

SUBARCTIC RHODOLITH BEDS PROMOTE LONGEVITY OF CRUSTOSE CORALLINE ALGAL BUILDUPS AND THEIR CLIMATE ARCHIVING POTENTIAL

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ABSTRACT: The rocky, photic benthos of Arctic and Subarctic Biogeographic Regions has a characteristic seaweed flora that includes an extensive high-magnesium calcium carbonate basal layer of crustose coralline red algae. The thickest (10–40 cm) and oldest parts of the crust (previously reported as up to 640–830 years old), primarily at mid-photoc depths of 15–25 m, are composed of buildups of the genus *Clathromorphum*. Due to its annual growth increments and cycling of Mg content with temperature, *Clathromorphum* has recently been developed as a high-resolution climate archive. The age of the archive is primarily limited by the boring of mollusks that reduce structural integrity, remove the record, and induce local diagenesis. Depressions and gentle slopes in the deeper portions of Subarctic rocky bottoms often collect mixed bioclastic and siliciclastic sediments, including a dense cover of rhodoliths (*Lithothamnion glaciale* and *Lithothamnion tophiforme*). In this paper we describe a transition zone of these two environments that forms on cobble/boulder glacial erratic bottoms in northern Labrador. *Clathromorphum compactum* buildups on the boulders and cobbles projecting through rhodolith beds can be preserved by fine-grained anaerobic sediments that in turn reduce mollusk boring. This significantly enhances preservation and longevity of *C. compactum* crusts. We describe specimens of ages up to 1200 years BP, and discuss how greater ages can be obtained for archiving high-resolution climate information.

INTRODUCTION

An understanding of variations in Subarctic and Arctic climate over the last several thousand years is essential to modeling and managing anthropogenic climate change. In lower latitudes, abundant tree ring and pollen data in the terrestrial environment and coral and bivalve data can provide that understanding in marine environments. However, given the crucial role that sea ice plays in controlling earth's solar radiation budget (IPCC 2014), reliance solely on midlatitude data and newer mollusk data from the Arctic fringes is inadequate to support the accurate modeling of global climate processes. Recent studies have shown that crustose coralline algae, particularly species of the genus *Clathromorphum*, abundant in shallow high-latitude seas, can record an array of paleoclimate information at high resolution (e.g., Adey et al. 2013; Halfar et al. 2013). Analysis of yearly cycles of the growth, reproduction, and carbonate chemistry of these calcified red algae can provide a detailed (~ monthly) understanding of Holocene climates in Arctic and Subarctic regions. In this paper, we describe a Subarctic mixed siliciclastic-bioclastic facies in which crustose corallines (rock-attached crusts) and rhodoliths occur together, and we show how that combination considerably extends the history available from archival corallines.

Corallines are structurally complex calcified red algae. In the large order Corallinales (> 40 genera and > 600 species), primary high-Mg calcite (5%–25% Mg) is deposited metabolically within organic cell walls; a variety of secondary calcifications can present a wide range of

carbonate mineralogy (Adey et al. 2013; Nash et al. 2013). Corallines occur from Arctic/Antarctic to tropical waters and are ecologically highly diverse, ranging from small parasitic and epiphytic crusts to massive biohermal structures such as algal ridges in the tropics (Adey 1978). Two life forms are prominent: (1) smooth, leafy, or protuberant crusts, more-or-less firmly attached to rock, coral, or other hard substrate; and crusts bearing more or less narrow diameter, bifurcating structures (typically called branches) that can build carbonate centimeters to meters in thickness; and (2) detached fragments of those crusts, especially those with branching morphologies, that can continue to grow (and sometimes reproduce) in periodically mobile sedimentary environments. The former are referred to as crustose coralline algae and the latter as rhodoliths. Rhodoliths range from branch fragments to large concretions (> 30 cm) with and without a hard central core; maerl is a European term for more fragmentary growth forms (morphologies). Adey and Macintyre (1973) modeled the environmental relationship of these life forms as a function of wave energy and depth, and Freiwald and Henrich (1994) described the relationship between attached crusts of the branching *Lithothamnion glaciale* and related bioclastic deposits of *L. glaciale* rhodoliths in northern Norway.

Through the stratified growth patterns and chemistry of their complex skeleton, corallines (both crusts and rhodoliths) are being used to develop the science of rhodochronology. Other authors have used the broader terms sclerochronology (Wanamaker et al. 2011) and algochronology (Kamenos and Law 2010, Kamenos et al. 2012), but we prefer



rhodochronology because the Corallinales are a prominent order of the Rhodophyta, or red algae, and the seasonal layering and mode of formation (intercalary meristem = cambium) is superficially similar to that in the trees used in dendrochronology.

Climate Archives from *Clathromorphum* Species

Extensive encrustations of *Clathromorphum* species are common on photic rocky surfaces throughout the Subarctic and parts of the Arctic (Fig. 1A–D; F–H). Halfar et al. (2013) inferred the age of one *C. compactum* specimen from the Labrador Coast to be 646 years, based on the thickness of collected specimens, radiocarbon dating, and counting of annual growth increments using seasonal Mg variations (Fig. 2). In the Aleutian Islands, *Clathromorphum nereostratum* has been reported to reach a thickness of 50 cm (Lebednik 1976), and a thickness/growth rate equivalent of 700 years has been estimated by Frantz et al. (2005). A radiometrically determined age for a live-collected specimen of *C. nereostratum* of 850 years was later reported by Halfar et al. (2007). The high-magnesium carbonate skeleton of the genus *Clathromorphum* has shown considerable value as a proxy for temperature, salinity, and sea ice cover based on variations in Mg/Ca composition as well as changes in annual growth increments (Chan et al. 2011; Halfar et al. 2011, 2013; Hetzinger et al. 2012; Adey et al. 2013). Furthermore, coralline algal trace element and stable oxygen and carbon isotope variations have also been employed as paleoenvironmental proxies (Halfar et al. 2007; Williams et al. 2011; Hetzinger et al. 2013).

No biological age limit is known for *Clathromorphum* carbonate buildups. Species of the genus have developed a unique type of crystalline carbonate reinforcement that likely increases skeletal strength (Adey et al. 2013); the latter authors suggest that this high-magnesium crystalline calcite structure increases potential age, and has evolved as a successful form of space competition. However, the boring of bivalves and polychaetes can destroy the structural integrity of the older parts of crusts (Fig. 1C–D), and this process generally limits maximum crustal accretion on rocky surfaces in both North Pacific and North Atlantic/Arctic Oceans (Chenelot et al. 2011, Adey et al. 2013). In the northwestern Atlantic Subarctic, the typical maximum thickness for *Clathromorphum compactum* is 5–10 cm (Adey et al. 2013). At published growth rates of 130 $\mu\text{m}/\text{year}$ for *C. compactum* on the north central Labrador Coast, 70 $\mu\text{m}/\text{year}$ in Arctic northern Baffin Island and 400 $\mu\text{m}/\text{year}$ for *C. nereostratum* in the Aleutian Islands (Adey et al. 2013), the maximum thickness of collected specimens produces a minimum age of 1200 years in the North Pacific and 1600 years in the Labrador Sea. However, proxy information has been limited to < 700 years BP, largely because the extensive mollusk borings can obliterate the paleorecord.

Rhodoliths

Rhodoliths (including maerl) are free-living, generally spherical coralline nodules or branch fragments that form abundant shallow-water marine facies worldwide. Reviewed several times (Adey and MacIntyre 1973; Bosence 1983; Foster 2001), rhodoliths occur most abundantly on flat-lying surfaces below coral and rocky slopes. Although there are some large isolated flat banks in which rhodoliths are clearly self-supporting (Amado-Filho et al. 2007; Basso et al. 2009), rhodoliths are often supported by nearby rocky or reef crust reservoirs (see e.g., Freiwald and Henrich 1994; Piller and Rasser 1996).

Rhodoliths generally roll with current and wave action (Basso et al. 2009). While formal studies are few, Marrak (1999) showed that not only are waves and currents important in different situations, but bioturbation can also play a significant role (also, James 2000). Rhodoliths are known to occur abundantly in the Arctic and Subarctic (Foslie 1895; Adey and Hayek 2011). However, only a few formal studies have been carried out in these regions (Spitsbergen, Teichert et al. 2014; Newfoundland, Gagnon et al. 2012; Greenland, Kamenos et al. 2012). This is the first description of a rhodolith bed on the Subarctic shorelines of Labrador. While not yet widely investigated, it has been generally assumed that the sediment underlying rhodolith beds is largely built by the fragmented accumulations of the rhodoliths themselves (Foster 2001).

