THE DEEP-SEA GORGONIAN CORAL *PRIMNOA RESEDAEFORMIS* AS AN OCEANOGRAPHIC MONITOR

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ABSTRACT

Primnoa resedaeformis is a deep-sea gorgonian coral with worldwide distribution and a lifespan of at least several hundred years. Recent work has suggested that it may be possible to obtain extended, high-resolution records of ambient oceanographic conditions from *Primnoa* skeletons. This thesis focuses on specimens recently collected live from the Northeast Channel, SW of Nova Scotia, from depths of 300-500m.

Skeletal microstructure was examined as a prerequisite to geochemical sampling. Skeletons exhibit periodic growth at three distinct scales. Concentric annual rings throughout the skeleton, and sub-annual laminae in the horny axis, measure 200 +/- 100 microns and 15 +/- 10 microns, respectively. Fine-scale striae in the outer calcite cortex measure 1.5 +/- 2 microns. The dark, gorgonin-rich portion of annual rings in the horny axis forms in winter, when currents in the NE Channel are most energetic. Growth in these animals is apparently tied to the passage of currents at seasonal, lunar and tidal frequencies. Annual ring widths in the horny axis could not be successfully cross-dated, however, a prominent dark ring that appears to have been formed in 1976 is present in several of the colonies examined. Prominent dark rings may serve as useful benchmarks in sclerochronology.

Mg/Ca and Sr/Ca were measured by laser ablation ICP-MS in the predominantly calcite axial cortex. Across a 1.5^0C gradient, Mg/Ca is positively related to temperature. Sr/Ca also increases with temperature, but this may be explained by the influence of Mg/Ca on Sr partitioning, rather than temperature. Near annual-resolution timeseries profiles of Mg/Ca are consistent within and among colonies having different growth rates. Conversion of Mg/Ca profiles to temperatures using a provisional calibration

[Mg/Ca (mmol/mol) = 4.88(+/- 1.09) T (^{0}C) + 70.92 (+/-6.79)] yields a range of values and trends that are consistent with the observational data. Mg/Ca in *Primnoa,* therefore, is a viable means of monitoring bottom-water temperatures. The North Atlantic Oscillation (NAO) is responsible for a significant component of inter-annual temperature variability in the Scotia-Maine region. Mg/Ca records from older corals could therefore provide extended proxy records of the NAO.

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INTRODUCTION

Fishermen in the Canadian Maritimes have long known that where there are corals, there are fish. “Forests” of gorgonian corals, often exceeding 4m in height, provide habitat for a variety of commercially important groundfish species. Concerned with increasing destruction of the crucial habitat by “factory” trawlers, a group of long-line fishermen presented specimens to scientists at Dalhousie and McMaster Universities in 1995. Scientific knowledge of Canada’s deep-water corals at that point was virtually non-existent, except for the work of a McMaster University graduate student, Jodie Smith, who was pioneering the use of deep corals as paleo-climate monitors (Smith, 1997). Fishermen’s fears thus formed the impetus for recent work on deep gorgonian corals and this thesis. Great lifespans of deep corals make these organisms priceless archives of climatic data, an aspect rendering their conservation even more compelling.

This thesis focuses on the gorgonian *Primnoa resedaeformis*, which, alongside *Paragorgia arborea,* is the most abundant coral species living off Nova-Scotia (Breeze, 1997). Both species have arborescent, or fan-shaped morphologies that bend and sway in currents as a means for individual polyps to capture food. *Paragorgia* deposits a skeleton of amorphous, sponge-like mesoglea, useless for climate records, while *Primnoa* deposits a heavily calcified structure in discrete layers, like those of a tree.

Scientific literature on *Primnoa* is limited. Bayer (1955) outlined the gross morphology and phylogenetic affinities of the Primnoidea. Grasshoff and Zibrowius

(1983) outlined the differences between the flexible, horny axis and stiff calcite "crust," or cortex, of axial skeletons of *Primnoa* and related species. More recently, Risk et al. (2002) studied lifespans and growth patterns in *Primnoa* collected from the Scotian Shelf region; a sub-fossil fragment was found to have lived for at least 350 years. Andrews et al. (2002) validated annual timing of concentric rings in *Primnoa* using radiometric techniques. Heikoop et al. (2002) showed that surface productivity data could be obtained from $\delta^{15}N$ and $\delta^{13}C$ in the horny layers. Heikoop (unpublished) has also shown that Mg/Ca in calcite layers reflect temperature.

This thesis expands upon the work of Risk et al. (2002) and Heikoop et al. (2002). There are two parts, each one a separate manuscript intended for publication. Part One, entitled "Climatic significance of growth patterns in the deep-sea coral *Primnoa resedaeformis*" was submitted to *Marine Ecology Progress Series* in February, 2002, and was accepted for publication pending minor revision. The revised manuscript is presented here. It investigates skeletal micro-structure in colonies of *Primnoa* recently collected live from the Northeast Channel. Evidence is given for annual, monthly, and tidal-scale banding, and possible causes of formation are offered. The findings suggest that proxy environmental records could be obtained from *Primnoa* skeletons with a temporal resolution comparable to that of reef corals, but with worldwide coverage. Part One also formed the material for two abstracts published in 2001 (Appendix: Publications).

Part Two, entitled "NAO record from Mg/Ca in skeletons of the deep-sea gorgonian coral *Primnoa resedaeformis,*" is intended for submission to *Geochimica et Cosmochimica Acta.* It surveys Mg/Ca and Sr/Ca in NE Channel *Primnoa* specimens. Following recent work by Heikoop (unpublished), I determine a provisional calibration relating Mg/Ca to temperature across a depth gradient. Calibrated temperatures are compared with the observational record over the last thirty years, and a case is made for using Mg/Ca in Primnoa as a monitor of bottom temperatures, and the North Atlantic Oscillation. Part Two formed the basis of an abstract published in 2002 (Appendix: Publications).

PART ONE:

Climatic significance of growth patterns in the deep-sea coral *Primnoa resedaeformis*

ABSTRACT

Skeletal structure in the deep-sea gorgonian *Primnoa resedaeformis* is investigated for potential use in paleoceanographic applications. Specimens collected from depths of 280-450m in the NE Channel, SW of Nova Scotia, exhibit periodic growth at three distinct scales. Concentric annual rings throughout the skeleton and sub-annual laminae in the horny axis measure 200 +/- 100 microns and 15 +/- 10 microns, respectively. Fine-scale striae in the outer calcite cortex measure 1.5 +/- 2 microns. The dark, gorgonin-rich portion of annual rings forms in winter, when currents in the NE Channel are most energetic. Growth in these animals is apparently tied to the passage of currents at seasonal, lunar and tidal frequencies. Annual ring widths in the horny axis could not be successfully cross-dated, however, a prominent dark ring that appears to have been formed in 1976 is present in several of the colonies examined. Prominent dark rings, and possibly their unique geochemical signatures, may serve as useful benchmarks in sclerochronology. Future geochemical sampling of growth increments could yield century-scale proxy environmental data at annual, or better, temporal resolution. Worldwide distribution of *P. resedaeformis* implies global coverage of these reconstructions.

1. INTRODUCTION

There is increasing interest in the potential climate records contained in the skeletons of deep-sea corals. Analyses of trace inclusions in the carbonate skeletons of reef corals have generated a multitude of proxy records (reviewed in Druffel, 1997); but these are restricted to the photic zone in tropical waters. Deep-sea corals overcome these spatial restrictions: they range from the continental shelf to abyssal depths at all latitudes. In addition, these organisms are generally slow growing and may live to a thousand years or more (Druffel et al., 1990, 1995; Smith, 1997a; Risk et al., 2002). Recent work on deep-sea corals has shed information on the variability of millennial-scale climate processes (Edwards et al., 1993; Smith et al., 1997b; Adkins et al., 1998; Mangini et al., 1998; Goldstein et al., 2001) as well as episodic phenomena (Smith et al., 1999).

A major limitation with deep-sea corals, however, has been a poor understanding of their growth (e.g.: Mikkelson et al., 1982; Lazier et al., 1999). A general lack of unequivocal growth layers has made it difficult to obtain tracer records with a high degree of temporal resolution (annual-decadal). Study of climate processes in the high latitudes, for example, would benefit from annual-scale reconstructions (e.g.: Petrie and Drinkwater, 1993; Marsh et al., 1999).

Primnoa resedaeformis is a gorgonian coral distributed worldwide, from 50m to 3.5km depth (Smithsonian holdings), usually in areas of fast currents (e.g.: Tunnicliffe and Syvitski, 1983). Off the Canadian Maritimes it is found in submarine canyons that intersect the shelf break (Breeze et al., 1997). Skeletons are composed of calcite and horny, sclerotized collagen called gorgonin (Marks, 1949; Goldberg, 1974,1976). Younger parts of the skeleton have abundant gorgonin and older parts are massively calcified (Bayer, 1955; Grasshoff and Zibrowius, 1983). Like other gorgonians (Grigg,

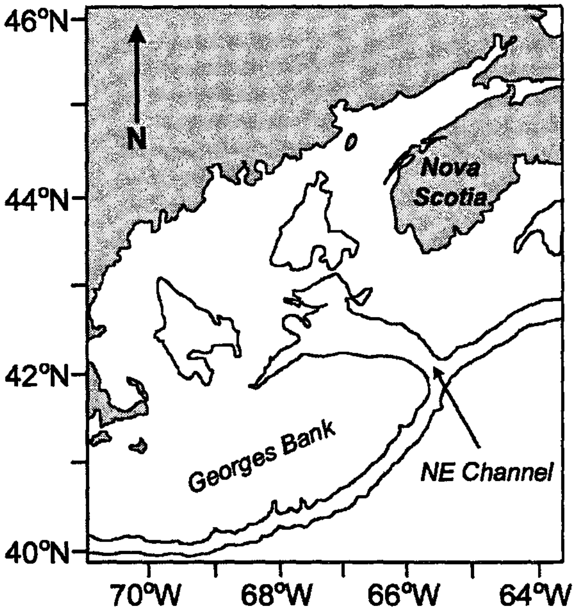

Figure 1. Map showing location of *Primnoa* collection. 200m and 1000m isobaths are shown.

1974; Szmant-Froelich, 1974; Goldberg, 1976; Mitchell et al., 1993), concentric growth rings in *P. resedaeformis* appear to be annual (Andrews et al., 2002; Risk et al., 2002). In addition, sub-annual rings in the skeleton appear to form with a periodicity related to tides (Sherwood et al., 2001; Risk et al., 2002;). Life spans of individual colonies may exceed 300 years (Risk et al., 2002). Preliminary geochemical analyses have shown that there is a possibility of obtaining proxy temperature, salinity and productivity data from these corals (Heikoop et al., 1998; Sherwood et al., 2001; Heikoop et al., 2002).

In this paper, we present a detailed investigation of the skeleton of *P. resedaeformis*. Only superficial descriptions of this coral exist (Bayer, 1955; Grasshoff and Zibrowius, 1983; Risk et al., 2002). The nature, timing, and possible causes of incremental growth in *P. resedaeformis* are examined in light of their underlying skeletal microarchitecture. In addition, patterns of growth are evaluated for their inter-colony reproducibility; if deep-sea corals are utilized for geochemical tracer studies, it must be established that individual colonies respond to environmental conditions in a consistent manner.

2. METHODS

Specimens of *P. resedaeformis* were collected from the Northeast Channel, SW of Nova Scotia (Figs. 1 and 2). Fishermen supplied 11 specimens, collected from a depth of 450m with long-line gear in August, 2000. A specimen was supplied by a Canadian Department of Fisheries and Oceans deep-sea habitat survey in July, 2000 (331m). It was collected live and held for 2 weeks in an aquarium before dying. Two more specimens were collected with the remote operated submersible *ROPOS* in August, 2001 (410m, 475m).

