.g., degree of sphericity or some related measures) changes from discoidal to spheroidal as rhodolith transport increases (Bosellini and Ginsburg 1971, Bosence 1976, Prager and Ginsburg 1989, Bosence 1991). Logistical considerations did not allow a comparison of the degree of sphericity of rhodoliths from shallow and deep water. However, we found that shallow rhodoliths were more than 180% larger at Holyrood than St. Philip's and that a larger proportion (70% versus 46%) of rhodoliths at the latter site had a spheroidal, compact shape. In contrast, shallow rhodoliths at Holyrood were predominantly platy or bladed, and their longest axis was 35% longer. The position of our study sites along the coast may partly explain this pattern. The St. Philip's site is much closer to the mouth of Conception Bay than the Holyrood site, which is located at the end of a narrow cove that forms the deepest inland portion of the bay. Rhodoliths at the St. Philip's site may have been exposed to stronger and more frequent offshore swell, locally-generated waves, and tidal currents than those at Holyrood; hence, they are more likely to be eroded or broken into smaller pieces.

The above findings are consistent with the postulate of wave-induced changes in size and shape of rhodoliths within and between our study sites; however, they also contradict patterns of rhodolith distribution seen elsewhere. For example, rhodoliths in Mexico remained spherical, though branch density and size generally decreased along depth-related gradients of water motion and sedimentation (Steller and Foster 1995), whereas rhodolith volume (size) decreased with increasing depth in Brazil (Riul et al. 2009, Bahia et al. 2010). Littler et al. (1991) found that rhodoliths living between 67 and 91 m along the eastern margin of the Bahamas were larger and more spherical than those from deeper water. Rhodolith growth and morphology can vary with temperature, sedimentation, light, nutrients, movement, and species (King and Schramm 1982, Potin et al. 1990, Foster 2001, Blake and Maggs 2003, Wilson et al. 2004, Steller et al. 2007, Riul et al. 2008, Martin and Gattuso 2009). Given that such data are not currently available for rhodoliths of Newfoundland and Labrador, our interpretation concerning the variation in rhodolith morphology in our study sites remains to be tested. Nevertheless, our results suggest that the conditions for growing rhodoliths were better in deep than shallow water at St. Philip's; moreover, shallow rhodoliths experienced better conditions at Holyrood than St. Philip's; the presumably milder hydrodynamic conditions at the former than the latter (see above) may also limit sedimentation and particle resuspension at St. Philip's, which could promote higher water clarity (assuming similar

Table 3 Mean (and associated standard error, SE) size (mm), density (individuals m^{-2}), and biomass (g m^{-2}) of invertebrate macrofauna in eight taxonomic groups associated with shallow (8–10 m deep) rhodoliths collected in July 2009 in 7–9 and 7–10 quadrats at the St. Philip's and Holyrood sites, respectively.

Taxonomic group	Variable	Study site				p-Value
		St. Philip's		Holyrood		
		Mean	SE	Mean	SE	
Asteroidea	Size (disc diameter)	5.5	0.7	4.7	1.1	0.27
	Density	25.9	5.2	24.4	5.7	0.43
	Biomass	7.3	2.9	7.0	4.6	0.48
Echinoidea	Size (test diameter)	9.3	1.5	9.2	1.3	0.48
	Density	76.5	10.4	48.9	9.5	0.033
	Biomass	37.7	14.7	25.8	8.4	0.22
Ophiuroidea	Size (disc diameter)	5.6	0.3	6.1	0.2	0.055
	Density	898.8	110.5	2026.7	151.0	<0.001
	Biomass[a]	188.2	36.3	573.1	65.1	<0.001
Bivalvia	Size (shell length)	7.8	0.9	9.4	1.1	0.14
	Density	66.7	22.3	21.1	6.1	0.027
	Biomass	13.1	6.4	4.3	2.1	0.096
Gastropoda	Size (shell length)	5.9	0.8	6.3	1.9	0.42
	Density	61.7	10.7	12.2	2.6	<0.001
	Biomass	3.1	0.7	1.1	1.0	0.067
Polyplacophora	Size (shell length)	6.5	0.2	6.2	0.1	0.095
	Density	749.4	158.8	417.8	65.2	0.030
	Biomass	41.5	17.6	16.6	4.6	0.085
Crustacea	Size (body length)	11.7	0.3	15.7	3.2	0.13
	Density	106.2	12.3	46.7	8.6	<0.001
	Biomass	4.3	0.8	1.9	0.4	<0.01
Annelida	Size (body length)	–	–	–	–	–
	Density	13.6	7.1	15.6	7.6	0.53
	Biomass	–	–	–	–	–
Total	Biomass[b]	107.0	25.9	56.7	10.7	0.041

