A technical report to the Monterey Bay National Marine Sanctuary

Investigations of bamboo coral age and growth from Davidson Seamount

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Abstract

Estimates of age and growth for bamboo coral (*Keratoisis* spp.) have been difficult to determine and only a few of these estimates had an actual temporal context. In this study, two bamboo coral colonies were collected from Davidson Seamount and analyzed for age and growth using lead-210 dating. The findings from both colonies converged on a radial growth rate of approximately 0.055 mm/yr. The calculated age of each colony was 89 years (range of 74-106 years) for a colony that stood 70 cm tall, and 145 years (upper limit of 450 years) for a large colony with irregular shape and height. Linear extension rates for each colony varied considerably with a range of 0.093 to 1.0 cm/year between the two colonies, which may indicate that linear growth rates are unreliable as an indicator of colony age.

Introduction

Deep-sea corals can provide high-relief habitat that is ecologically diverse and intrinsically valuable (McDonough and Puglise 2003, Friewald et al. 2004, Freiwald and Roberts 2005). These coral habitats are often inhabited by assemblages of invertebrates and fishes that are unique (Heifetz 2002, Husebo et al. 2002, Rogers et al. 2007). The value of the deep-sea environment created by corals is often related to some form of benefit to man, like essential fish habitat, but it should also be considered important from a perspective of world heritage because these living habitats are very fragile (Willison et al. 2001). Once these communities are disturbed or removed many of the corals and the habitat they create will not recover within our lifetime (e.g. Andrews et al. 2002). With many fish stocks on the decline, there is increasing utilization of deep-water habitat for fishing purposes. The impact to corals by fishing activity is increasing worldwide and has been devastating in some cases (Auster and Langton 1999, Clark and Koslow 2007). It is essential that these habitats, especially those that have not been impacted, be identified, conserved, and studied in more detail before irreversible damage occurs (NOAA 2007).

Information about the life history of habitat-forming corals, such as age, growth, and longevity, is necessary before their sensitivity and importance can be fully understood. Age determination studies to date have found that deep-sea corals can attain ages that are on the order of tens to

hundreds to perhaps thousands of years (e.g., Andrews et al. 2002, Adkins et al. 2004, Love et al. 2007). Age and growth of deep-sea corals can typically be determined from outgrowth studies in the field, growth zone counts in the skeletal structure, radiometric techniques (e.g. lead-210 dating), or a combination of these techniques.

Some deep-sea coral species can be aged by counting growth zones in skeletal structures using axial cross sections (Grigg 1974, Andrews et al. 2002, Risk et al. 2002, Marschal et al., 2004, Thresher et al. 2004, Roark et al. 2005, Sherwood et al. 2005); however, establishing a temporal context is essential for these estimates to be useful in understanding the biology of the organism. Several radiometric methods are available for confirmation of growth zone counts, which can also be used to establish growth rates that are independent of zone counts. Thresher et al. (2004) found good agreement between zone counts in a *Keratoisis* sp. using two radiometric schemes and Roark et al. (2005) used bomb radiocarbon ($\Delta^{14}C$) to independently measure growth rates for bamboo corals.

Lead-210 dating is a technique that uses the radioactive decay of lead-210 as a natural chronometer that can reveal estimates of age and growth. How this process works begins with the natural incorporation of lead-210 from seawater into the coral skeleton. As the coral grows like a tree, laying down growth rings, the radioactivity of lead-210 decreases from the youngest (outer edge) to the oldest (center) material of the skeleton. The reason lead-210 activity decreases is because it slowly decays away (radioactive decay) at a known rate (half-life of 22.26 years). To measure this change in radioactivity and relate it to age, a series of samples are taken from the edge to the center of a skeletal cross section. By taking this series of lead-210 measurements, the decrease of lead-210 activity can be used to determine the age and growth of the deep-sea coral (Druffel et al. 1990). This approach is useful to about 100 years of age at which time the activity of lead-210 decreases to background or supported levels (Figure 1).