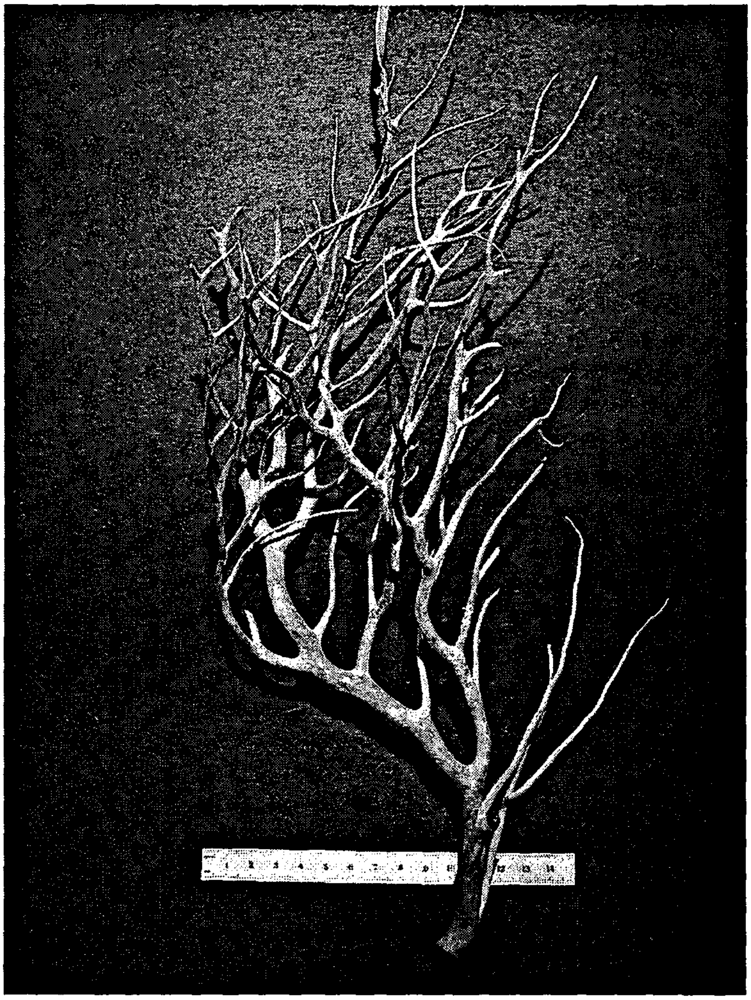

Figure 2. Colony of *Primnoa resedaeformis*. Lifespan was 35 years. (Ruler, for scale, is 15cm)

Corals were rinsed in freshwater and left to air dry for several weeks prior to examination. Several preparation techniques were used, depending on the desired imagery. Polished thin and thick sections generally yielded the highest quality images. Sectioned axes were embedded in epoxy (Buehler Epothin) under high vacuum. During grinding and polishing of embedded specimens, water lubricant caused the organic fraction of the skeletons to swell; kerosene was therefore used. Sections were etched in 2% acetic acid to view calcite crystal fabric, or in commercial bleach to remove the organic fraction.

Skeletal structure was examined with SEM (Phillips ESEM), transmitted light and Nomarski reflecting light microscopy. For SEM, sections were gold sputter coated to a thickness of 7ηm. Image analysis was performed with National Institute of Health (NIH) "IMAGE" software.

Parts of bleached, powdered, and ultrasonically cleansed skeleton were examined by XRD to determine percent calcite vs. aragonite. Percent organic material in the horny axis (see below) was measured by loss on ignition (550^0C for 3 hours).

3. RESULTS

Stems of *Primnoa* have three distinct zones: a central rod; a horny axis, brown with gorgonin; and a calcite cortex, which is massive and white (Fig. 3A). All three zones are present in basal sections; the calcite cortex is missing in more distal sections (Fig. 3B). Dark rings are sometimes seen in the outer calcite cortex that may represent death/re-growth surfaces. Cracks are common in the central rod and horny axis; these are artifacts of drying. XRD confirmed that calcite is the carbonate phase in all three zones. The central rod and horny axis contain about 23% (Loss on ignition, s.d. 1.8, n = 5) and

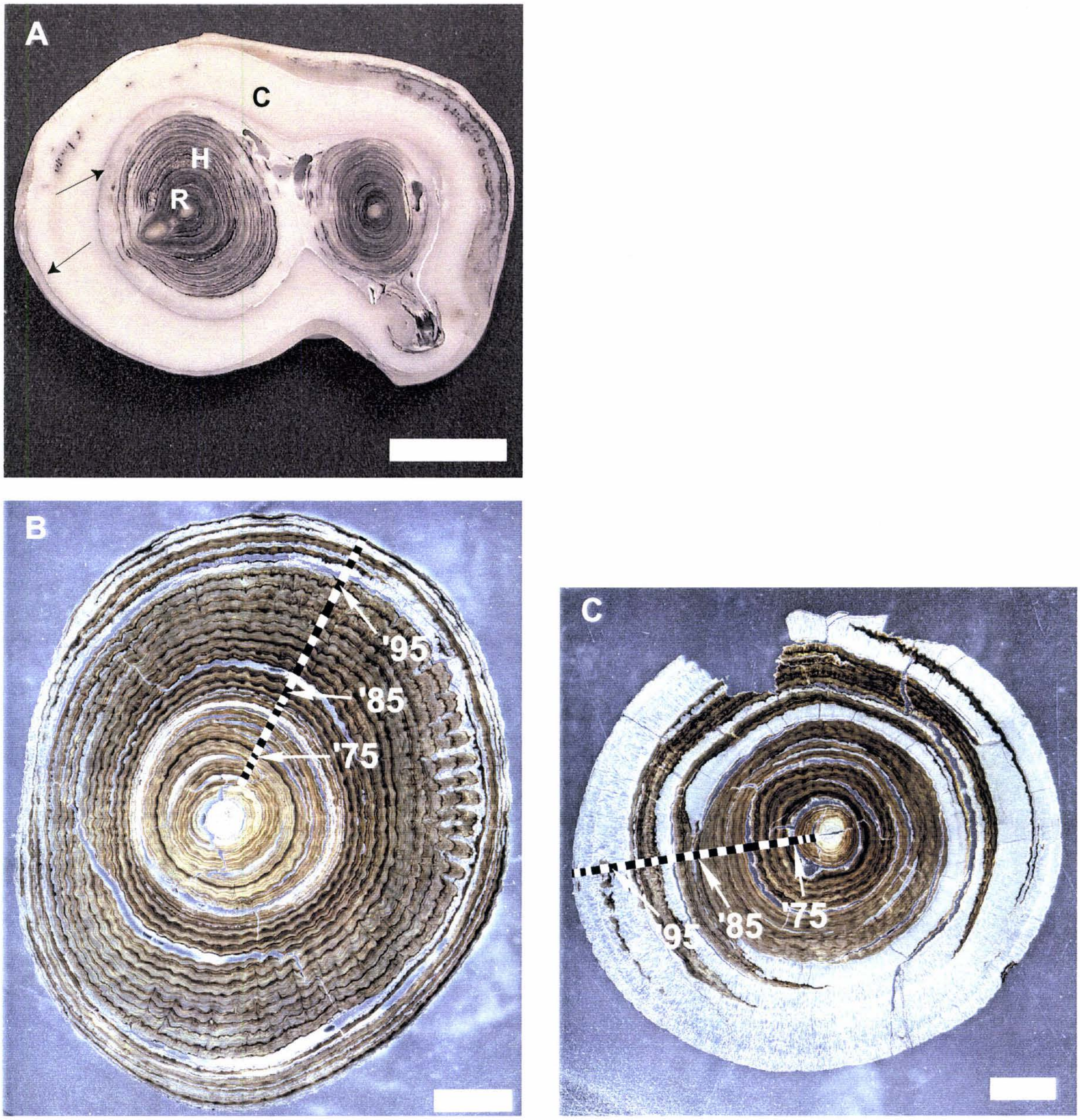

Figure 3. A) Polished basal section of large Primnoa specimen. R: central rod; H, horny axis; C, calcite cortex. Two growth axes are present. Note possible death surfaces in the calcite cortex (arrows). Specimen lived for approximately 250 years, based on ^{210}Pb dating (see Part Two). (Scale bar = 2cm). **B)** and **C)**Younger specimens collected live in August, 2001. Concentric rings are annual. Cracks are artifacts of drying. Note the prominent dark band that appears to have been formed in 1976. (Polished thin sections in transmitted light; scale bars = 2mm).

28% organic material (s.d. 1.8, n = 5), respectively. Organic inclusions in the calcite of the outer cortex are negligible.

3.1 Investigation of skeletal structure

3.1.1 Central rod

The central rod is solidly mineralized all through the lengths of colonies. It averages about 2-3mm in width. Transverse sections show laminated, annular lobes, suggestive of loculi (Lewis et al., 1992) that have been fused (Fig. 4). At the periphery of the rod, lobes grow laterally outward. At the nucleus, lobes are chaotic and appear to grow inward.

3.1.2 Horny axis

The horny axis shows concentric rings, as in trees, that are easily visible to the unaided eye (Fig. 3). Radiometric measurements have confirmed annual periodicity (Andrews et al. 2002). Rings are continuous and form by alternating proportion of gorgonin. A sharp transition from gorgonin-poor to gorgonin-rich defines the inner boundary of each ring. The wavy, undulating nature of rings is reflected in longitudinal striae on the outer margin of the skeleton. Rings average 200 +/-100 microns in width (Table 1). A striking feature of annual rings is their variation in relative abundance of gorgonin from year to year. Some annual rings are particularly gorgonin-rich. A prominent dark ring that appears to have been formed in 1976 is consistently present on several of the studied specimens (Fig. 3B,C).

Fine-scale laminae are present within annual gorgonin rings (Fig. 5; also see Risk et al., 2002). These are best seen with Nomarski interference optics; the differences in hardness between laminae accentuate micro-relief during polishing. Laminae often thin and lap in the trough of the early part of an annual ring. Laminae average 15 +/- 10

Figure 4. Central rod showing laminated, annular lobes growing laterally inward at the nucleus, and outward at the periphery. (Polished transverse section under Nomarski light; scale bar = 250 microns)

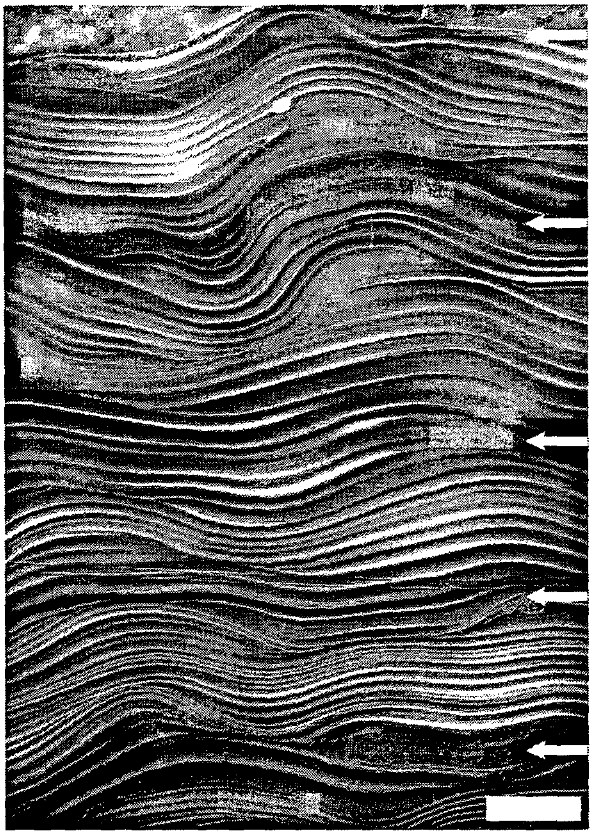

Figure 5. Growth patterns in the horny axis. Variation in the proportion of gorgonin to calcite (greater in the darker areas) forms annual rings (arrows). Sub-annual laminae number 15-20 per year. Note truncated laminae. Growth directed to top of image. (Polished transverse section in Nomarski light; scale bar = 100 microns)

microns in width and there are an average of 13-18 laminae per year (Table 1). The widest laminae are found in the dark, gorgonin-rich portion of annual rings.