Corallines and the Shallow Subarctic Benthos

Adey and Hayek (2011) graphically described the rocky benthos of Subarctic shores, especially the algal (seaweed) components, and related community structure, relative to depth, wave energy, and sea urchin grazing (see also Himmelman 1991). Adey et al. (2013) presented the extent of development of *C. compactum* crusts in an ecosystem graphic. Here we add the location of principal rhodolith development to that graphic (Fig. 3). The areal extent of *Lithothamnion* rhodoliths, in any given locality, is a function of the availability of local flat-lying terrain within the zone of transition from rocky to sediment bottom (Adey and Hayek 2011).

Geologic and Geomorphologic Background

The central Labrador Coast was extensively glaciated by the Laurentide ice sheet until 10,000–12,000 years BP, and valley glaciers persisted until 7000–8000 years BP (Smith et al. 2003). The later valley glaciers carved out several fjords, including Hopedale Run in the area covered in this paper (see below). With postglacial sea level rise between 10,000 to 8000 years BP, the coastline rose from the –80 m level of late glacial time to about 40 m above present sea level. Raised shorelines are

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FIG. 1.—A) Extensive bedrock-covering encrustation of *Clathromorphum compactum* with a thickness of 0.5–3 cm (from 15–17 m depth at Grady Island, Groswater Bay, southern Labrador; Lat 53°48'N; Long 56°24'W). B) *C. compactum* mound of 4.5 cm thickness (approximately 250 years old) collected from 18–20 m depth at Great Island, Southern Labrador (Lat 52°17'N; Long 55°36'W). C–D) Specimen of *C. compactum* collected from broad rock surface at 18–20 m depth at East Kingitok Island, Labrador. C) Upper surface showing only small scattered holes marking the locations of boring mollusks. Dark crusts are areas of a noncalcified red alga growing on dead *C. compactum* surface. D) Lower surface showing extensive boring. Approximately one quarter of the mound was cut off for analysis (upper left), but the only attachment to the rock substrate for this part of the specimen is indicated by the patch to the right of the label. With over 90% of its attachment surface removed by boring invertebrates, this specimen would have been easily detached with minimum wave action or bioturbation. Specimen 2011–15, 18–20 m, deposited in Coralline Collection, U.S. National Museum. E) Surface topography 0–40 m above sea level and resembling nearby submarine topography (Arlorkak Island, Kingitok Island Region, northern Labrador, Lat 55°25'N; Long 59°25'W). Abundant boulders and cobbles (glacial till erratics), largely cleared of original glacial silts and clays, occur in depressions and swales. Beginning 2–3 m above sea level, depressions become filled with vegetation and peat, creating apparent green “meadows” with boulders projecting through the vegetation. F) Abundant boulders and cobbles encrusted mostly with *C. compactum* at margins of rhodolith bed composed of *Lithothamnion glaciale* at 15–17 m depth in the Kingitok Island complex. Kelp bush (*Agarum clathratum*) to left and in background (view A). While patchy in rhodolith beds, this species can form a thick but patchy seaweed savanna on rocky bottoms (see Adey and Hayek 2011). G) Thick *C. compactum* crust on a buried cobble in the central part of the Kingitok rhodolith bed. Mound is approximately 25 cm wide. H) *C. compactum* head thickly encrusting a cobble (not visible) embedded in rhodolith bed. Specimen approximately 20 cm wide. Rhodoliths and sediment partially cleared in foreground. Specimen takes on gray appearance where it was embedded (lower left), and sediment (lower right) is clearly gray-black due to anaerobic conditions.

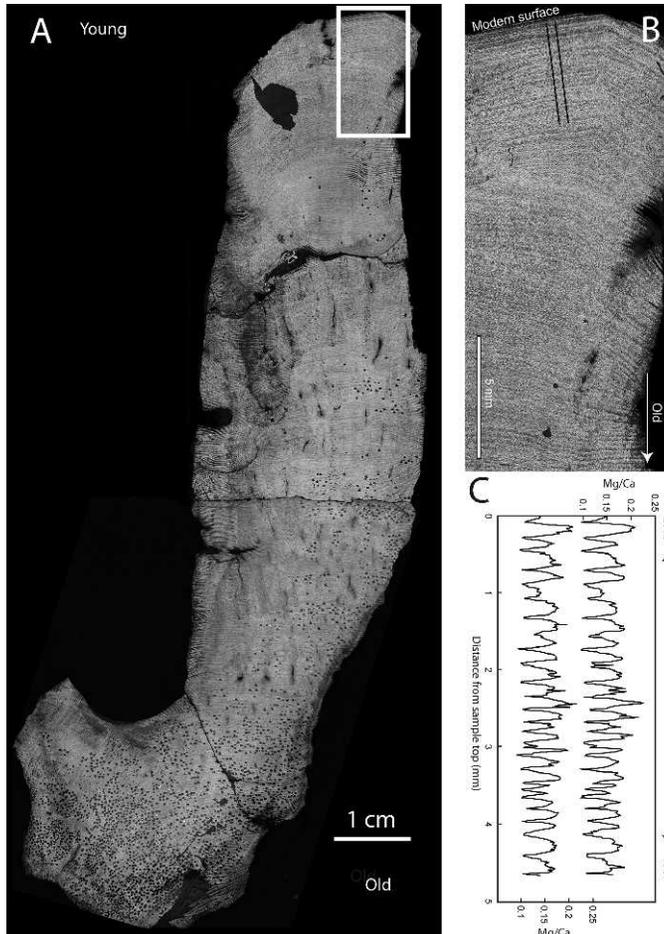


Fig. 2.—646-year-old polished section of *C. compactum* specimen. A) Specimen 2011–15, 15–17 m, East Kingitok Island, Labrador; deposited in Coralline Collection, U.S. National Museum. B) Detail of view A. C) Annual cycles of Mg/Ca ratios measured by electron microprobe, on two parallel transects along main axis of growth on uppermost 5 mm of specimen shown in view B (modified from Halfar et al. 2013).

abundant throughout the complex (being particularly evident where the coast is gravelly or sandy); crustal rebound has lifted those shorelines approximately 30–40 m (Clark and Fitzhugh 1991). In spite of the rebound uplift, and because of the valley glaciation that preceded the rapid sea level rise, today the north central Labrador Coast presents a drowned topography. The resulting 20–40-km-wide island complex consists of thousands of islands and skerries, punctuated by a few drowned glacial valleys crossing the island complex (Fig. 4). The glacial till that thinly covered the region following glaciation has been washed of silts and clays by at least one transgression of sea level. The crustal rebound primarily of the 8000 to 3000 years BP period affords an opportunity to visualize the subtidal topography on land. Glacial erratic cobbles and boulders are common everywhere in this terrain, with larger erratics often forming conspicuous skyline silhouettes. However, the majority of the smaller boulders and cobbles tend to be collected, by gravity and wave action, in local depressions in the rock basement (Fig. 1E).

In this paper, we will discuss how the resulting geomorphology creates ideal conditions for the close association of rocky bottom with sediment-accumulating rhodolith beds. This situation in turn significantly increases the potential age limit of the *C. compactum* proxy archive, although

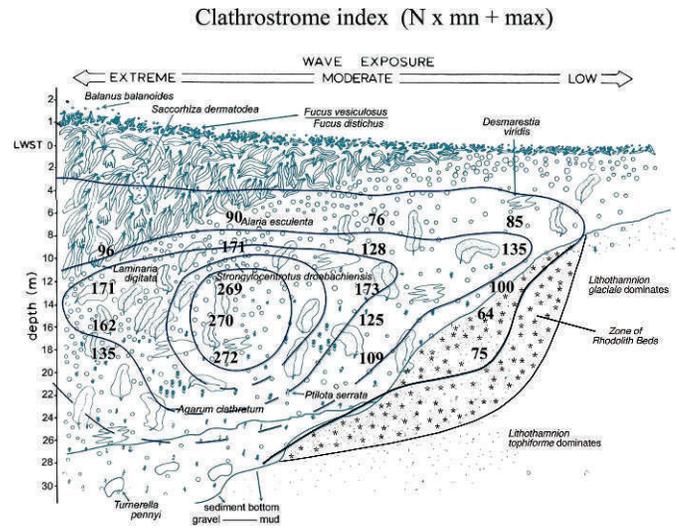


Fig. 3.—Benthic ecosystem structure relative to depth and wave exposure in the photic zone of the rocky Labrador Coast, with *C. compactum* development index ($N \times mn + max$) overlaid and contoured. Modified from Adey et al. 2013 to show rhodolith beds at the junction of rock substrate and deeper sediments; for each station-depth zone, N = number of specimens, mn = mean thickness and max = maximum thickness in cm; see Adey et al. 2013 for details of *Clathromorphum* index and biotic component symbols.

the rebound itself likely places a limit of about 3000 years BP to *Clathromorphum* archives on this coast. Because of the integral relationship between archival age and the *Clathromorphum* crusts and rhodoliths found in this study, we cored the underlying sediment in the central area of a rhodolith bed. Since the accumulating sediment clearly increased the potential of finding large specimens which were largely undamaged, we sought to determine the contribution of the rhodoliths to the underlying sediment.