Ages were estimated in a recent study of bamboo coral from Davidson Seamount (Andrews et al. 2005). The results from various growth zone counting interpretations led to a wide range of estimated age. For a cross section 8 to 11 mm in radius, estimates of 80 to 220 years were determined for the bamboo coral colony. Support for the older age estimates prevailed based on

a series of lead-210 dating samples taken in that study. This line of work has been further applied to other species of bamboo coral from New Zealand and related to possible indicators of ocean climate change (Neil et al. In Press, Tracey et al. In Press).

In the current study, additional specimens were collected from Davidson Seamount in 2006 to better refine estimates of age using fine scale lead-210 dating. The aim of the collections was to obtain two relatively large bamboo coral colonies of the same species from two different locations to determine if growth differed between locations. In addition, a series of upper limbs or tip portions from colonies within and between various locations were collected with an arbitrary target number of approximately 30 samples. The purpose was to compare growth and potential environmental markers in the growth structure between and within sites; however, this portion of the study was abandoned for reasons discussed here. As is often the case with deep sea studies, ideal collections were not realized. Discussed in this report are: 1) the results of sample collections and its affect on the proposed study; 2) the successful application of fine scale lead-210 dating to two colonies of bamboo coral; and 3) continued support for, and refinement of, findings in the previous study (Andrews et al. 2005).

Materials and Methods

Specimen collection and identification

Bamboo coral specimens were collected from Davidson Seamount during surveys made January 26 to February 4, 2006. Two full bamboo coral colonies were collected using the ROV *Tiburon* from the R/V *Western Flyer* toward the end of surveys on February 2-3 for the purpose of applying lead-210 dating (Table 1). Collection of the colonies from the chosen locations was more opportunistic than the plan to collect from habitats that appeared to have favorable or unfavorable growth conditions; fewer stands of bamboo corals were encountered than anticipated. Colony T948-A2 (Figures 2 & 3) and colony T950-A10 (Figure 4) were both classified as *Keratoisis* sp. based on the branching pattern observed with the ROV. In addition to these specimens a third colony that was collected in 2002 (T428-A10) from Davidson Seamount was used in this study (Table 1); a preliminary analysis was performed on this specimen for Andrews et al. (2005) and it was added to this study for reasons that will be presented in the

results and discussion. The bamboo coral colony was similar in appearance to T948-A2 and was also identified as a *Keratoisis* species (T428-A10; Figure 5).

Specimens were stored frozen until used for age determination and specific identification. Coral specimens were identified to genus by taxonomists specifically studying bamboo corals. Specimens were provided to Dr. Les Watling (University of Hawaii at Manoa) and Dr. Scott France (University of Louisiana at Lafayette) for a future role in a plan to monograph the subfamily Keratoisidinae.

Growth and environmental marker comparisons

An attempt was made to collect approximately 30 branch-tip segments from within and between individual colonies with a standard length (~30 cm) from different bamboo coral sites. Only 11 tips were collected during the surveys because there were fewer locations visited than expected where bamboo corals were present. These branch-tip segments were examined after collection and found to be inadequate for the kind of analysis originally proposed. Most of the segments were in poor condition because of their fragility; most were broken into pieces and had large sections missing. Among those segments that may have been used for this purpose, there was no consistency in length or skeletal diameter that could be used to provide a reference for growth between locations. It was proposed that the segments would be cross sectioned in at least one location (at a set distance from the tip) and examined for growth zone patterns, but most had damage or loss that made this impossible to do; hence, no sections were made and the attempt to discern patterns between sites was abandoned.

Lead-210 dating

Radial sampling of skeletal cross sections was chosen over sampling along the axis of the colony because length or height was highly variable throughout the colonies collected. For each colony, a section of the skeletal structure was chosen near the base of the colony. The sections were cut in cross-section and mounted to glass slides for sample extraction using a New Wave® micromilling machine (Figure 6). Serial samples were extracted using a 0.5 mm bit, beginning at the exterior edge and progressing to the center, along a path that followed the radius of the section. Eight concentric paths were taken from a single section that was from colony T428-

A10. A series of thinner sections were necessary for colony T948-A2 because of its small diameter. Eight radial samples from a series of six thin (~2 mm) sections were extracted to provide sufficient sample from each radial path (Figure 7). Target sample weight was no less than 0.02 g per sample to reduce count times and the margin of error during alpha-spectrometry based on previous activity observations.