Table 1: Characteristic widths (in microns) of 3 scales of incremental growth.

	Average width	St.dev.
Annual rings	200	100
Sub-annual laminae	15	10
Finescale striae	1.5	2

SEM images show that sub-annual laminae in the horny axis arise from a complicated arrangement of calcite and the collagen fibers that form a significant component of gorgonin (Fig. 6). When acid etched, the laminae that stand out on both transverse and longitudinal surfaces consist of dense, longitudinally oriented collagen fibers (Fig. 6A). The intervening valleys consist of loosely packed, more circum-axially oriented fibers. When the skeleton is bleached, a similar pattern emerges from the mineralized component, with calcite in the form of shorter, needle shaped crystals (Fig. 6B).

3.1.3 Outer calcite cortex

The outer calcite cortex begins to form when axial diameter exceeds approximately 1.5cm. The transition to calcite cortex is usually gradual, resulting in a zone of horny axis inter-layered with discrete bands of massive calcite. Likewise,

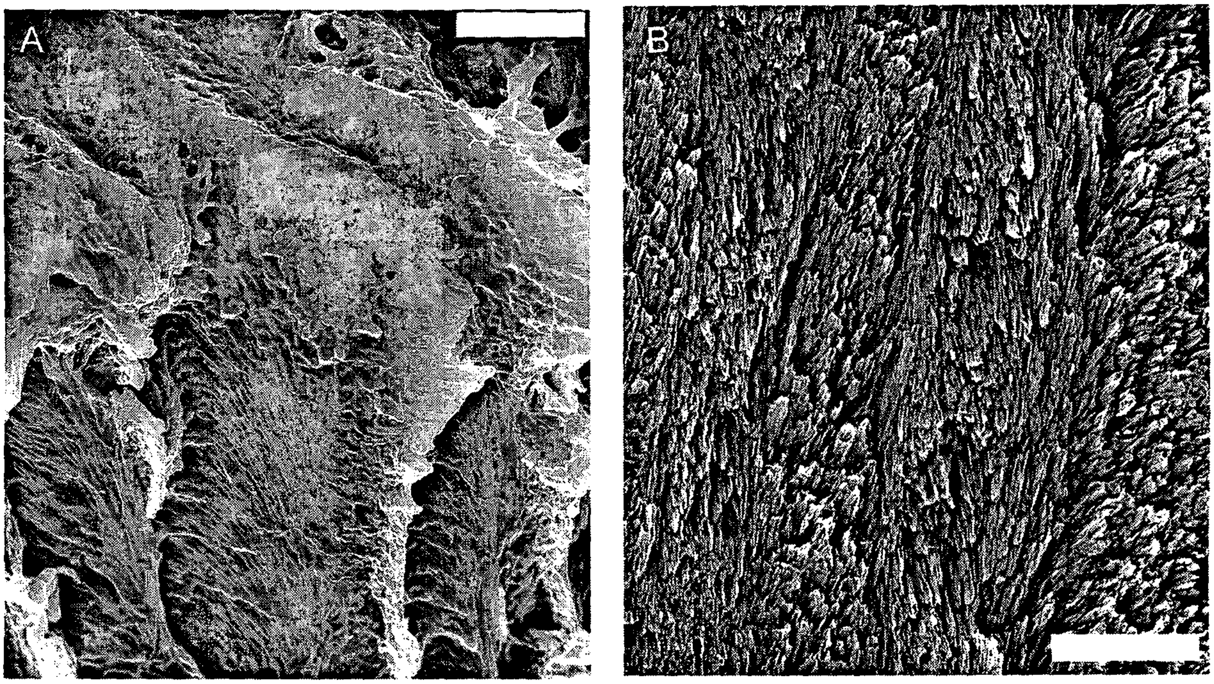

Figure 6. SEM images of sub-annual laminae in the horny axis. **A)** Longitudinal section etched in 2% acetic acid. Upper third of image shows the transversely-sectioned surface. Note longitudinal aspect of collagen fibres on laminae etched into prominence. Fibres in intervening valleys are more circum-axially oriented. **B)** Longitudinal section bleached to remove organic material. Note needle shaped crystals alternating between longitudinal (vertical) and more circum-axial (horizontal) orientations. (Scale bars = 10 microns)

discontinuous gorgonin layers are sometimes present in the outer calcite cortex. Concentric rings are barely visible by slight differences in translucence (Fig. 3B); and they average around 200 microns or less in width. Work by Andrews et al. (2002) suggests that, as with horny rings, rings in the cortex are annual. We were unable to improve ring discrimination by any of: higher magnification; use of Nomarski optics; staining with Alizarin Red; or charring the skeleton in a flame. SEM images show why these rings lack easily discernable boundaries. Horizontally aligned, fibrous crystals form fan-shaped, spherulitic bundles that compete for space as they grow outwards (Barnes, 1970; Fig. 7A). The first layer of fans nucleates on a flat surface provided by the preceding horny lamination. Subsequent layers of fans branch and become more randomly oriented owing to less uniformity in their sites of nucleation. Thus, fan boundaries often become more indistinct with increasing distance from the horny axis. Organic inclusions have a strong effect on crystal orientation: when a horny layer is deposited later in the calcite cortex, the first few layers of fans subsequent to it are "re-aligned", resulting in more distinct rings. Periodic growth of calcite fans is demonstrated by fine-scale striae averaging 1.5 microns (Fig. 7B).

3.2 Ring and laminae counts

Reproducibility of annual ring counts was assessed among multiple operators. Two axial sections having about 10% cortex were used. Counts were reproducible (Table 2), in agreement with counting experiments by Andrews et al. (2002). Thus, counting rings may be a quick and easy way of ageing young specimens with an average error of a few years. It becomes increasingly difficult to age older specimens (>50 years), owing to more poorly discernible growth rings in the outer calcite cortex.

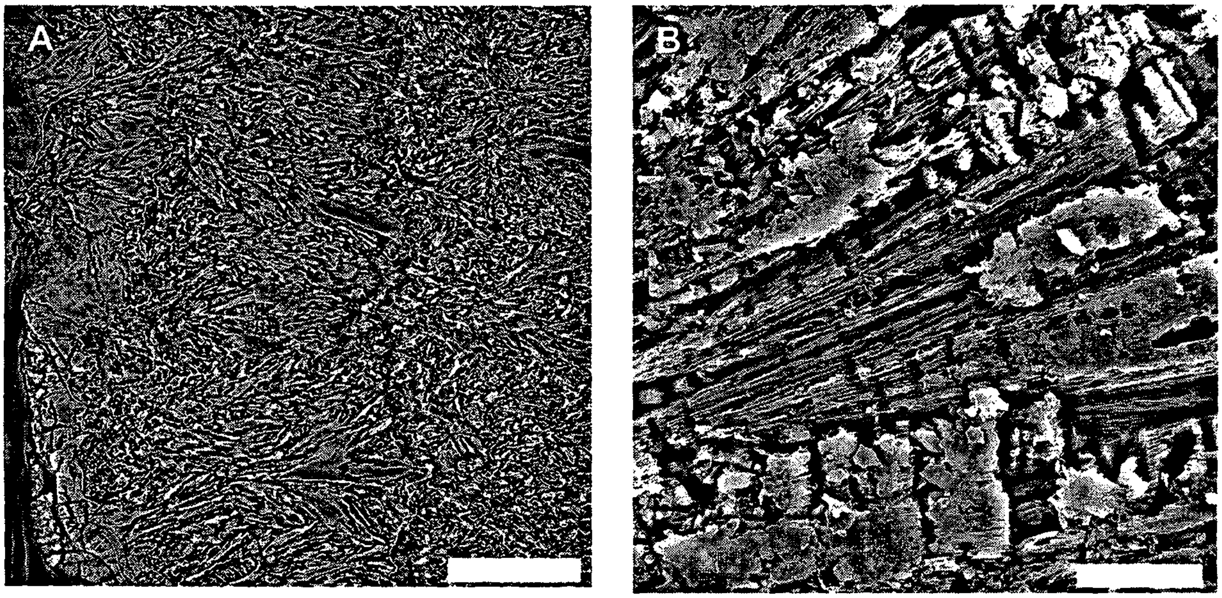

Figure 7. SEM images of the calcite cortex. **A)** Longitudinal section etched in 2% acetic acid. Radiating crystal fans grow peripherally to the right. (Scale bar = 100 microns)
B) Striae measuring 1-2 microns demonstrate periodic deposition of fan-shaped crystal bundles in the cortex. (Scale bar = 10 microns)

Table 2: Results of age determinations with three amateur counters.

Counter	DFO2000-A3	DFO2000-C3
1	33	35
2	30	36
3	31	37

A comparison of the widths of annual rings in the horny axis was made on specimens that had a covering of live coenenchyme when collected in July/August, 2000 (Fig. 8). Attempts to cross date (Stokes and Smiley, 1968) the widths of annual rings failed. This stems from the wavy, undulating nature of gorgonin rings and a rather subjective determination of the boundaries of annual rings (Fig. 5). Timing of annual ring formation was estimated by comparing the width of the most recent ring with the preceding ten rings (except specimen HH2000-2 which only had five years of growth). The most recent annual ring averages 54% (+/- 17%, n=5) of the average growth in the period 1990-1999. Since all the specimens were collected in July/August, the dark, gorgonin-rich segment of an annual ring appears to form in winter.

4. DISCUSSION

4.1 Patterns of growth

Growth in skeletons of *P. resedaeformis* occurs in two overlapping phases. Younger skeletons have dense gorgonin (collagen plus proteinaceous matrix) deposited alongside a fibrous calcite component. The central rod and horny axis have the same architectural characteristics, except that annular lobes in the former are discontinuous and lighter brown in colour. Concentric rings in the horny axis form by alternating proportion

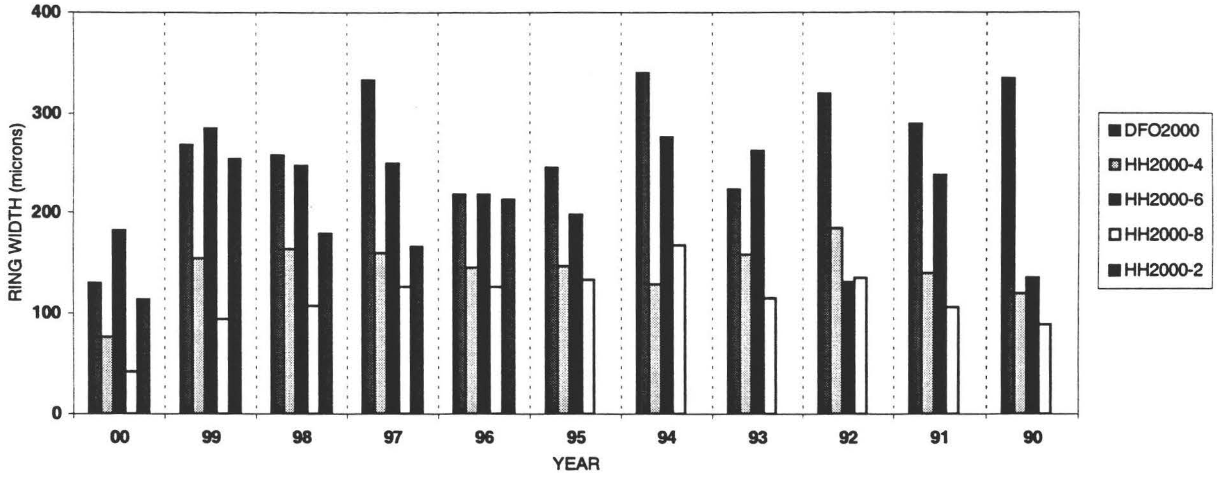

Figure 8. Timeseries comparison of widths of annual rings in the horny axis. Only colonies collected live (July/August, 2000) with clear banding patterns were used. Most recent rings average 54% +/- 17% relative to previous 10 years growth (5 years for specimen HH2000-2)

of gorgonin with annual periodicity (Andrews, 2002; Risk et al., 2002). When the skeleton reaches 1 to 1.5 cm in axial diameter, dense calcite is deposited in concentric layers around the basal regions. The transition from horny axis to dense calcite cortex occurs in response to the accumulation of the load imparted by the overlying arborescent mass of the colony. There are three distinct scales of growth (Table 1). Annual rings in both the horny axis and outer calcite cortex average 200 microns in width. In the horny axis, sub-annual laminae average 15 microns. And in the outer calcite cortex, periodic striae on calcite fans average 1.5 microns.