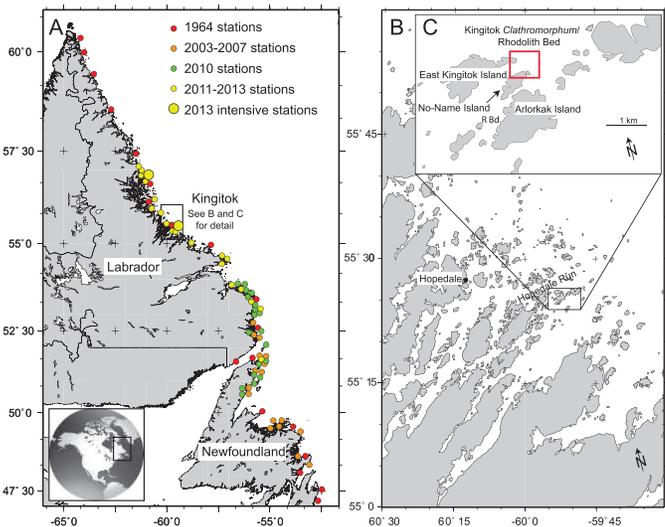


Fig. 4.—A) Map of Labrador and Newfoundland showing 137 *C. compactum* sampling stations. Some dots represent multiple stations. B) Hopedale Run area of the north central Labrador island complex. Hopedale Run, passing from west southwest to east northeast on north side of East Kingitok Island, is a drowned fjord. C) Detail of Kingitok area showing combined *Clathromorphum*-rhodolith bed (red rectangle) detailed in this paper plus location of more protected bed (RBd) without projecting *Clathromorphum* (2 km to southwest of prime work site).

MATERIALS AND METHODS

Cruises onboard the R/V *Alca i* in 2010, 2011, and 2013 were dedicated to examining the potential for the Subarctic coralline species *Clathromorphum compactum* to provide a long-term, high-resolution climate archive for the coastal waters of northern Newfoundland and Labrador (Adey et al. 2013). Incorporating a 1964 SCUBA-based coralline analysis (Adey 1966), and later field studies (2003–2007, Adey and Hayek 2011), an extensive subtidal network of 137 depth-zoned SCUBA stations was developed for the coast of Newfoundland and Labrador facing the Labrador Sea to determine coralline cover and the relative abundance of *C. compactum* (Fig. 4). Here we focus on findings relating to *C. compactum* specimens with unprecedented longevity, located within a *Lithothamnion glaciale* rhodolith bed, at three stations (five sites) near Kingitok Islands off Hopedale, Labrador at latitude 55°26'N and longitude 59°52'W (Fig. 4).

Land-fast sea ice, generally with extensive snow cover, blankets the northern Labrador coastal region for seven to eight months of the year from about early December until late June. Summer sea-surface temperature in the middle of the island complex rises to 7–10 °C during August (personal observation W.H. Adey 1964, 2011, 2013); however, the benthic community we describe here is below the thermocline for much of the warmer period, and temperatures reach no more than 6 °C in August and September (Fig. 5A, B). During the winter months of each year, we have assumed that the water temperature at the depth of formation (15–18 m) of the thick *C. compactum* crusts and the rhodoliths described in this paper is constant at less than –1.5 °C (due to the sea ice cover interacting with deeper water brought in by tidal currents from offshore; field observation, W.H. Adey). Bottom temperatures in early July 2013 ranged from –1 to –2 °C; and had risen to 4.8 °C by mid-August. A temperature profile at Crab Island (2 km from the Kingitok Site) taken on August 1, 1964 showed temperatures 6.5–7.1 °C from the surface to 12 m depth; temperatures at the depth of the rhodolith bed in 1964 were 5–6 °C. This suggests that surface temperatures rapidly reach a peak of 7–10 °C in July, and with reducing insolation and greater summer cloudiness, begin falling in August; however, at the depth of the Kingitok rhodolith bed, peak temperature is later, in August to September, but still well below peak surface temperatures (Fig. 5B).

Formal current analyses were not undertaken while working at the Kingitok site. An east-west alternating semidiurnal flow was apparent to the divers on the bottom as silt stirred up by their activities wafted either to the west or east across the rhodolith bed. However, during these dives it was never strong enough to affect the divers or overturn rhodoliths. Although the Kingitok site is one of intermediate wave activity, it is moderately open (20° angle) to the Labrador Sea 18 km to the northeast (Fig. 4). On several occasions diving had to be suspended because of incoming high seas. Although bathymetry was cross checked with SCUBA depth gauges, most relevant depth data were taken by sounder transects using a dive skiff and a hand-held, recording GPS unit. Bathymetry was plotted using ArcGIS with bottom characteristics verified by SCUBA. Still and video underwater imaging were both employed to better understand the topography and coralline communities on the bottom. The dimensions of collected *C. compactum* specimens, in particular the thickness of each sample, were measured with calipers.

To provide information on the sedimentary characteristics of the rhodolith bed, four pieces of copper pipe (6.1 cm diameter) were hammered into the central area of the bed to a depth of 10–15 cm below the loose rhodoliths. Cores were capped and returned to the surface upright to preserve the sediment layers. Cores were extruded in the boat lab where the total length was measured before the core was sectioned into 3 regions from surface to bottom (0–5 cm, 5–10 cm, and 10 cm–end). Once sectioned, cores 1 and 2 were sieved by hand into three size fractions, to determine the relative contribution of each particle size to the

sediment matrix of the rhodolith beds. The size fractions were > 2.1 (2.0) mm, > 50 (62.5) µm, and < 50 (62.5) µm (numbers in parentheses are the Krumbein scale separation points for gravel/sand/silt). The exterior surfaces of each core section were removed prior to sieving to avoid capturing rhodolith fragments that may have been transported into the sediments during the coring process. Cores 3 and 4 were passed through an automated grain size analyzer (Camsizer, NOVA Southeastern University). All sieved sections were dried to a constant weight. Thin sections were made from the sand fraction of all samples and the invertebrate, coralline, and siliciclastic components quantified (300 counts per sample). The gravel fraction was likewise quantified (150 counts per sample). Several random samples of the silt size fraction were mounted for observation by SEM.