p-Values (p) denote statistical significance of between-site difference in mean values of corresponding variables (one-tailed t-tests, α=0.05). [a]Approximation based on complete and incomplete individuals (see Materials and methods for details). [b]Excluding Ophiuroidea and Annelida.

terrestrial runoff) that, in turn, leads to better light penetration that stimulates rhodolith growth.

Rhodolith macrofauna

The analysis of invertebrate macrofauna associated with shallow rhodoliths indicated that brittle stars and chitons largely dominated (up to 94% of total macrofauna altogether) at both sites, though species richness was similar. The shift in dominance in both brittle stars and chitons between sites may partially explain the decrease in abundance of individuals in all but two (Asteroidea and Annelida) of the six other invertebrate taxa at Holyrood. The daisy brittle star (*O. aculeata*) and the mottled red chiton (*T. marmorea)* that dominated the area are facultative deposit feeders and grazers, respectively. We propose that the great abundance (>2000 individuals m^{-2} and >570 g tissue m^{-2}) of *O. aculeata* and relatively high abundance of *T. marmorea* at Holyrood resulted in low larval recruitment and high predation on early post-larval stages in other (and possibly their own) species of invertebrates. Furthermore, we noted the presence of a thin film of red filamentous seaweeds within interstices of exposed surfaces of some rhodoliths at Holyrood, but not St. Philip's. These patterns, and the fact that the rhodolith bed at St. Philip's supported higher densities of *T. marmorea* and the grazing sea urchin, *S. droebachiensis*, suggested that algal recruitment on rhodoliths may be higher at Holyrood, which could have also reduced invertebrate settlement and recruitment. The above noted differences in invertebrate abundances could have also resulted from uneven larval supply at the two sites, which are likely related to variation in water motion (see above).

Size frequency distributions of brittle stars and chitons did not differ between the two sites. This finding, together with the overall small size of rhodolith-associated invertebrates, suggests that rhodolith bed communities were stable and maintained at early stages of development by ecological processes that most likely included predation and competition. Chitons were also the dominant macrofaunal species in a shallow (12–18 m deep) rhodolith bed discovered in the summer of 2004 in the North Pacific (Konar et al. 2006). Globally, our findings support the idea that rhodolith beds can form nursery areas for a number of invertebrates, including bivalves, gastropods, echinoderms, and polychaetes. For example, Foster et al. (2007) found 114 cryptofaunal taxa