Examination of sub-annual laminae in the horny axis reveals an interesting arrangement of collagen and calcite. Alternating collagenous and mineralized laminae are deposited cylindrically. When the skeleton is decalcified, the undissolved collagen can be peeled away, lamination by lamination. There appear to be distinct alternations in the orientation of both the elongate, fibrous collagen and needle shaped calcite components through one lamination (Fig. 6). Longitudinally oriented collagen fibers impart to the skeleton tensile strength while mineralization accommodates compressive forces (Lewis et al. 1992). Collagen fibers oriented more circum-axially perhaps add further resistance to torsion (Wheeler, 1994). Variations in both the extent of mineralization and orientation of collagenous and mineralized components through one lamination would therefore seem to create differences in the ability to accommodate bending and twisting. This structural arrangement is particularly significant to life in areas of high current velocities (Tunnicliffe and Svitsky, 1983); the inherent ability to bend and twist (Jeyasuria and Lewis, 1987) allows the animal to minimize drag forces, yet remain in a more or less upright position (Spongaule and LaBarbera, 1991). Further investigation is required to determine the exact nature of these variations in fiber orientation, as well as the significance and degree of sclerotization throughout the horny axis (e.g.: Szmant-Froelich, 1974; Goldberg, 1978).

4.2 Origins of growth periodicity

4.2.1 Annual rings

Annual cycles in growth rate have been observed in many gorgonians and their possible causes include spawning (Grigg, 1974; Hartnoll, 1975; Coma et al., 1995), temperature changes (Velimirov, 1975; Coma et al., 1998a), and trophic constraints (Coma et al., 1998a) related to a combination of food availability (Ribes et al., 1999), currents (Velimirov, 1975) or both (Fabricius et al., 1995; Coma et al., 1998b). Observations of the behaviour of *P. resedaeformis* do not exist, but experiments on asymbiotic, shallow water gorgonians may be applicable. These studies point to heterogeneity of gorgonian diet (Coma et al., 1994; Ribes et al., 1999) and the importance of detrital POC (Leversee, 1976; Lasker, 1981; Coffroth, 1984; Ribes et al., 1999; also see review in Gili et al., 2001). Ribes et al. (1999) found that detrital POC accounted for 86 +/- 14% of ingested carbon in *Plexaurella clavata.* Since particle capture rates depend on flow (Dai and Lin, 1993; Fabricius et al., 1995), feeding in gorgonians is strongly regulated by current regime (Gili et al., 2001).

Polyps on *P. resedaeformis* point down, which is likely an adaptation allowing for the direct interception of particulate matter as the colony bends in strong currents. The strength of currents in the NE Channel is clearly evident in video footage from the *ROPOS* submersible dives (Scott et al., 2002), which shows the horizontal transport of particulate material at speeds of up to 60 cm/sec. October to May is the season of strongest current velocities, occurring in bursts both into and out of the NE Channel (Ramp et al., 1985). The dark portions of annual rings in *P. resedaeformis* coincide with this period, thus, stronger currents and the associated lateral advection of detrital POC may be inherently liked to their formation. Increased feeding at these times may result in increased rates of gorgonin synthesis (Risk et al., 2002). Alternatively, the dark portions of the annual rings may reflect the preferential deposition of collagen in response to the tensile forces imposed currents in the more energetic winter months.

4.2.2 Sub-annual laminae

In a preliminary survey of a sub-fossil specimen of *P. resedaeformis* also from the NE Channel, Risk et al. (2002) counted approximately 26 sub-annual laminae per year, and suggested a link with spring tides. With Nomarski interference microscopy and a larger number of samples, we see that the number of laminae range from 13 to 26, with an average of about 15, dependent upon the year (Fig. 5). Laminae present within the horny axis probably reflect current variability. There are, in fact, about 19 times per year in the study area in which tidal amplitude is "larger than average" (Canadian Hydrographic Service, 2000). Determination of the true provenance of sub-annual laminae requires more samples from different regions, but present data suggest that the timing of sub-annual laminae is driven by tidal currents.

4.2.3 Fine-scale striae

Striated crystal fans in the outer calcite bear a striking resemblance to calcite structures in some tropical gorgonians (Lewis et al., 1992) and to aragonite structures in deep-sea scleractinia (Sorauf, 1972; Sorauf and Jell, 1977; Lazier et al., 1999). Both Sorauf and Jell (1977) and Lewis et al. (1992) have suggested daily periodicity of these striae. Daily banding is also known in tropical scleractinia (Risk and Pearce, 1992) and in fossil rugosan corals (Wells, 1963). Compared to the width of annual rings in *P. resedaeformis*, striae measure slightly too large to be daily. Striae may perhaps be related to currents in the tidal to 4-day frequency range (e.g.: Ramp et al., 1985; Brown, 1998), but it is difficult to establish a link.

4.3 Paleoclimatic considerations

The presence of secondary calcite precipitate would significantly hinder attempts to obtain proxy records from skeletons of *P. resedaeformis*. In some gorgonians, hollow central cords are subject to secondary mineralization (Goldberg, 1976; Lewis et al., 1992). This does not appear to be the case in *P. resedaeformis*, since the central rod is solid in the youngest branch tips and throughout the axis. Crystal fabric in the central rod demonstrates growth peripherally, except at the very nucleus, where growth occurs by a chaotic intermingling of discrete lobes. These lobes are probably primary deposits. Thus, the central rod is suitable material for obtaining a "birth date" by radiogenic means (e.g.: Andrews et al., 2002). Risk et al. (2002) warned that calcite bands present within the horny axis may be secondary. SEM shows that all the massive calcite deposited in the studied specimens in the form of incrementally deposited calcite fans (Fig. 7). Peripheral growth of these fans demonstrates primary precipitation.

Gorgonians exhibit great plasticity in growth and morphology in response to changes in their microhabitat and metabolism (Wainwright and Dillon, 1969; Grigg, 1972). This likely explains the poor correspondence of annual ring widths in five colonies examined here (Fig. 8); heterogeneous inter-colony growth rates (Coma et al., 1998b) probably swamp regional environmental effects. In tropical gorgonians, coenenchyme is known to retract up-axis with increasing age of the colony or when conditions become unfavourable to growth. With renewed favourable conditions, coenenchyme may migrate down-axis and deposit new skeleton. Certain parts of the axis may be subject to further necrosis (Feingold, 1988) or predation (e.g.: Harvell, and Suchanek, 1987; Brazeau and Lasker, 1992). In specimens of *P. resedaeformis* from the NE Channel, the basal reaches of some colonies were without coenenchyme and encrusted with filamentous fungi, ascidians or sponges. Some of the very old specimens show prominent dark stains in the outer calcite cortex that may be death surfaces (Fig. 2A). Serial geochemical data will be complicated by this fact, and the interpretation of these records should require comparison of records from several adjacent colonies. Although cross dating by means of ring widths was unsuccessful, prominent bands in the skeleton, like the dark band that appears to have been formed in 1976 in NE Channel specimens, and likely the unique geochemical signatures contained within, will serve as useful benchmarks in these endeavours.

The presence of three scales of periodic growth in *P. resedaeformis* presents an exciting new avenue for research in paleoceanography. Use of these corals may generate records of ocean climates from all latitudes and all depths over many hundreds of years with annual, or better, temporal resolution. Furthermore, the two-part nature of the skeleton means that stable isotope profiles from the proteinaceous fraction may augment coeval trace element profiles from the carbonate fraction (Heikoop et al., 1998; 2002). Future work includes looking for geochemical evidence of unique climatic events in specimens from the NE Channel, such as the documented storm tides of 1869, 1759 and 1976 (Desplanque and Mossman, 1999) and episodic warm water (Brooks, 1987) and cold-water incursions associated with the North Atlantic Oscillation Index (Colton, 1968; Petrie and Drinkwater, 1993; Marsh, et al., 1999).

5. CONCLUSIONS

1. Specimens of *P. resedaeformis* collected from the NE Channel exhibit three scales of incremental growth apparently related to current variability at seasonal, lunar and tidal frequencies.

2. Young specimens can be aged with relative ease. Due to poorly discernable growth rings in the outer calcite cortex and possible death/re-growth surfaces, age estimates of

old (>50 years) specimens should be validated by radiometric methods. Heterogeneous inter-colony growth rates probably obviate cross-dating of individuals by annual ring widths. A prominent dark ring that appears to have been formed in 1976, however, is present in several of the studied specimens. Rings like this may serve as useful benchmarks in sclerochronology.

3. Results presented here confirms recent work (Heikoop et al., 2002) suggesting that *P. resedaeformis* is a potential source of high-resolution proxy data with unprecedented global coverage.

PART TWO:

North Atlantic Oscillation record from skeletal Mg/Ca in the deep-sea gorgonian coral *Primnoa resedaeformis*

ABSTRACT

Primnoa resedaeformis is a deep-water gorgonian coral with worldwide distribution and a lifespan of at least several hundred years. Recent work has suggested that it may be possible to obtain extended, high-resolution records of ambient conditions from the annually-secreted rings in axial skeletons of *Primnoa*. In this paper, Mg/Ca and Sr/Ca are measured by laser ablation ICP-MS in the predominantly calcite axial cortex. Specimens were collected live from the Northeast Channel, Southwest of Halifax, from depths of 300-500m. Across the 0.5^0C gradient, Mg/Ca is correlated to temperature. Sr/Ca also increases with temperature, but this may be explained by the influence of Mg/Ca on Sr partitioning, and possibly other factors, rather than temperature. Near-annual resolution profiles of Mg/Ca are consistent within and among different colonies having different growth rates. Conversion of Mg/Ca profiles to temperatures using a provisional calibration [Mg/Ca (mmol/mol) = 4.88(+/- 1.09)T(^{0}C) + 70.92 (+/-6.79)] yields a range of values and trends consistent with the observational data. The North Atlantic Oscillation (NAO) is responsible for a significant component of inter-annual temperature variability in the Scotia-Maine region. Mg/Ca records from older corals could therefore provide extended proxy records of the NAO.

1. INTRODUCTION

High-resolution proxy records are critical in paleoceanography. Reef corals are useful since chemical tracers in their carbonate skeletons provide continuous records of ambient conditions over hundreds of years (e.g.: Cole et al., 1993; Beck et al., 1997; Hendy et al., 2002). Similar data from deep, azooxanthellate corals may extend the range of these re-constructions worldwide (Griffin and Druffel, 1989; Druffel et al., 1990, 1995; Smith, 1997a; Risk et al., 2002; Heikoop et al., 2002). Previous work has focused primarily on the deep scleractinian coral *Desmophyllum cristigalli.* Using stable isotopes, Smith et al. (1997b) found evidence of rapid change in deep-water ventilation during the Younger Dryas. Similar work on *D. cristigalli* used Cd/Ca and paired ^{230}Th-^{14}C dates to track deep-water ventilation (Adkins et al., 1998; Mangini et al, 1998; Goldstein et al., 2001).