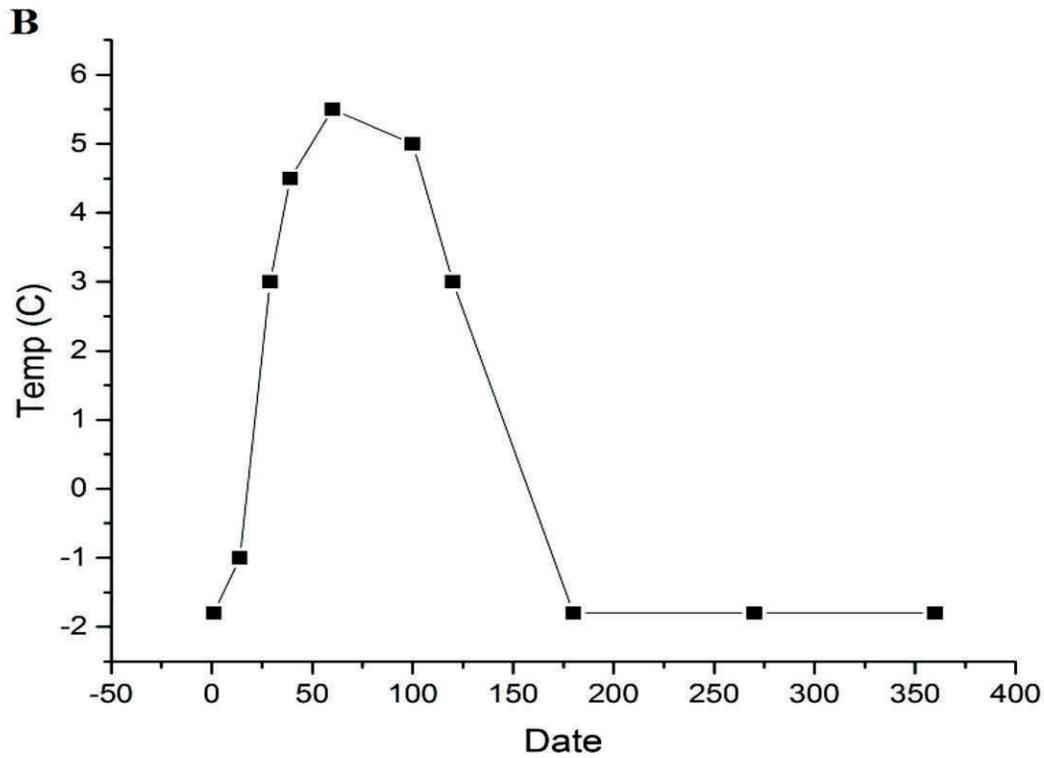
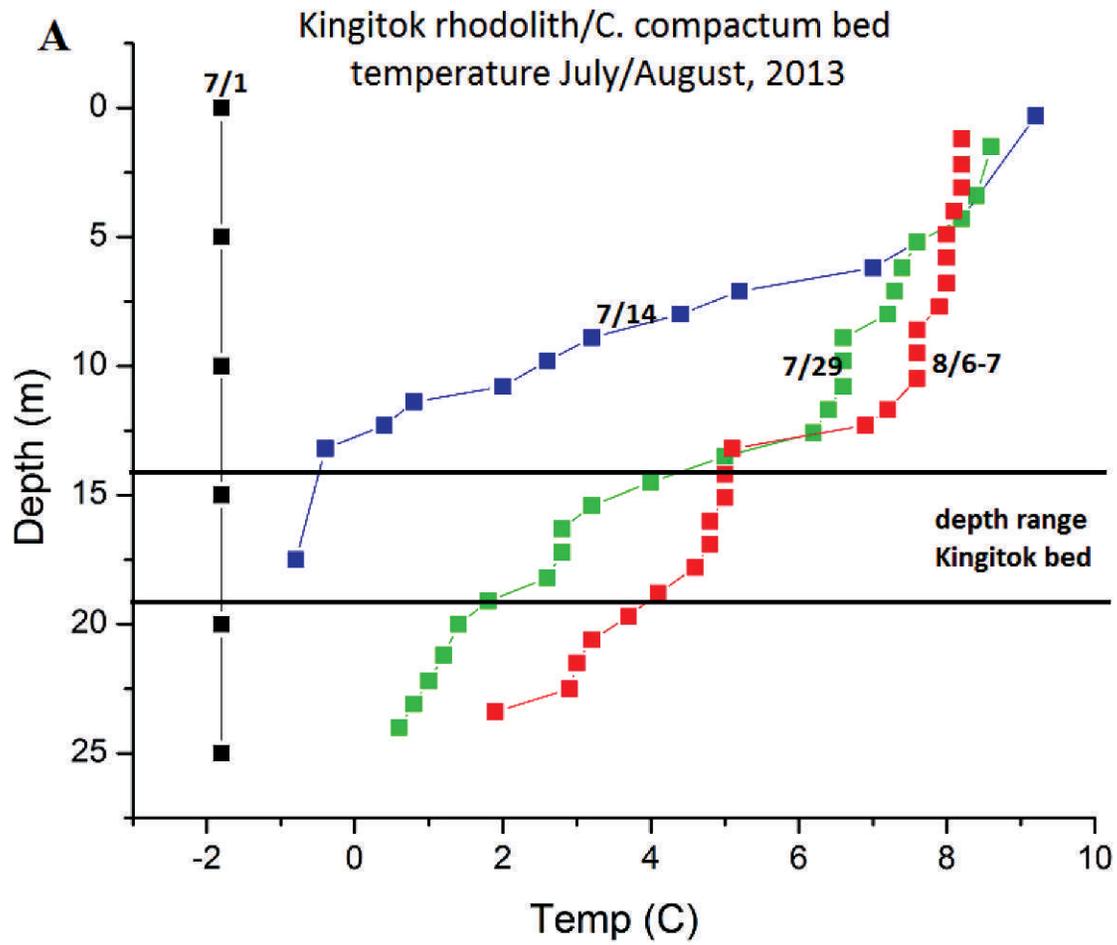
Two specimens from the Kingitok Site were sectioned, polished and yearly growth rates measured in a dissecting microscope. These rates were cross-checked using seasonal Mg variation with electron microprobe and laser-mass spectrometer analysis. These rates were compared with radiocarbon dates measured by BetaAnalytics Inc (<http://www.radiocarbon.com/>).

The collecting of *C. compactum* mounds in the 2010 and 2011 field seasons was comparable based on the time available at each locality for a single collecting diver (Thew Suskiewicz) on a single SCUBA tank (see Adey et al. 2013 for details). In 2013, once the rhodolith bed at the Kingitok Islands was defined by several exploratory dives, collecting was more intense per unit area than in the earlier seasons. It was still undertaken by a single diver (TS), the same diver that carried out the 2010 and 2011 collections, with the support diver taking photographs. However, on a typical dive, TS could extract only about a quarter as many samples from a rhodolith bed as he could from a comparable rocky bottom; 12 dives by TS were employed solely in collecting the reported *C. compactum* from the beds. The process required first exhuming sediments around the specimen and then removing the sample from the cobble or boulder on which it resided using either a chisel or a pry-bar (Fig. 1F–H). Thus it was more time consuming than the collecting procedure employed in 2010 and 2011, when the intersection of coralline crust and rock was more obvious. Also, considerable time was sometimes spent exhuming sediment from around a target specimen, only to find that the specimen was not of sufficient thickness. Clearly, considerably greater collecting effort was required per unit specimen in 2013 (Kingitok rhodolith bed) than in 2010 and 2011, and this information is crucial to one of the key conclusions derived below.

RESULTS

In the Kingitok region, as noted in the Introduction, the subtidal topography, to 30 m below sea level, mimics the terrestrial topography (Fig. 1E). Within the photic zone, which may extend down to more than 40 m below sea level, a complex seaweed community thrives (Fig. 1A, B); coralline crusts, primarily *Clathromorphum compactum* and to a lesser extent *Lithothamnion glaciale* and *Lithothamnion lemoineae* (in the 10–25 m range), cover the steeply sloping rock surfaces. The swale equivalents below sea level are filled to varying degrees with fine to coarse shelly sediments, frequently sheathed with rhodoliths; often coralline crust-covered glacial erratics project above the rhodolith surface (Fig. 1F–H); the abundance of the latter depends upon wave and current exposure and the resulting depth of accumulated sediment.

Where a more protected flat-lying bottom is present at roughly 8–28 m depth, large rhodolith beds form and accumulate fine sediment (Figs. 1F–H, 6). The rhodoliths support a rich community of invertebrates, often dominated by ophiuroids as seen in more southerly rhodolith beds (Gagnon et al. 2012). In more protected situations where the sedimentation rate is higher, projecting glacial erratics are lacking (Fig. 4C); they are presumably deeply buried in sediment. At depths of 10–30 m in the