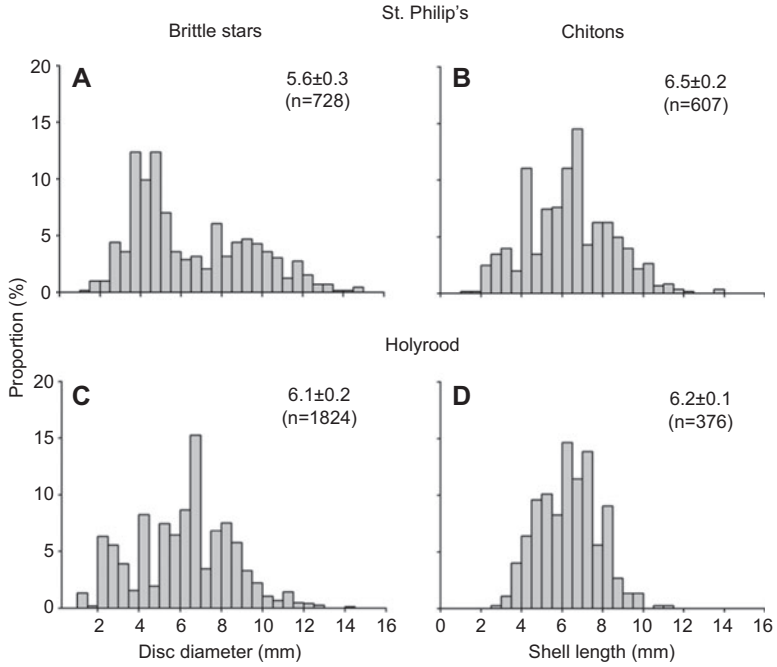

Figure 8 Size frequency distributions of (A and C) brittle stars [mainly the daisy brittle star, *Ophiopholis aculeata*] and (B and D) chitons [mainly the mottled red chiton, *Tonicella marmorea*] from shallow [8–10 m deep] rhodoliths collected at the St. Philip's and Holyrood sites in July 2009. Values in each panel represent mean [±SE] size [disc diameter of brittle stars and shell length of chitons] and sample size.

on only 15 shallow (2–8 m deep) rhodoliths in Mexico, and Sciberras et al. (2009) reported 244 animal and 87 algal taxa in an extensive (about 20 km^2) and deep (30–100 m) rhodolith bed in the Maltese Islands. The findings of the present work suggest a lower diversity of rhodolith-associated invertebrates along the coast of Newfoundland and Labrador. A few studies have shown that macroalgal richness and invertebrate abundance in rhodolith beds can vary seasonally (Steller et al. 2003, Figueiredo et al. 2007, Riosmena-Rodriguez and Medina-Lopez 2010). Therefore, conducting similar surveys in additional areas; expanding the relatively narrow temporal window (~1 month), over which we sampled rhodoliths; and using a finer taxonomic resolution to classify rhodolith-associated invertebrates would contribute to a better understanding of the biogenic potential of rhodolith beds on local and regional scales.

Owing to their complex architecture, rhodoliths can substantially enhance larval settlement and growth of ecologically and commercially valuable invertebrate species (e.g., Kamenos et al. 2004a,b, Steller and Caceres-Martinez 2009). Conversely, invertebrates such as sea urchins may also create moderate levels of bioturbation that maintain the structural integrity of rhodoliths while preventing fouling (James 2000). The occurrence of large mussel shells exhibiting various stages of colonization by red coralline seaweeds (mainly *L. glaciale*), as well as unusually large, hollow rhodoliths filled with fish eggs or containing adult urchins at one of our study sites suggested that facilitation (*sensu* Connell and Slatyer 1977) is a driving force in the creation and maintenance of rhodolith communities in Newfoundland and Labrador. We propose a successional sequence, whereby spores of red coralline seaweeds settle on shells of dead (or live) mussels and over the course of tens to hundreds of years form nucleated rhodoliths, eventually turning into hollow structures through mechanical abrasion or chemical dissolution of mussel shell cores (or inner tissues in non-nucleated rhodoliths) by some boring invertebrate species. Subsequent splintering of rhodolith tissue through excessive wave-induced movement could partly or completely expose the internal cavity of rhodoliths, which could then be used by fish for egg deposition and defense or urchins as a surface for grazing. As in other ecosystems, grazing by fish and invertebrates, such as urchins, chitons and gastropods, could inhibit biofouling of rhodoliths (Steneck 1986, Littler et al. 1995). These are also known to shed surface layers of cells (e.g., Keats et al. 1997) to prevent being overgrown by other organisms. Further research is required to test this postulate.

Conclusions and future research directions

Historically, research on the stability and structural and functional importance of benthic primary producers in the northwestern Atlantic has largely focused on kelp (Witman 1987, Johnson and Mann 1988, Chapman and Johnson 1990, Lambert et al. 1992, Scheibling et al. 1999, Gagnon et al. 2004, Steneck et al. 2004, Vadas et al. 2004, Gagnon et al. 2005) and seagrass (Schneider and Mann 1991, Laurel et al. 2003, Joseph et al. 2006, Selgrath et al. 2007, Thistle et al. 2010, Warren et al. 2010) habitats. This is the first integrated, quantitative examination of the structure and biogenic potential of rhodolith beds in this vast region. We showed that rhodolith