Despite these advances, high-resolution proxy records from deep corals remain elusive. Smith et al. (1997b, 2002) showed that paleo-temperatures from δ^{18}O are rendered unreliable by strong kinetic disequilibria. A technique based on the correlation between δ^{13}C and δ^{18}O overcomes this problem, but it is analytically time-consuming (Smith et al., 2000). Some researchers are now turning to elemental ratios, such as Sr/Ca, which appear to be less susceptible to kinetic partitioning in azooxanthellate corals (Cohen et al., 2002). The timing of skeletal banding patterns in *D. cristigalli* also remains unclear (Lazier et al., 1999). Additionally, the requisite testing of the fidelity of proxy records is usually impossible owing to the lack of instrumental data where deep corals are found.

There has been recent interest in deep corals living off Nova Scotia (Scott et al., 2002). Diverse communities of gorgonian corals and associated fauna live along the shelf break to depths of 500m or more (Breeze, 1997). One of the common gorgonians, *Primnoa resedaeformis*, has a life span of at least several hundred years (Risk et al., 2002). Potential to obtain paleo-records (Heikoop et al. 2002) has generated interest in the nature and timing of skeletal banding in *Primnoa* (Risk et al., 2002; also see Part One). The younger, horny axis is composed of concentric rings, about 200 microns wide, alternating in the proportion of gorgonin to calcite. Finer laminae within the rings may reflect the semi-monthly periodicity of tidal currents. Older parts of the skeleton are stiffened with a cortex of dense calcite in the form of spherulitic crystal bundles oriented radially. Bounding surfaces of the crystal bundles delineate faint concentric rings, also around 200 microns wide, that are only barely visible (i.e.: Fig. 3C, Part One). Radiometric age validation with ^{210}Pb-^{226}Ra (Andrews et al., 2002) has confirmed the interpretation (Risk et al., 2002) that the concentric rings in the horny axis and cortex are annual.

Few studies have concerned the geochemistry of calcite octocorals. Heikoop et al. (2002) showed that $\delta^{18}0$ in *Primnoa* may be dominated by growth-related kinetic isotope effects. Sr/Ca may also reflect growth rate (Heikoop et al., 2002). Weinbauer et al. (2000) reported similar findings on the Mediterranean gorgonian *Corallium rubrum*. It is known from experiments on inorganic calcite that Sr partitioning depends on precipitation rate and the concentration of Mg in the precipitate (e.g.: Mucci and Morse, 1990; Carpenter and Lohmann, 1992). Thus, Sr/Ca is an unlikely source of proxy environmental data in *Primnoa*. On the other hand, Mg/Ca in *Primnoa* calcite reflects temperature, and a preliminary calibration has been determined (Heikoop, unpublished). The slope of this calibration parallels other empirical calibrations from a variety of different octocoral species (Chave, 1954; Weinbauer and Velimirov, 1995; Weinbauer et al., 2000). Skeletal Mg/Ca is also governed by Mg/Ca of seawater (Velimirov and Bohm, 1976), but open-ocean residence times of these elements are > 10^6yrs, and compositions would have remained constant over the Holocene (Broeker and Peng, 1982). There is no evidence to link Mg/Ca with growth rate (Weinbauer et al., 2000), despite the observation that Ca and Mg are transported to the sites of calcification via different pathways that may respond differently to physiological influence (Kingsley and Watabe, 1985). In general, the above findings parallel temperature dependent partitioning of Mg in inorganic calcite (Mucci, 1987; Oomori, 1987; Mucci and Morse, 1990).

Studies using foraminifera (Rosenthal et al. 1997; Mashiotta et al., 1999; Elderfield and Ganssen, 2000), mussels (Klein et al., 1996) and ostracodes (Chivas et al., 1986) establish precedent for Mg/Ca paleothermometry. Field and culturing experiments with foraminifera have demonstrated that shell Mg/Ca is regulated primarily by temperature (Lea et al., 1999) although factors such as salinity, pH, and the presence of gametogenic calcite (Nurnberg et al. 1996; Lea et al., 1999) may distort the relationships. The purpose of this paper is to compare Mg/Ca and Sr/Ca in live-collected specimens to assess the feasibility of obtaining paleotemperatures from *Primnoa*. First, Mg/Ca and Sr/Ca are compared within and among different colonies to determine if they respond to factors other than temperature. Second, profiles of Mg/Ca and Sr/Ca obtained with laser ablation ICP-MS (LA-ICP-MS), a relatively new technique for high spatial resolution analysis of solids *in situ* (e.g.: Sinclair et al., 1998), are compared with instrumental temperature over the last thirty years.

2. HYDROGRAPHIC SETTING

Specimens were collected from the NE Channel, 200-500m deep, separating Browns and Georges Banks, southeast of Halifax (Figure l). Advection forces slope water, either cold Labrador Slope Water or Warm Slope Water, into the NE Channel and the Gulf of Maine (Gatien, 1976). Regional-scale episodes of cooling/freshening (up to 4°C and 0.6ppt at 200m depth) are related to increased southwestward flow of the Labrador Current around the tail of the Grand Banks (Petrie and Drinkwater, 1993; Loder et al. 2001; Drinkwater et al., in press). These episodes appear to follow the North Atlantic Oscillation (NAO) with a lag-time of 1-2 years (Marsh et al., 1999; Drinkwater et al., in press). The NAO, which describes the movement of atmospheric mass between the Azores high and the Iceland Low, modulates the production of Atlantic mode waters that drive the thermohaline circulation (e.g.: Dickson et al., 2002). The NE Channel is therefore an ideal setting to study Mg/Ca temperature-dependence in Primnoa: inter-decadal temperature variability exceeds everywhere else in the North Atlantic at that depth (Levitus, 1989); and proxy temperature/NAO records that extend the range of instrumental data would be profoundly significant to our understanding of anthropogenic climate change.

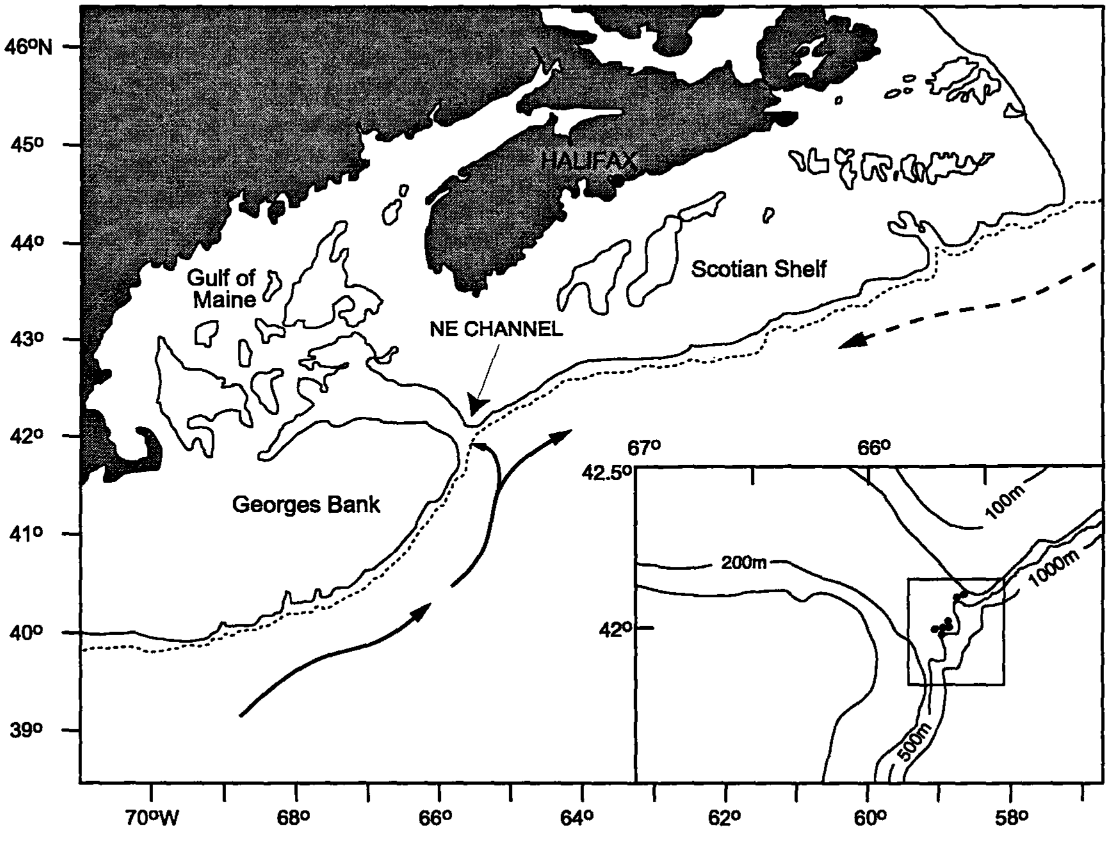

Figure 1. The Gulf of Maine region, with schematic trajectories (200m depth) of Warm Slope Water (solid arrows) and Labrador Slope Water (dashed arrow) under conditions of low deep Labrador current transport (adapted from Drinkwater et al., in press). The 200m and 1000m isobaths are depicted by solid and broken lines, respectively. Inset shows locations of of*Primnoa* collection and temperature data retrieval grid.

3. METHODS

3.1 Instrumental temperature data

Temperature data were accessed online from the Marine Environmental Data Service of Fisheries and Oceans Canada (http://www.mar.dfo-mpo.gc.ca/science/ocean/database/data-query.html). Temperature statistics were retrieved from the 0.35^0 by 0.40^0 grid centered at 41.98^0N/65.10^0W, from 200 to 500m in depth (Fig.1, inset). Unfortunately, timeseries data >300m were incomplete. To obtain a complete timeseries at 450m, the 300m data were scaled by the difference in climatological mean temperature between 300m and 450m.

3.2 Specimen collection and preparation

Colonies of *Primnoa* were collected from depths of 250-500m with long-line fishing gear (August 2000) or by the remotely operated submersible *ROPOS* (August 2001). The Bedford Institute of Oceanography provided an additional specimen, collected with video grab apparatus (July 2001). Details are listed in Table 1. Specimens were scraped clean of adherent tissue, rinsed in freshwater and left to air dry for several months. All measurements were performed on axial cross sections taken from near the base of the colony.

3.3 Age determination

Axial cross sections expose concentric rings in the different growth zones (Figure 2). In the horny axis, age may be determined by visual counting of the annual rings, as in dendochronology or otolith ageing (Andrews et al., 2002; also see Part One). Greater

Table 1. Summary of collection details, growth rates and elemental composition of colonies of *Primnoa*. Range of Mg/Ca and Sr/Ca reported as percentages.