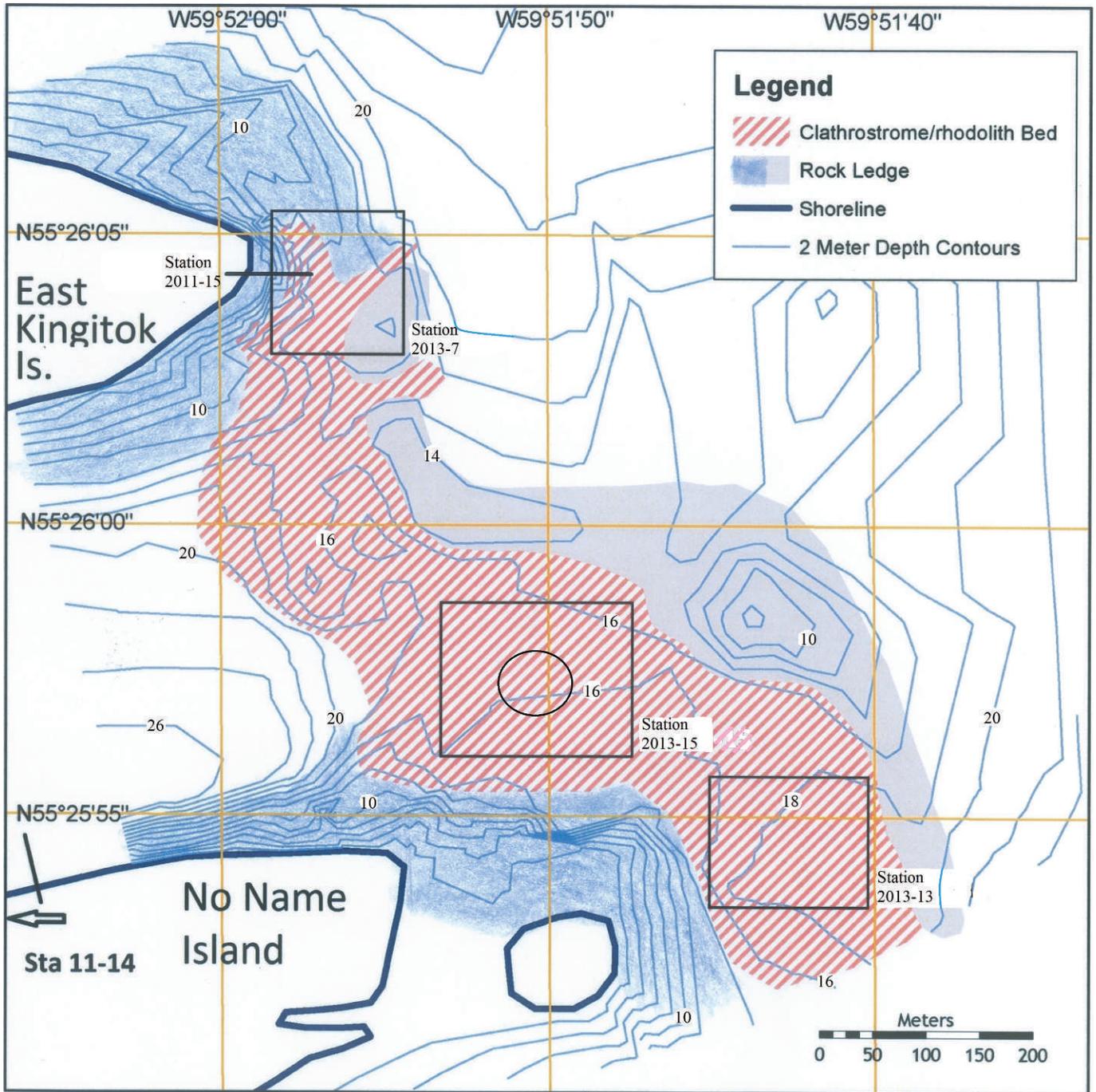


FIG. 6.—Benthic topography at Kingitok site derived from echosounder, GPS, and SCUBA surveys. Bedrock extends from the island shores to 15–18 m, depending upon slope and exposure (blue). Submerged ridge (light gray) to the right (at 8–20 m depth) represents a rocky divide with the bottom sloping steeply to the right (northeast). To the left of rhodolith bed, topography slopes westward between East Kingitok Island and No Name Island to the south. Flat-lying rhodolith bed at depth of mostly 15–17 m has modest east-west–flowing tidal current of approximately 0.5 km/hour (maximum). Three rectangles show collecting areas described in this paper. Location of sediment cores indicated by the ellipse located in the Station 2013-15 rectangle. The coordinates shown on this map were taken on site with a hand-held GPS device; they take precedence over the map-derived coordinates shown in Figure 4.

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FIG. 5.—A) Temperature relationships with depth and time at Kingitok rhodolith bed in summer of 2013. B) Estimated yearly temperature at bed surface based on above data and assuming that when shore-fast ice cover is present that bottom temperatures are < 1.5 °C. X-axis scale, days after July 1.

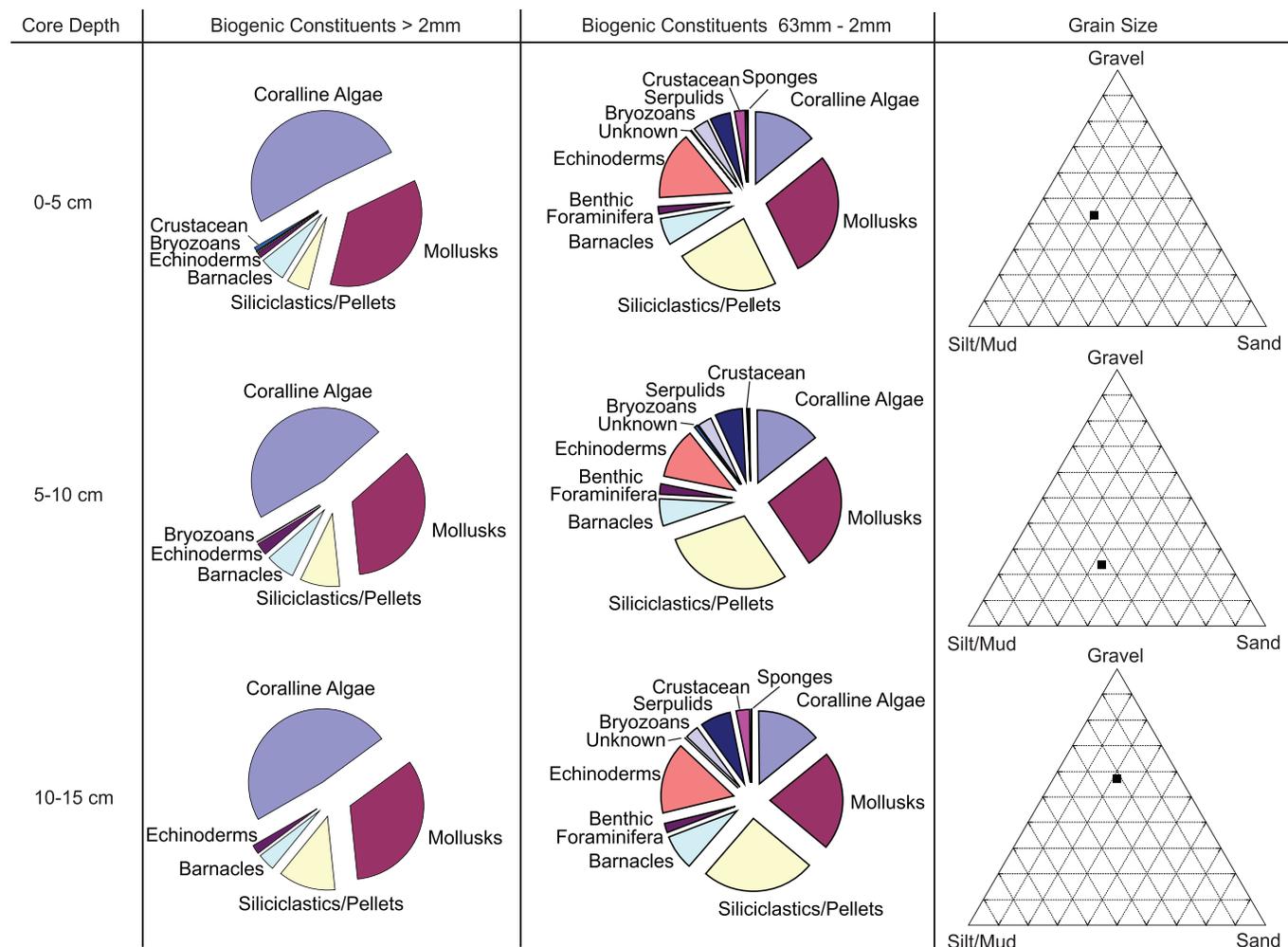


Fig. 7.—Mean abundance of biotic constituents in the coarser (gravel and sand) fractions with depth in the cores. Ternary diagrams showing an approximate equal amount of sand, gravel, and silt/mud with core depth. Note that sediment is dominated by silt and gravel with a relatively small sand component. See Table 1 and text for full analysis.

Subarctic, the rhodolith beds are made up of both the wide-ranging *Lithothamnion glaciale* and the more Arctic *Lithothamnion topiforme* (Adey et al. 2005). In this study, *L. glaciale* highly dominated at depths < 20 m, with *L. topiforme* intermixing deeper and becoming dominant > 25 m. The Kingitok *C. compactum*/rhodolith bed covers an area of ~ 0.15 km² (Fig. 6). Cobbles and boulders, with buildups of *C. compactum*, were scattered throughout the bed; they were intensively sampled in the areas delimited by rectangles on Figure 6.

The 3-dimensional structure of the rhodolith bed, as shown by sediment cores taken approximately within the circle shown in the 2013-15 rectangle in Figure 6, reveals little internal depth stratification. Point-counted biogenic constituents remain uniform downcore; the grain size data similarly show no significant stratification (Fig. 7). Siliciclastic silts (including fecal pellets) provide roughly 45% of the total accumulated sediment. Not including the fecal pellet component (made up largely of siliciclastic silt; Fig. 8), bioclastic gravel (39%) and sand (16%) provide most of the remainder. Rhodolith fragments make up approximately 24% of the total sediment below the rhodolith surface veneer (Fig. 7; 49% of

the gravel fraction and 8% of the sand fraction consists of coralline fragments). Invertebrate skeletons provide a larger fraction (31%) of the bioclastic components. The silt, as seen in SEM mounts, is primarily crystalline material intermixed with a small amount of silica diatom frustules and sponge spicules. No coralline fragments were observed. The accumulating, organic-rich sediment of the rhodolith beds becomes anaerobic below a few cm depth, as seen in the *Clathromorphum* mound broken from its cobble substrate (Fig. 9).

Most of the *C. compactum* specimens collected in the 2010 and 2011 cruises were taken from rocky bottoms, largely from mid-exposure (wave/iceberg) shores. Figure 3 shows a plot of *C. compactum* development as a function of wave exposure, depth, and community structure relative to the typical rhodolith beds of the region (modified from Adey et al. 2013). When a level expanse of bottom occurs within that range, rhodolith beds can be extensive. As discussed in the Introduction, when cobbles and boulders occur on those level surfaces and fine-grained sedimentation is modest, *C. compactum* mounds remain uncovered on the tops of the boulders. Figure 4C shows the location of a more protected site, with

Fig. 8.—A portion of two of ten sections of core epoxy-embedded coarse fraction (63 μm–2 mm). Note dark-colored fecal pellets (Plt), benthic foraminiferal tests (Frm), echinoderm spine (Ech) section, and bivalve mollusk fragment (Mlk). Internal composition of fecal pellets, seen at larger magnification, closely resemble largely siliciclastic fine fraction (< 50/62.5 μm) as seen in SEM mounts (see text). Scale bar = 1 mm.