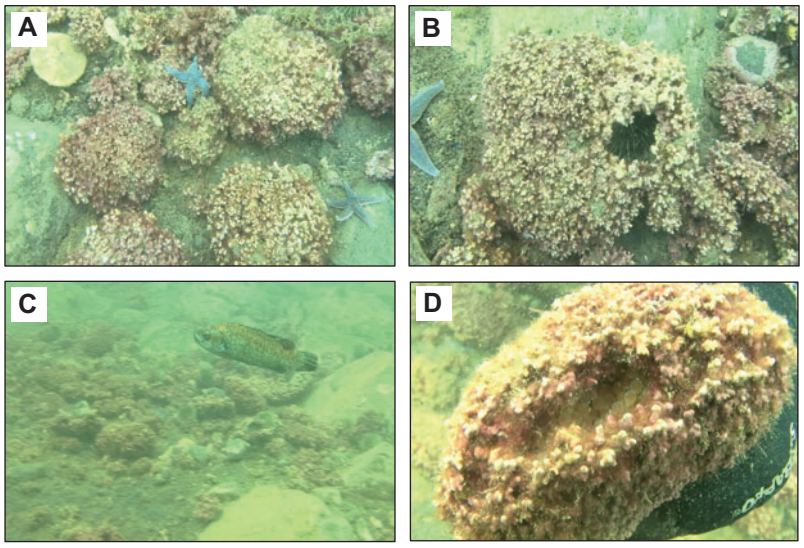

Figure 9 Portions of the rhodolith bed at Holyrood and associated communities of benthic and pelagic organisms. (A) Large [>15 cm] rhodoliths surrounded by live northern sea stars [*Asterias vulgaris* (Verrill)], green sea urchins [*Strongylocentrotus droebachiensis*], and dead sand dollars [*Echinarachnius parma* (Lamarck)]. (B) Green sea urchin inside the cavity of a large [>15 cm] rhodolith. (C) Large [~20 cm long] cunner [*Tautogolabrus adspersus*] patrolling a portion of the bed. (D) Large [>15 cm], hollow rhodolith filled with fish eggs.

biomass and the abundance of associated invertebrate macrofauna can be high (>25 kg of rhodoliths and >0.6 kg of invertebrate macrofauna m^{-2}), yet vary significantly within small bathymetric and geographic ranges in Conception Bay. Our study was designed to provide key information about the morphology of rhodoliths and their biogenic potential as opposed to examining the detailed structure and function of the two rhodolith beds from which they were extracted. Other observations along the coast of Newfoundland in the last two years indicated rhodolith habitats are widespread, at least along the east coast of the province (P. Gagnon, unpublished data). Therefore, patterns in this study likely reflect part of a broader spectrum of rhodolith morphology, biogenic potential, and abundance within beds along the coast of Newfoundland and Labrador and in other parts of the northwestern Atlantic.

We know little about the distribution and abundance of rhodolith beds in the northwestern Atlantic (but see Adey and Hayek 2011). The general lack of data on the taxonomy of rhodolith-forming species and effects of environmental variability (e.g., temperature, salinity, and grazing pressure) on growth and survival of those structurally complex seaweeds in this region limited our ability to establish causes and consequences of patterns we observed. For example, it is possible that part of the observed morphological differences was due to variation in rhodolith-forming species. Although we can ascertain that *L. glaciale* was the dominant red coralline seaweed that formed rhodoliths in the two beds examined, it is possible that other coralline species were present, though to a much lesser extent, in those rhodoliths. Molecular and genetic tools should be used to help clarify this question. Current knowledge suggests that rhodolith beds in Europe and along the west coast of North America are sensitive to anthropogenic factors, and that conservation measures must be established to preserve their high biogenic potential and capacity to provide nursery grounds for commercial shellfish and fish species (BIOMAERL 1999, Barbera et al. 2003, Grall and Hall-Spencer 2003, Hall-Spencer et al. 2003, Steller et al. 2003). Our data generally support the proposed models of rhodolith bed formation and maintenance (Foster 2001). However, further research, including long-term field studies and laboratory experiments are required to determine more accurately the occurrence and extent of rhodolith beds and the processes by which physical factors such as currents, light and temperature, regulate these assemblages in the northwestern Atlantic.

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