Specimen	Lat(°N)/Lon(°W)	Depth(m)	Growth rate (mm/yr)	Mg/Ca (range) (mmol/mol)	Sr/Ca (range) (mmol/mol)	n**
HH2000-4 [a]	42.050/65.583	450	.150	97.26 (20)	3.260 (13)	21
HH2000-11 [a]	42.050/65.583	450	.165	99.60 (23)	3.196 (32)	36
COHPS2001-1 [b]	~42.00/~65.55	378	.090*	103.15 (21)	3.204 (22)	89
COHPS2001-2 [b]	~42.00/~65.55	378	.115*	102.96 (17)	3.311 (12)	63
R637052 [c]	42.047/65.577	474	.160	99.91 (11)	3.097 (12)	11
R639009 [c]	41.983/65.633	410	.370*	99.09 (23)	3.252 (43)	73
R640013 [c]	41.988/65.633	423	.130	100.35 (11)	3.124 (16)	12
HUDVg-15 [d]	42.017/65.667	321	n/a	105.59 (10)	3.300 (4)	6

Samples collected by: [a] Fishermen, Aug. 2000 and [b] 2001;
[c] ROPOS, Aug. 2001; [d] DFO cruise, Jul. 2000
* Dated by $^{210}Pb_{ex}$, all others by visually counting annual rings
** Number of laser ICP-MS spot analyses

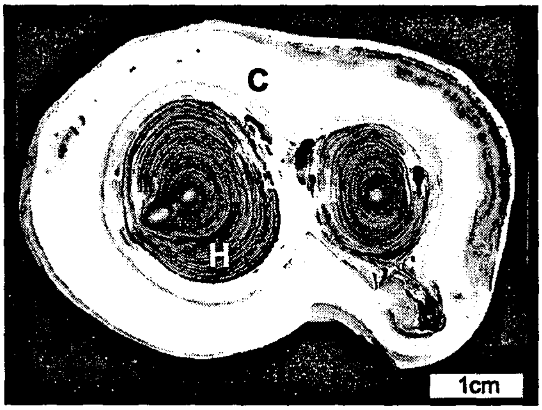

Figure 2. Axial section of Primnoa, showing horny axis (H) and calcite cortex (C).

ambiguity of rings in the cortex renders counting more difficult. In some specimens, an average annual growth rate may be estimated from the widths of rings in the calcite (and adjacent discontinuous horny layers if they are present; i.e.: Fig. 2b, Part One). In other cases, the growth rate may be determined by measurement of ^{226}Ra -^{210}Pb (e.g.: Druffel et al., 1990; Andrews et al., 2002).

Radiometric analyses were carried out a GEOTOP, Montreal, Canada. Measurement of ^{210}Pb was done by alpha spectrometry of its daughter product, ^{210}Po, while ^{226}Ra was measured by thermal ionization mass spectrometry with isotope dilution. Axes were sectioned into 15mm-thick slabs and sub-samples were cut parallel to the growth increments (Figure 3a), and crushed in an agate mortar. Powder was oxidized in peroxide held at pH 8 by addition of ammonium hydroxide, washed with de-ionized water and dried at 60°C. The cleaned powder was weighed into a teflon beaker, along with suitable amounts of ^{209}Po and ^{228}Ra spikes, and dissolved in 100ml 0.5N HCl. A silver disc mounted on a Teflon post was immersed in the solution, which was stirred and heated to 90^{0}C for 5 hours. Under these conditions, Po self deposits on the silver disc. Counts of ^{209}Po and ^{210}Po were measured in a EG&G 576 spectrometer (Flynn, 1968). Radium was isolated from the remaining solution. First, Ra, Ba, Sr and Ca were co-precipitated with MnO_2. Radium and Ba were purified with cationic exchange resin (50W-X8). Radium was then purified with Sr Spec resin (Andrews et al., 1999). The final Ra fraction was loaded onto Re filaments with 1 µl of Ta-HF-H3PO4 activator, and analyzed with a VG-54 mass spectrometer. Precision is better than 0.5% on the isotopic ratios.

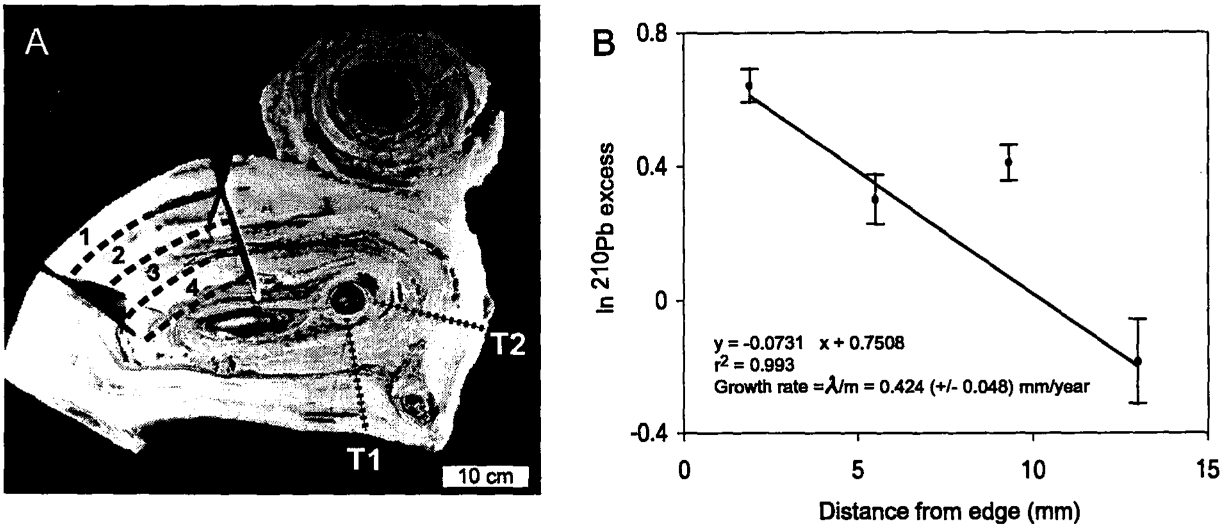

Figure 3. (A) Basal section taken from specimen R639009. Samples (1-4) cut parallel to growth lines were measured for ^{210}Pb and ^{226}Ra (Table 2). Also shown are the locations of transects (T1 and T2) used to generate Mg/Ca profiles. (B) Plot of natural log transformed values of unsupported lead ($^{210}Pb_{ex}$) versus distance from edge of skeleton. Error bars are 1σ. Contamination by additional ^{210}Pb is suspected in sample 3 (see Table 3), so it was excluded from the regression. Calculation of the growth rate (0.424mm/yr) follows Andrews et al. (2002).

Table 2. Summary of radiometric analysis of specimen R639009. Errors (in brackets) are 1σ

Sample	Distance from edge (mm)	^{210}Pb (dpm/g)	^{226}Ra (dpm/g)	$^{210}Pb_{ex}$ (dpm/g)
1	1.9	2.005 (+/-.085)	0.1026 (+/- .012)	1.9024 (+/- .097)
2	5.5	1.462 (+/- .088)	0.1088 (+/- .014)	1.3532 (+/- .102)
3	9.3	1.605 (+/- .074)	0.0983 (+/- .008)	1.5067 (+/- .082)
4	13	0.927 (+/- .098)	0.0955 (+/- .015)	.8315 (+/- .113)

Results of radiometric determinations on specimen R639009 are listed in Table 2. Calculation of the growth rate involves plotting natural log transformed values of unsupported Pb ($^{210}Pb_{ex}$) against distance, and dividing the decay constant by the slope of the line of best fit (Figure 3b; Andrews et al., 2002).

3.4 ICP-MS techniques

3.4.1 Cleaning

Sections of *Primnoa* (3mm thick) were cleaned of organic and authigenic ingrowths prior to elemental analysis. 1) Oxidative leaching used a bath of concentrated lithium hypochlorite (commercial swimming-pool shock chemicals). The sections were left in the bath, held at 90°C, for one week with periodic ultrasonic agitation and rinsing. 2) Sections were rinsed in milli-Q water then triply agitated (10 min each) and rinsed in 0.1% HNO3 (trace metal grade) to remove authigenic phases. 3) Sections were then triply agitated (20 min each) and rinsed in milli-Q water. The cleaned sections were epoxy-embedded (Beuhler Epothin), polished to 1-micron relief and finally agitated and rinsed in milli-Q water to remove polishing residues.

3.4.2 LA-ICP-MS analysis

Mg/Ca and Sr/Ca were measured by LA-ICP-MS at the Department of Geological Sciences, Queen's University, Canada. The setup consists ofa 213nm U.V. laser (New Wave LUV) and a magnetic-sector ICP-MS (Finnigan Element). Analytical parameters are listed in Table 3. Spot analyses with a 100 micron diameter beam were taken 200 microns apart, along radial transects of axial cross sections. The laser produced "clean " pits, with minimal deposition around the crater rim. Pit depths were less than one half the pit diameter.

Data acquisition involved monitoring for ^{25}Mg, ^{43}Ca, ^{44}Ca, ^{86}Sr and ^{87}Sr in low resolution mode. Background counts were measured before each spot analysis and subtracted. Counts were normalized to ^{43}Ca to correct for difference in ablation yield. After completing a transect, repeats were measured adjacent to the first three spots as a check on drift. Standardization using NIST SRM 612 followed that of Arrowsmith (1987) and Feng (1994). Calculation of instrumental response (count rate divided by elemental concentration) used the concentrations given in Pearce et al. (1997). Ca concentration in coral was calculated from calcite stoichiometry. Ca response in NIST612 and calcite differed by a factor of 5. The difference, called matrix effect, arises from the differences in the physical properties of the two materials (e.g.: Morrison et al., 1995). Since data are reported as elemental ratios, rather than absolute abundances, no attempt was made to correct for matrix effect.

Reproducibility, determined from repeat spot analyses of coral within two days (repeat spots were parallel to the growth layers, positioned as close to the originals as possible without overlapping) was 2.5% for Mg/Ca and 6% for Sr/Ca (Table 4).

3.4.3 Solution analysis

As a check on the accuracy of LA-ICP-MS, and to perform additional measurements, solution analyses were made on a quadrupole ICP-MS (PE Elan 6000) at

Table 3: Laser and ICP-MS parameters

Laser: New-Wave LUV		**ICP-MS:** Finnegan Element	
Type:	Nd:YAG	Type:	Magnetic sector
Pulse rate:	2 Hz	Mode:	low resolution, peak jumping
Beam diameter:	100-200 microns	Aquisition delay:	30 sec.
Power:	0.8mJ	Replicates:	20
		Scan time:	15 sec.

Table 4. Reproducibility of paired LA-ICP-MS measurements made within 2 days. Average difference and range are listed as percentages

Ratio	Average difference	Range	n
Mg/Ca	2.5	0.07 - 7.3	14
Sr/Ca	5.8	0.1 - 16.7	14

Table 5. Comparison of laser and solution ICP-MS analyses performed on adjacent skeleton. Average difference and range are listed as percentages. Laser Mg/Ca data are scaled by 0.73 to correct for analytical bias.

Ratio	Average difference	Range	n
Mg/Ca	1.9	0.1 - 7.3	24
Sr/Ca	3.6	0.4 - 11.4	25

the School of Geography and Geology, McMaster University. Powder samples (~0.1mg) were obtained from the same cleaned sections used in laser sampling with a computerized micro-milling machine (Merchantek). The samples were dissolved in 2% nitric acid (trace metal grade) in polyethylene vials and diluted following standard procedures. ^{24}Mg, ^{44}Ca and ^{88}Sr were analyzed on the same aliquots. External calibration used gravimetric standards (Plasmachem). Reproducibility, based on the standard deviation of repeated analysis of calibrated solutions, is approximately 1.5% for Mg/Ca and Sr/Ca.

Comparison of laser and solution ICP-MS measurements made along parallel transects reveals a systematic offset in values of Mg/Ca. Considering the matrix problem inherent to standardizing laser data with NIST 612 (e.g.: Morrison, 1995), the solution values are considered more accurate. Scaling the laser Mg/Ca data by 0.73 (the average offset) brings the values to within 2% of the solution values (Table 5). The Sr/Ca values match to within the analytical error without scaling.

3.4.4 Contaminants

Preliminary tests showed that Mg/Ca in the horny layers were 2-3 times greater, and more variable, than in the cortex. This was not the case for Sr/Ca. The source of higher Mg/Ca was thought to derive from the presence of organic Mg in the gorgonin, and the cleaning routine described in section 3.3.1 was employed to remove it. After a week in hot bleach, however, oxidation would visibly penetrate only about 1-2mm into the surface of the skeleton and Mg/Ca values in the horny layers did not lower. It is unclear if cleaning was insufficient, or if calcite associated with the horny layers has higher lattice-bound Mg content. In any case, the calcite and gorgonin are so intimately admixed (Risk et al., 2002; also see Part One) that it is probable that more rigorous cleaning involving crushing (e.g.: Shen and Boyle, 1988) is required for Mg/Ca analysis of the horny layers. Subsequent analyses were limited to the cortex, assuming that organic inclusions would be negligible in that zone.