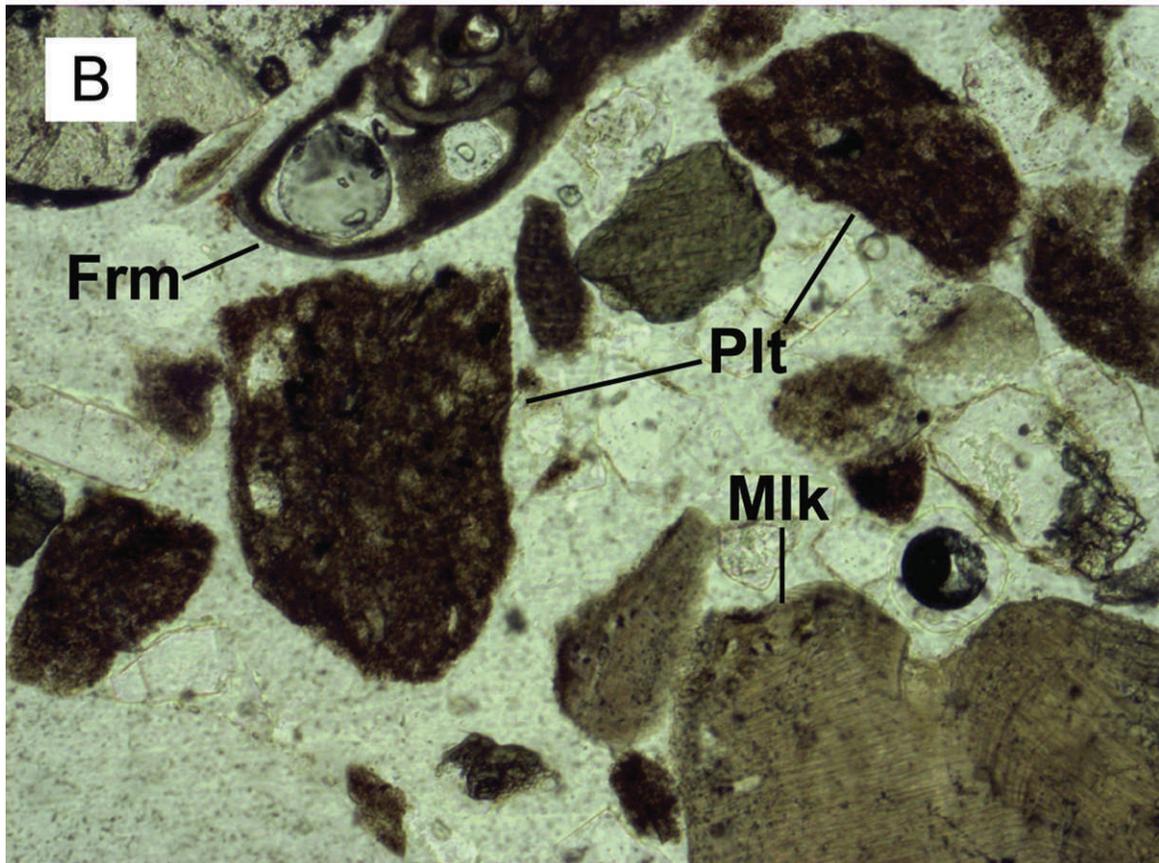
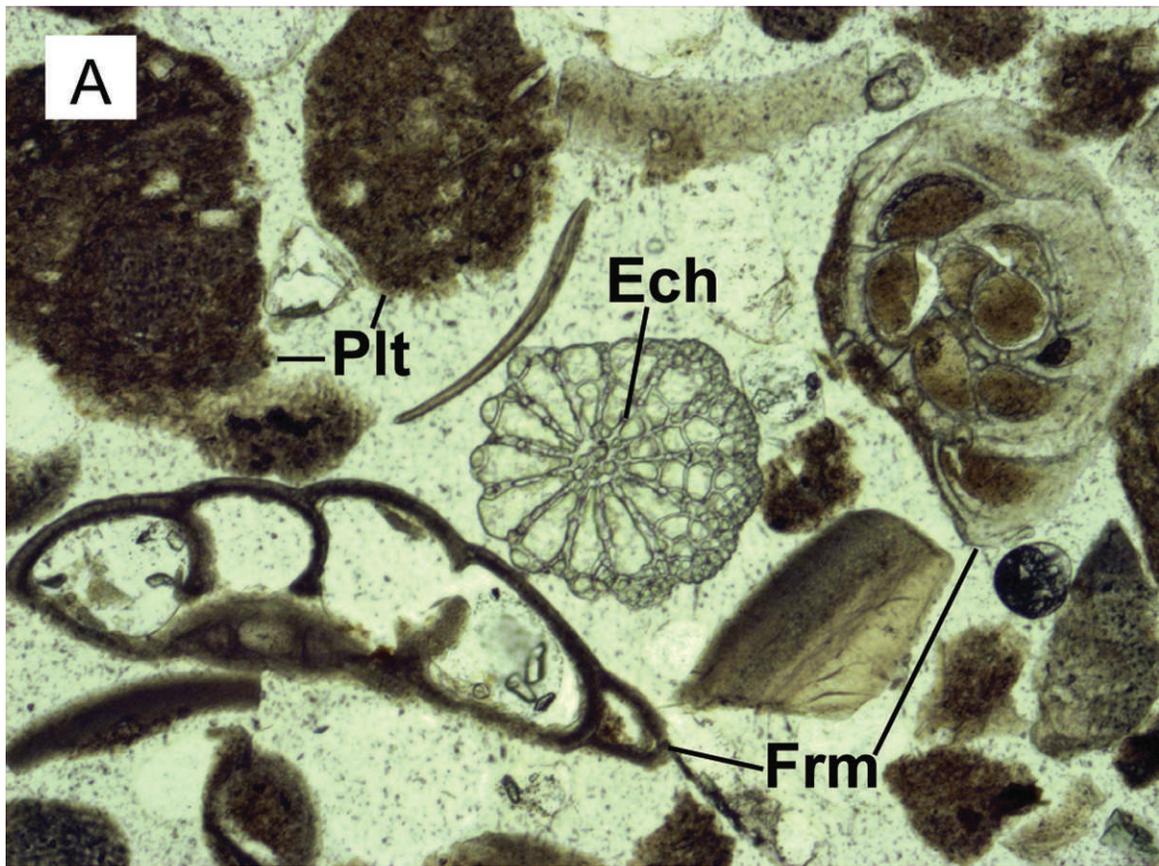




FIG. 9.—*C. compactum* extracted from its rock base. Pink portion on top is surface layer of calcified red alga that was living when collected. While mollusk borings are common (holes in crust), they are more limited in the older part of specimen that was embedded in anaerobic sediment. Specimen is about 14 cm in thickness and three quarters of its thickness was submerged in rhodolith-covered anaerobic sediments. Specimen 2013-13(6), 15–17 m; deposited in Coralline Collection, U.S. National Museum.

greater sedimentation, that is totally dominated by rhodoliths; the cobbles and boulders with their *C. compactum* mounds are likely buried under the fine sediment.

Most of the thick samples of *C. compactum* from the area of this study were embedded in epoxy and sliced vertically at the point of their greatest thickness (Fig. 10). The counting of yearly layers on polished surfaces (Fig. 2B), cross checked with seasonal variations in Mg using electron microprobe and laser scanning, allowed the determination of yearly thickness (i.e., yearly growth rate; Fig. 2C). Those data, representing at least 50 years of measurement for each specimen, were cross checked with ^{14}C analyses, presented in Figure 11 and Table 1. As shown in Figure 12, the mean thickness of the specimens collected from rock surfaces in 2010 in southern Labrador was 16.8 mm (approximately 93 years, based on the growth rates published for that region by Adey et al. 2013). The mean sample collected in 2011 in north central Labrador was only slightly thicker at 17.6 mm; however, with the lower growth rates of that region (see Adey et al. 2013), that represents an increase of 45% in average age of 136 years.

At East Kingitok Island, during the 2011 cruise, a single specimen of 104 mm thickness was taken from a cobble lying in a rhodolith bed, roughly 10 m from the base of the overlying rocky slope (Station 2011–15 in Fig. 6). The base of this specimen was embedded in gray-black (anaerobic) silt trapped by the rhodoliths; it also had many fewer borings of the bivalve *Hiatella arctica* (see Adey et al. 2013 for a description of these borings). This specimen was dated by a combination of annual layer counting and radiocarbon to an age of 646 years (Halfar et al. 2013). In the 2013 season, collection concentrated on the *C. compactum* encrustations on the projecting cobbles and boulders in this rhodolith bed. The three sites in this bed produced a mean *C. compactum* thickness that was 6 times larger (at approximately 634 years) than those taken in 2010 and 2011 from rocky bottoms (Fig. 12). Visually, these samples, many with their bases embedded in anaerobic sediment (Figs. 1F–H, 9, 10), are much denser and less bored than the samples taken on rocky bottoms (Fig. 1C, D).

DISCUSSION

By enhancing the structural integrity of their carbonate skeletons with interfilament calcification, species of the Subarctic and Arctic genus *Clathromorphum* have developed a longevity strategy to deal with the

intensive space competition that occurs on Subarctic rocky bottoms (Adey et al. 2013). This produces the potential for millennial ages of plants in optimal localities, making them among the longest-lived marine organisms (Frantz et al. 2005). The postglacial rebound provides a potential upper age limit of several thousand years for *Clathromorphum compactum* on the Labrador Coast. However, there are other potential limitations on the long-term persistence of these calcified red algae growing on rocky substrate in high-energy habitats.

Icebergs, sea ice, wave action with rock tools (moving pebbles and cobbles), and downslope movement of rock in a recently glaciated environment, all potentially limit the long-term crustal buildup of these species, favoring their accumulation on the subtidal slopes of more protected islands without sea cliffs. At the other end of the energy spectrum, the ability of the deeper-water *Clathromorphum* species to withstand the heavier terrigenous sedimentation of the inner coastal region appears limited. There the crustose coralline branching species *Lithothamnion glaciale* dominates; since the branch tips project above the periodically heavy sediment loading, growth is less affected than in the unbranched crustose species. Also, as described by Adey (1965) and elaborated by Adey et al. (2013), *Clathromorphum* species have evolved a long-lasting photosynthetic surface tissue (epithallium) and have formed a mutualism with grazing limpets and chitons (Steneck 1982). This has resulted in the loss of the surface sloughing characteristic of the barklike epithallium of most corallines. Less able to remove sedimentary detritus from their surface, the competitive capabilities of *Clathromorphum* are further limited in protected parts of the coast.

Finally, invertebrate borings, carried out to provide protected habitat (probably mostly through the use of acidic secretions), are abundant in *C. compactum* crusts. Invertebrate borings weaken the carbonate skeletons and provide pathways for interaction of seawater with the older parts of the crusts, leading to diagenesis. *Clathromorphum compactum* mounds on broad rocky surfaces can achieve millennial ages without large numbers of invertebrate borings and subsequent diagenesis only occasionally. However, *C. compactum* reproduces seasonally and builds crust continuously; it does not have a significant consumer. The abundant green sea urchin only occasionally feeds on *C. compactum*, and the common grazing chitons have a mutualistic relationship, keeping the surface clean of other algae that could easily outgrow this slow-growing crust. *Clathromorphum compactum* is highly abundant at mid-depths (10–25 m) and mid-exposure on rocky shores in Labrador (Adey et al. 2013). The Labrador Coast is about 600 km long; the rocky shore, with its many bays and islands, presents extensive subtidal rocky surface and adjacent bottom with rhodolith beds that in turn provide scattered optimum sites for these crusts to develop and continue their growth for many centuries. This provides an extensive potential climate archive.

As pipe core sections show (Figs. 7–8), the rhodoliths in the Kingitok bed formed less than a quarter of the underlying sediment. Even though 90% of the gravel fraction and 73% of the sand fraction size component of the sediment is bioclastic, invertebrate skeletons dominate over the coralline fragments. The total sediment is 45% siliciclastic silt (including fecal pellets), largely derived from the water column, and invertebrate shells provide 31% as bioclastic gravel and sand within the framework of the rhodolith bed itself. It seems likely that rhodoliths, and probably the many filter-feeding invertebrates associated with the rhodolith bed as well (Chenelot et al. 2011; Gagnon et al. 2012), trap fine-grained siliciclastic suspended sediments from the passing of the rather moderate tidal currents. In addition to hydrodynamic trapping, the infaunal filter feeders collect organic and inorganic fine suspended sediment and form mucoid-coated fecal pellets. These aggregations of suspended silt and diatoms from the water column (Fig. 8) are fecal pellets dropped on the underlying sediment, and can be seen in the slides of the gravel/sand fraction denoted as siliciclastic. Perhaps in part because of the fecal pellet mucus, and their incorporated organics, and the long period of ice cover

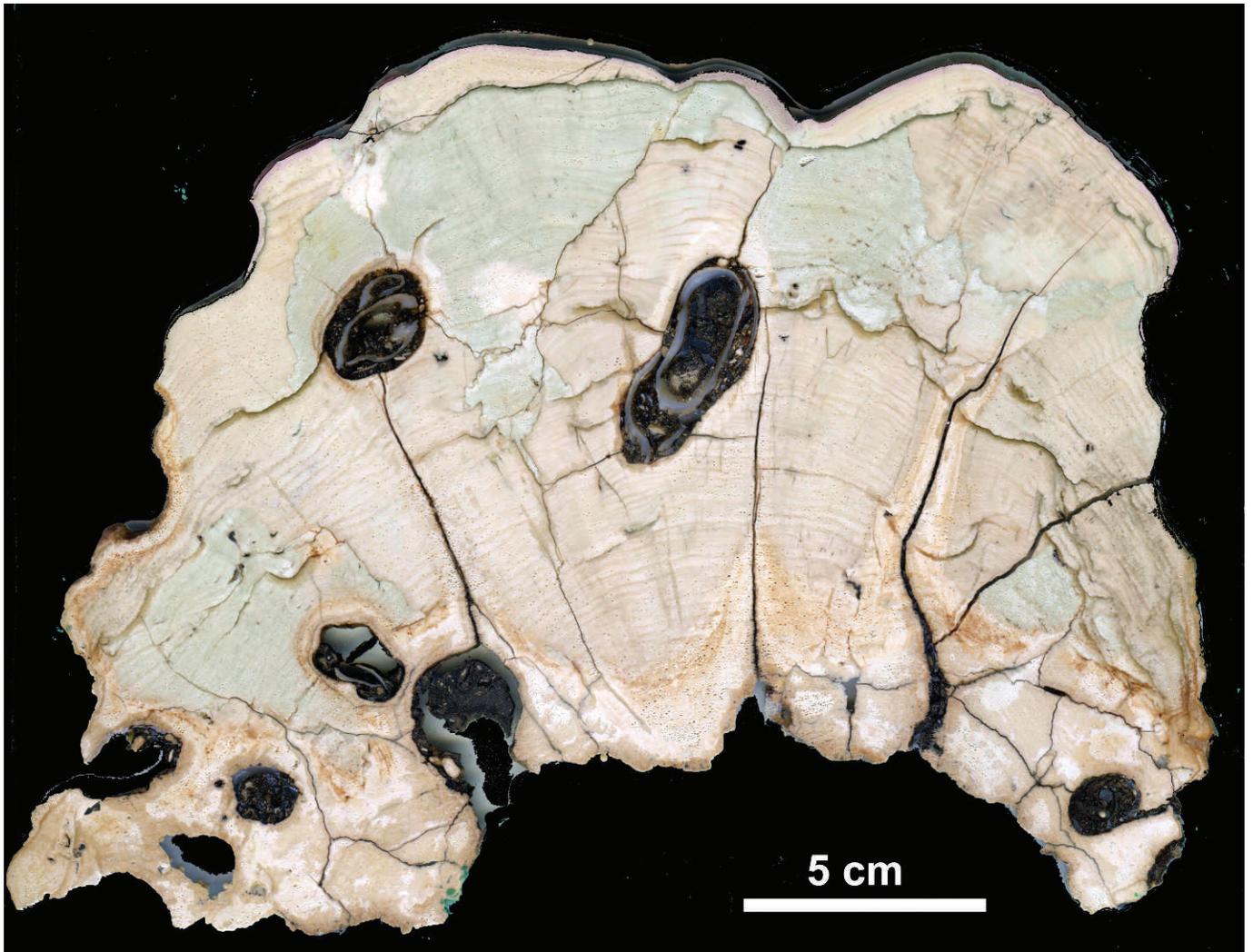


FIG. 10.—Large specimen of *C. compactum* broken from a cobble base in the Kingitok rhodolith bed. Based on the growth data cited in Fig. 11 and Table 1, this specimen is approximately 1000 years old. It has few *Hiatella* borings compared to the very rare specimens this size from broad rock surfaces (see Adey et al. 2013, fig. 25). When found, the latter are often too fragmented to provide useful archives.