Embedding resin was checked for potential to contaminate the coral skeleton with additional Mg, Sr or Ca. A laser spot analysis showed that levels of these elements within the resin were at or below background levels and therefore did not pose a contamination problem (also see Allison, 1995). To check if use of lithium hypochlorite would bias Mg/Ca or Sr/Ca, a section of *Primnoa* was subjected to the routine described in section 3.3 .1 without the oxidative leach. Five samples were milled randomly from the surface of the cortex. The section was cleaned again with oxidation and another five samples, adjacent to the first set, were collected. Analysis by solution ICP-MS revealed no differences in Mg/Ca and Sr.Ca between the two treatments. Thus, the oxidative leach does not appear to introduce a bias to Mg/Ca or Sr/Ca measurements in the calcite cortex.

4. RESULTS

4.1 Evaluation of the method

Table 1 lists bulk compositional values in the different colonies of *Primnoa*. Measurements by LA-ICP-MS are averages over at least ten years' worth of cortex (except specimen HUDVg15 where only about 2 years of cortex was present). Average values agree with previous measurements made on *Primnoa* with an ion microprobe (Mg/Ca ~ 100 mmol/mol; Heikoop, unpublished; Sr/Ca ~ 3.12; Heikoop et al., 2002). The average within-colony range of Mg/Ca and Sr/Ca is about 20%, well in excess of the reproducibility of both laser (2.5% and 5.8%; Table 4) and solution ICP-MS (~1%) techniques. Between-colony variation (~ 7% for both Mg/Ca and Sr/Ca) is smaller, but still within analytical resolution.

4.2 Assessment of elemental heterogeneity

Elemental heterogeneity was examined by taking samples at intervals around the circumference of a contemporaneous growth surface. Analysis by solution ICP-MS (each sample represents an amount of skeleton equal to ~3years) yielded standard deviations of 1.3% for Mg/Ca and 6% for Sr/Ca (n=6). The larger value for Sr/Ca, representing around one third of within-colony variation, suggests that timeseries profiles taken along skeletal transects will be unreliable.

Mg/Ca and Sr/Ca were also compared with estimates of the skeletal growth rate, but there were no significant relationships of either elemental ratio with this parameter (Table 1). In particular, specimen R639009, which had a growth rate twice that of any of the other colonies, had Mg/Ca and Sr/Ca values that were equivalent to other colonies growing at that depth.

4.3 Bulk Mg/Ca and Sr/Ca

Within the defined geographic grid (Figure 1, inset), temperature from 200-500m,

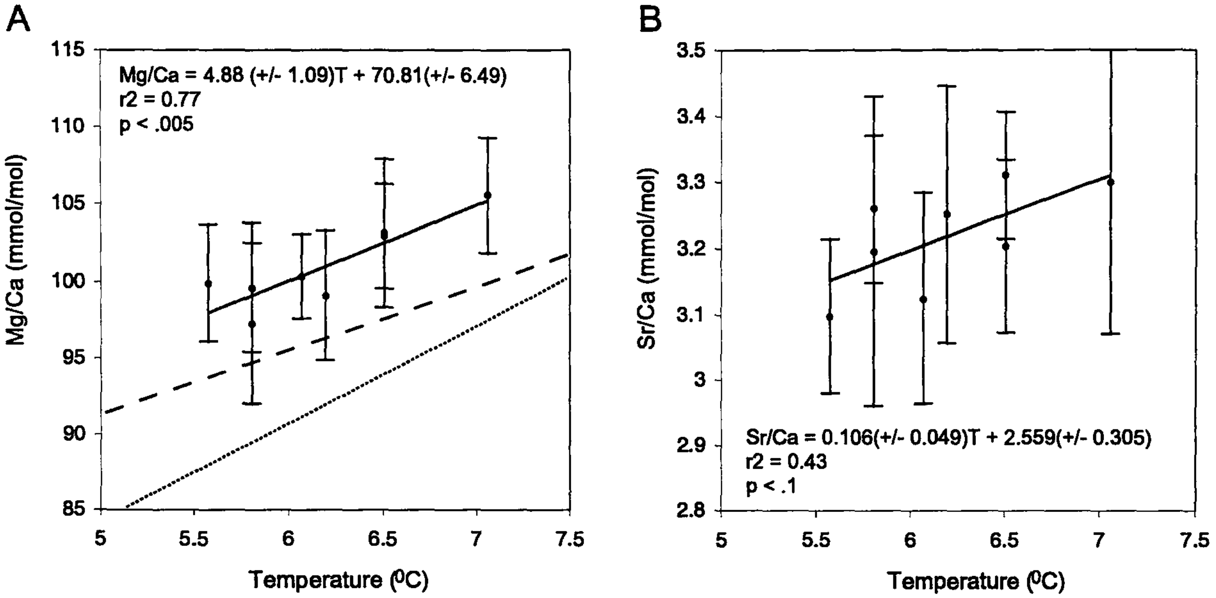

Figure 4. Relationship with temperature of bulk Mg/Ca (A) and Sr/Ca (B) in the cortex of eight different colonies of *Primnoa*. Error bars are 1σ from total number of laser spot analyses on each coral Additional lines in (A) are Primnoa calibrations from Heikoop (unpublished): dashed line, temperature data from World Ocean Atlas, 1998; dotted line, some Levitus 1994 data used instead. See Table 6 and text for explanation.

Table 6. Comparison of the temperature dependence of Mg/Ca (mmol/mol) in octocorals established in this and some other empirical studies.

Slope,	Intercept	Temp.range (^{0}C)	Species	Reference
4.88(+/- 1.09)	70.81(+/- 6.79)	5.5-7.1	*P. resedaeformis*	this study
4.12	70.79 [a]	6-9.5	*P. resedaeformis*	Heikoop (unpub.)
6.42	52.15 [b]			
5	40	13-16	*Corallium rubrum*	Weinbauer et al.(2000)
4.35	7.71	16-21	various	Weinbauer and Velimirov (1995)
3.35	62.42	0-25	various	Chave (1954)

[a] temperature data from World Ocean Atlas 1998
[b] some Levitus 1994 data used instead

decreases linearly at the rate of 0. 97^{0}C per 100m. Mean ambient temperature may therefore be calculated at the depths where each of the colonies lived. Bulk Mg/Ca values are correlated with temperature (Figure 4a) by the relationship:

$$\mathrm{Mg/Ca\ (mmol/mol)} = 4.88(+/\ 1.09)\mathrm{T}(^{\circ}\mathrm{C}) + 70.92(+/\ 6.79)$$

$$r^2 = .78,\ p < 0.005$$

where the 95% confidence intervals are in brackets. Though provisional, the relationship roughly parallels calibrations by Heikoop (unpublished) covering a 4^{0}C temperature range (Table 6; see discussion). Sr/Ca is also correlated with temperature, and is significant at the 90% level (Figure 4b).

4.4 Timeseries profiles

Mg/Ca profiles taken along radial traverses of the cortex are shown in Figure 5a. Data are from only those colonies having a covering of live coenenchyme at the time of collection; it is therefore assumed they were actively depositing calcite until then. Profiles generated from other corals are not included since it could not be determined when calcite deposition ceased. Chronology of each profile was established independently by applying a linear growth rate, calculated from either ^{210}Pb$_{ex}$ measurement (R639009; Figure 3b) or from the average width of annual rings counted in thin section (R637052, HH2000-11; see Part One, Figure 3C). Profiles R639-T1 and R639-T2 were taken on different sides of the same axial section of specimen R639009 (see Figure 3a). R639-T1 was measured by LA-ICP-MS at a resolution of about 2 samples per year. R639-T2 was measured with solution ICP-MS at a resolution of about 1.5 samples per year for the first half of the series and one sample every 2 years for the

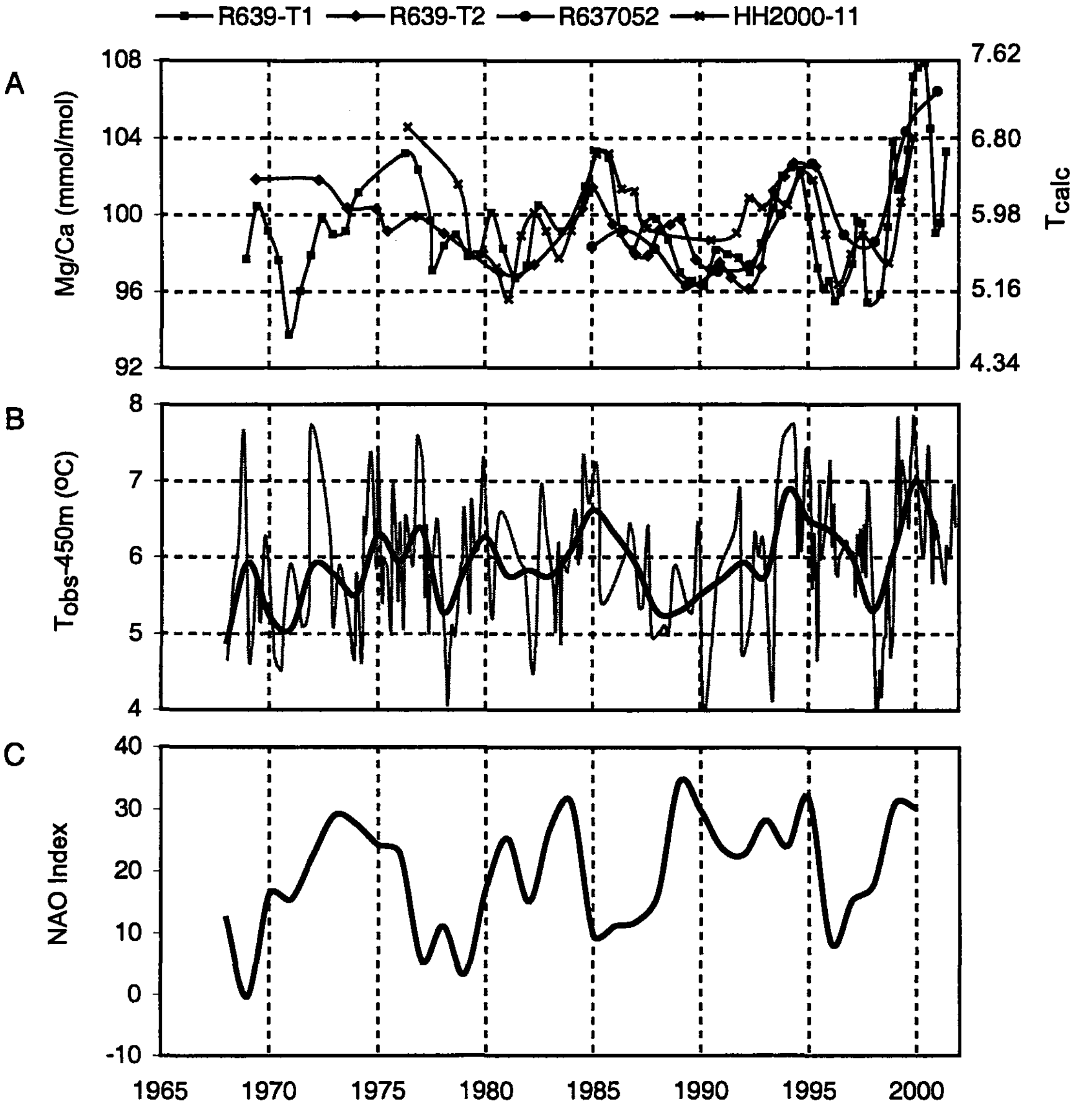

Figure 5. A) Mg/Ca profiles, smoothed with a 3-yr running mean, from live-collected specimens. Chronology established independently by $^{210}Pb_{ex}$ (R639), or by visual counts of annual rings in thin section (R637052, HH2000-11). R639-T1 and R639-T2 measured on the same axial cross section by laser and solution ICP-MS, respectively (see Fig. 3A). T_{calc} (right-hand axis) used calibration of this study. **B)** Temperature data from NE Channel at 450m. Grey line, raw data; black line, smoothed with 3-yr running mean. **C)** NAO index.

second half of the series. The other two profiles were measured by LA-ICP-MS at resolutions of 1.5 samples/yr (HH2000-11) and 0.7 samples/yr (R637052). Once smoothed (a 3-year running mean was chosen more or less arbitrarily), all the profiles closely match, thus demonstrating consistency of Mg/Ca within and among colonies.

A significant amount of noise is evident in each profile. By "stacking" profiles together (Fig. 5a), the correspondence with observed temperature improves. Lower Mg/Ca values track cold spells around 1971, 1981-1983, 1988-1993 and 1998, and higher values track the warm years in-between. Conversion of Mg/Ca to temperature (T_{calc}), using the calibration established above, yields a range of temperatures consistent with the observed data (T_{obs}). Using timeseries software (Paillard et al., 1996), the smoothed profiles were re-sampled at even 1-year increments to perform regression analysis. A plot of T_{calc} *vs.* T_{obs} is significant; a slope of <1 may be explained by a combination of noise, smoothing, and data filtering (Figure 6).

5. Discussion

5.1 Mg/Ca

The findings support the hypothesis that Mg/Ca in *Primnoa* calcite would reflect ambient temperature. The Mg/Ca *vs.* temperature calibration (Figure 4a) is significant over a range of only 1.5°C. Since bulk Mg/Ca values integrate at least ten years of skeleton, it can be assumed that they are good approximations of the climatological mean. The one exception to this, specimen HUDVg15, had only 2 years worth of cortex, but removing this value does not change the relation. The slope lies close to the average 5

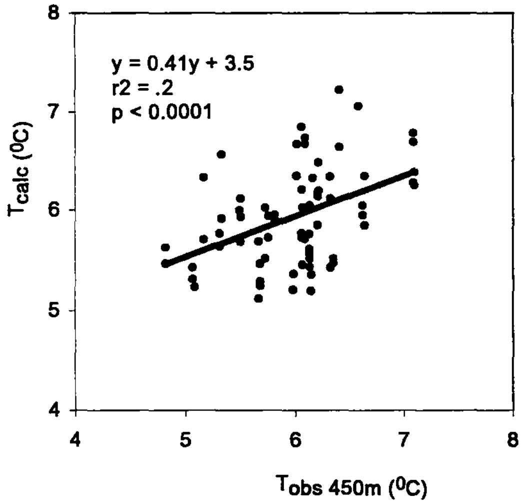

Figure 6. Temperatures calulated from timeseries Mg/Ca data (T_{calc}) shown in Fig. 5a, plotted against instrumental temperature (T_{obs})at 450m. Data resampled at even, 1 year increments

mmol/mol per °C established in some earlier empirical calibrations (Table 6). Noteworthy is that fact that empirical calibrations in deep-water species rely on temperature data that may have been extrapolated over large amounts of space and time. Indeed, the two different calibrations by Heikoop (unpublished) depend on whether temperatures at the collection sites were estimated from World Ocean Atlas (1998) or with some values from Levitus (1994) instead, which had better coverage over continental slope areas but poorer quality control (Heikoop, pers. comm.). By comparison, the temperatures used in the present study are more tightly constrained, but the range is smaller. For a given value of Mg/Ca, this calibration predicts a temperature 1-1.5°C cooler than that of Heikoop (unpublished); the offset may be due to bias introduced by analysis by ion microprobe *vs.* LA-ICP-MS. Given the limitations, the present calibration is provisional, but encouraging. Future work should focus on the collection of live specimens over a wider depth/temperature gradient with high-precision measurement of Mg/Ca by isotope dilution ICP-MS (e.g. Lea et al., 1999).

Correspondence of Mg/Ca profiles obtained from within and between corals having different growth rates (Figure 5a) supports the idea that temperature is the primary control on skeletal Mg/Ca. Noise and scatter in profiles (Figure 5a) could arise from analytical uncertainty, presence of residual organic contamination in the cortex, or factors, besides temperature, influencing Mg/Ca. Weinbauer et al. (2000) found no relationship between Mg/Ca and skeletal density in the axes of *C. rubrum*. Certainly, work on inorganic calcites has shown that Mg/Ca is not influenced by precipitation rate (Mucci and Morse, 1983; Mucci et al., 1985; Zhong and Mucci, 1989). Thus, it is unlikely that differences in crystal "growth" within the calicoblastic epithelium would account for the noise in Mg/Ca. Salinity, pressure, and physiological transport mechanisms are aspects worth the consideration of future studies.

5.2 Sr/Ca

Heikoop et al. (2002) found a weak negative correlation between Sr/Ca in *Primnoa* and temperature. The results here demonstrate a weak, positive relationship with temperature (Figure 4b). Sr/Ca in abiotic (Mucci and Morse, 1983) and biotic calcites (Carpenter and Lohmann, 1992) increases linearly with Mg/Ca content. Mucci and Morse (1983) explain this by an increase in lattice deformities induced by incorporation of smaller Mg cations; neighboring cells accommodate a greater proportion of larger ionic radius Sr. In *Primnoa*, Sr/Ca is positively correlated with Mg/Ca at both within-colony and between-colony levels (Figure 7). Therefore, increasing Sr/Ca with temperature observed in *Primnoa* may, in part, reflect increasing Mg/Ca. The correlation is weak, suggesting that factors such as kinetic partitioning of Sr (Heikoop et al., 2002) may also affect Sr/Ca.

5.3 Paleoceanographic potential

When Mg/Ca profiles from the three different colonies are smoothed and stacked, the overall trend through time offers a reasonably good approximation of instrumental temperature. Over an amplitude of about 2.5°C, calculated temperatures at any time in the stacked series are within 1°C of observed temperatures. This is not the case for individual profiles, due to noise. Increasingly, researchers are turning to multi-proxy/multi-record climate reconstructions with corals (e.g.: Hendy et al., 2002). With

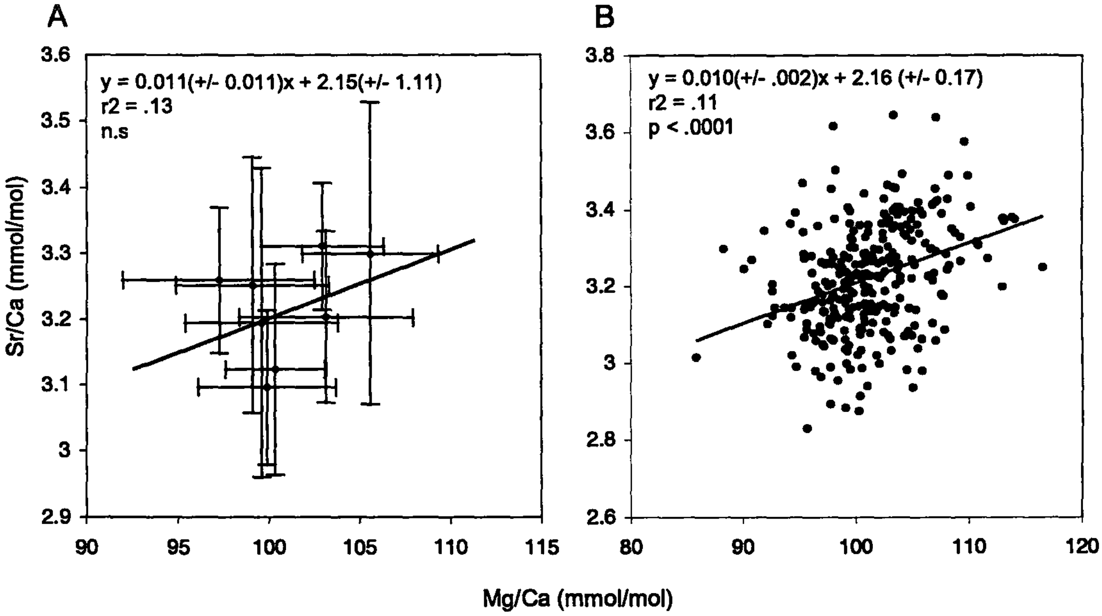

Figure 7. Plot of Sr/Ca versus Mg/Ca between colonies (A) and within colonies (B). Error bars in A are 1σ, brackets in equations are the 95% confidence intervals.

techniques used in this study, reliable temperature reconstructions at interannual-interdecadal scales could be obtained from multiple colonies/profiles of *Primnoa* (at least three).

Low NAO-index phases lead to a weakening of cold westerlies over the Labrador Sea and a warming and strengthening of the southwestward Labrador Current. Downstream in the Scotian Shelf/Gulf of Maine region, the front separating cold Labrador Slope Water from Warm Slope Water migrates south, and the region cools (see Drinkwater et al., in press). Over the period 1969-2000, the NAO went through four high-low index phases (Figure 5c). Similarly, Mg/Ca profiles in *Primnoa* exhibit 4 warm-cold phases that lag the NAO by 1-2 years (Figs. 5a-c). Because of the mechanistic link between NAO and temperature, Mg/Ca data faithfully record the inter-annual variability in NAO over the last 30 years.

It has already been suggested that *Primnoa* may be a valuable archive of proxy oceanographic data (Heikoop et al., 1998; Heikoop et al., 2002; Risk et al., 2002; Part One). The findings reported here suggest that Mg/Ca in the skeletons of fossil *Primnoa* will be a useful monitor of inter-annual changes in bottom temperatures far into the past. The significance of this finding is emphasized by the fact that other monitors of bottom conditions are limited to a temporal resolution of a few centuries in only the very best cases. Data on past deep-ocean circulation is a gaping hole in our knowledge; recent observations provide evidence that deep convection in the Labrador Sea, an important component of the global heat budget, can fluctuate at the scale of a few years (e.g.: Sy et al., 1997; Dickson et al., 2002). Particularly in the Scotian Shelf/Gulf of Maine region, the link between NAO and temperature means that proxy records from *Primnoa* will help to elucidate fundamental aspects of the coupled ocean-atmosphere climate system. Worldwide distribution of these organisms offers the possibility of reconstructing a number of mid and deep-ocean processes throughout the Quaternary.

6. CONCLUSIONS

1. Mg/Ca in the calcite cortex of *Primnoa* increases linearly with temperature. A provisional calibration established here confirms recent work by Heikoop (unpublished). We anticipate that high-resolution ICP-MS analyses of specimens collected over a greater depth-temperature range will constrain the calibration.

2. Timeseries Mg/Ca data from three recently collected colonies having different growth rates are consistent within and among each other. Stacked profiles track the instrumental temperature variability at that depth, thus establishing the fidelity of Mg/Ca as a temperature proxy. As a consequence of the link with temperature, extended proxy records of the NAO are possible.

3. Sr/Ca is positively correlated with temperature and also with Mg/Ca. The relationship with Mg/Ca may be consistent with the lattice-deformity hypothesis where higher Mg/Ca contents in calcite favour increased partitioning of Sr (Mucci and Morse, 1983), though other factors may influence Sr/Ca.

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APPENDIX: PUBLICATIONS

Sherwood OA, Risk MJ and Pearce TH (2001) Patterns of skeletal banding in the deep-water octocoral *Primnoa resedaeformis*. Eleventh Canadian Paleontology Conference, Sept. 22-24, 2001, London, Ontario, Program and Abstracts, 11:44

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Sherwood OA and Risk MJ (2002) North Atlantic Oscillation record from deep-sea corals. Geochim Cosmochim Acta 66: A706 (abstr.)