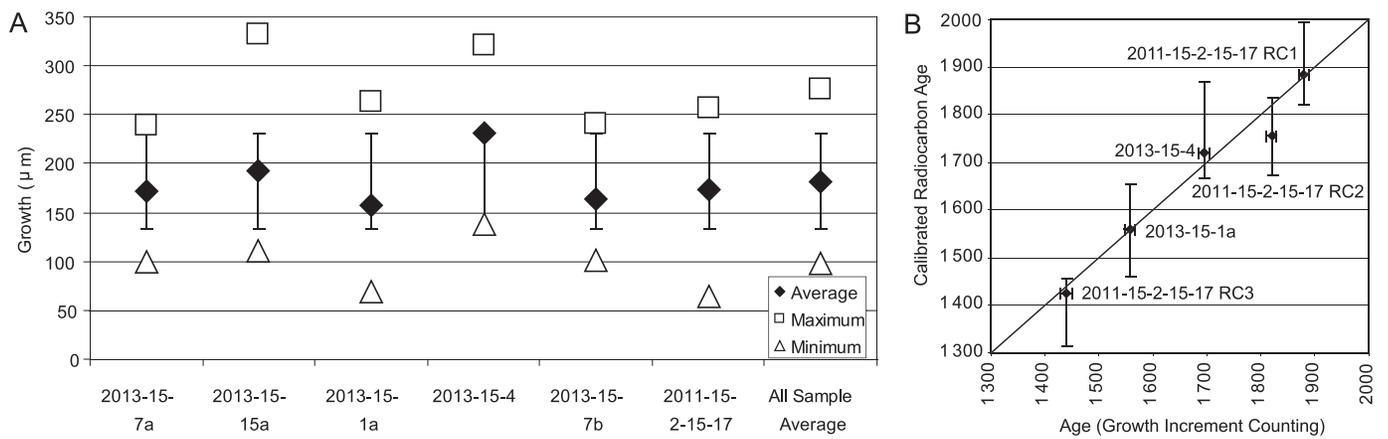


FIG. 11.—A) Growth rates of six samples of *Clathromorphum compactum* from the Kingitok rhodolith bed. At least 50 yearly thickness increments were measured from each sample. The average yearly increment was 182 μm. Data were collected by counting growth rings on polished sectional surfaces (see Table 1). B) Radiocarbon age (AD) correlated with growth increment count age of *C. compactum* specimens from the Kingitok site.

TABLE 1.—Results from AMS radiocarbon dating Utilizes MARINE13 database (Reimer et al. 2013). Marine reservoir value: $\Delta R = 96 \pm 38$. Asterisk indicates age determined by age model based on growth increments.

Sample #	Measured age (BP)	$^{13}\text{C}/^{12}\text{C}$	Conventional age	2 σ Calibration	Expected age*
2013-15-4	280 \pm 30	-1.9‰	660 \pm 30 BP	Cal AD 1660–1885	1685–1705
2013-15-1a	480 \pm 30	-2.0‰	860 \pm 30 BP	Cal AD 1460–1655	1547–1567
2011-15-2-15-17 RC1	140 \pm 30	-2.0‰	520 \pm 30 BP	Cal AD 1820–post 1950	1875–1880
2011-15-2-15-17 RC2	240 \pm 30	+0.5‰	660 \pm 30 BP	Cal AD 1670–1840	1815–1825
2011-15-2-15-17 RC3	670 \pm 30	0.0‰	1080 \pm 30 BP	Cal AD 1310–1440	1435–1445

with little disturbance, the surface silts become interlocked and “glued”. When the bed is subjected to moderate wave action, the rhodoliths remain largely on the surface of the “hardened” sediments, experiencing movement primarily when subject to periodic strong waves, and perhaps by the bioturbation of browsing fish. Strong northeast winds and swell during the four to five month ice-free period likely roll the rhodoliths back and forth across the compacted silts of the underlying sediment. Nevertheless, rhodolith branches apparently undergo little further degradation; while a significant part of the gravel fraction, they are only a minor part of the sand fraction and were not seen in the silt fraction. The underlying sediments, having little interaction with the water column and an abundant supply of fecal pellets from the infaunal invertebrates, become anaerobic, as indicated by their gray-black color. When this happens, invertebrate boring in the older parts of the partially buried *Clathromorphum* crusts growing on the embedded cobbles and boulders becomes significantly limited.

As we have shown, *Clathromorphum compactum* mounds collected in the Kingitok bed are on average six times thicker and older than those collected on rock surfaces; maximum ages are nearly twice as old

(Fig. 12). The lowest two depth zones of a single station collected in 2011 were at the margins of the Kingitok rhodolith bed. This included one of the largest specimens taken in the 2011 season. Thus, *C. compactum* mounds buried in the rhodolith bed provide significantly greater thickness and older specimens. Ages of the Kingitok rhodolith bed specimens were estimated by counting yearly layers, as described in this paper. These ages are likely minimum ages, since disconformities or unconformities exist in some of the specimens. The presence of an unconformity indicates that a specimen is older than a raw thickness measurement can document.

CONCLUSIONS

In this paper we expand our discovery of highly abundant multicentury encrustations of *Clathromorphum compactum* on moderately exposed Labrador Sea shores of Newfoundland and Labrador (Adey et al. 2013; Halfar et al. 2013) to include cases where *C. compactum* occurs on cobbles and boulders within rhodolith beds; this habitat produces millennial buildups in this species. In three seasons of SCUBA-based field work, we have been able to significantly increase the known age of *C. compactum* specimens with each season. As described above, these ages now reach approximately 1200 years BP. Much of this expansion has been based on increased understanding of the ecology of the species. Improved instrumental capability, for extensive coastal surveying and the location of rhodolith beds, would increase the limited bottom time available for collecting with SCUBA methodology. This would significantly increase the number of very old specimens available for climate archiving. Small boat surveying and instantaneous mapping, matching sonar with GPS, seem the most likely approach for identifying beds worthy of the more time-consuming SCUBA collecting. Subsurface seismic studies would also likely identify buried subfossil *Clathromorphum* buildups. Matching band patterns, as in dendrochronology, along with radiocarbon dating could extend climate archives to older times.

As shown by the research described here, *C. compactum* buildups, especially the largest and oldest specimens, hold a formidable potential to significantly enhance our understanding of prehistorical climatic variation. We think that a more extensive analysis of many localities and subsequent specimens could produce a more accurate climate and environmental history of the Labrador Coast. With the recent discovery of *C. compactum* with multicentury lifespans in northern Baffinland (Halfar et al. 2013), it is also likely that this work can be extended into the high Arctic, further contributing to a better understanding of the causes and consequences of global climate change. In particular, a detailed late Holocene climate history of the Arctic and Subarctic, one that includes the variability and extent of sea ice cover (Halfar et al. 2013), is well within our grasp.

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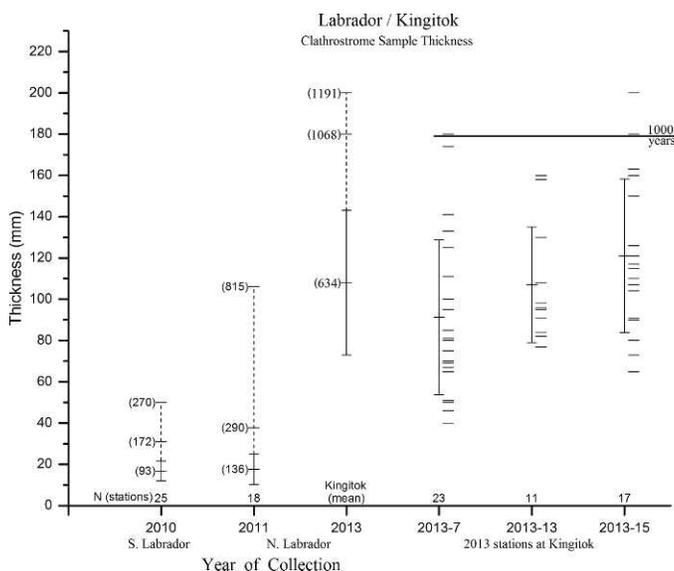


FIG. 12.—Comparison of individual specimen thicknesses from the 2013 Kingitok Stations (as shown in Fig. 6) with combined specimen thicknesses from the 2011 collections in northern Labrador and the 2010 collections in southern Labrador (see Fig. 4A). The ticks from top to bottom on the left three vertical bars represent: maximum thickness, mean maximum, plus standard deviation, mean and minus standard deviation, corresponding with the y-axis. Mean maximum is the mean of the largest samples from each collection site. The numbers in parentheses are ages inferred from specimen thickness and growth rates as determined by SEM analysis (180 $\mu\text{m}/\text{year}$, southern Labrador, 2010; 130 $\mu\text{m}/\text{year}$, northern Labrador, 2011; 181 $\mu\text{m}/\text{year}$, Kingitok, 2013; see Adey et al. 2013 and Figure 4 (above). Individual specimen measurements are shown for each 2013 Kingitok station to the right. The numbers to the lower right are sample numbers from each of the three 2013 Kingitok stations.

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