The decay of exogenous (unsupported) lead-210 across the radius of the skeletal structure was used to determine a growth rate. For samples with age that exceeded the utility of this method (about 100 years), the use of lead-210:radium-226 equilibrium was used to establish limits to calculated growth rate uncertainty. Lead-210 was measured via alpha-spectrometry of its daughter product polonium-210, and radium-226 was measured directly by counting atoms on an inductively-coupled plasma mass spectrometer (ICPMS). The specifics of determining lead-210 and radium-226 activities were based on a previously established protocol that is described elsewhere (Andrews et al. 1999, Andrews et al. 2002, Lundstrom et al. In Prep.).

Results

Specimen collection and identification

The bamboo corals collected were, at the time of collection, thought to be the same species (based on video observations); however, it was apparent that the colonies were very different upon closer inspection (Figure 8). While both have branching that occurs at the calcified nodes, colony T950-A10 was a much more robust colony with a deeper color. The polyp and branching arrangement was dense, polyps were longer, and the coenenchyme held together once thawed, maintaining a rather spongy texture. Colony T948-A2 was much more fragile and very light in color. The branching arrangement was spindly, polyps were smaller and more widely spaced, and the coenenchyme rapidly dissolved as the specimen thawed, turning to slime in minutes.

Dr. Les Watling and Dr. Scott France examined and compared the two samples collected in 2006 (T948-A2 and T950-A10) with a number of other specimens on hand. They focused on gross polyp morphology, within-polyp distribution, and density of each sclerite type, in concert with genetic data to date as a guide. They determined where each specimen grouped out based on the

phylogeny with respect to these morphological characters, and will later determine if the predictions hold once genetic sequencing is performed. Based on the brief analysis, they concluded that both colonies would be classified under current nomenclature in the genus *Keratoisis*, and appear to be related to different species in genetic clades B1 (T950-A10) and D1 (T948-A2). Specimens similar to T950-A10 have been collected by them from Aleutian Ridge, Gulf of Alaska. Specimen T428-A10 collected in 2002 was not made available for analysis.

Lead-210 dating

Inspection of colony T950-A10 resulted in an elimination of this specimen from the lead-210 dating because of its condition. The basal portion of this colony had an unusual shape that was explained by removing the coenenchyme (Figure 9). The skeletal matrix appeared to indicate the colony had a rather traumatic history; the colony had been broken into pieces, survived, and overgrown the numerous bits and chucks of broken skeleton. There was no clear way of sampling the scrambled matrix for lead-210 dating.

It was for this reason, coupled with apparent species differences, that the colony initially analyzed (T428-A10) in Andrews et al. (2005) was further examined in this study. Use of this colony provided additional information built on the findings of the previous study. In the previous study, lead-210 and radium-226 were measured in thick basal portions of the skeletal structure and in a younger section toward the tip of the colony. In the basal portion of the colony, activity ratios were near equilibrium, indicating the colony was more than 100 years old. In the younger section, whole skeletal segments were measured for lead-210 activity; activity decreased from the tip segment to the older segments. The combined findings indicated exogenous lead-210 was present in the skeletal system and that lead-210 dating could be applied when a careful extraction technique was developed.

The acquisition of a micromilling machine made this possible, and as a result a section was selected from T428-A10 for further analysis. The segment selected for analysis was one that measured 15 mm in diameter and was very nearly cylindrical. Extracted samples resulted from a series of 8 concentric extractions, ranging from the edge to the center, which provided enough

material for measurable activities (Table 2). Each radial path of extracted material was ~1 mm wide, with the exception of D02-1 and D02-3 which were ~0.5 mm wide.

Colony T948-A2 was smaller than T428-A10 and it was necessary to try a different approach to acquire enough mass from each radial sample. Colony T948-A2 had a small base that was fractured as a consequence of removal from the base rock. Because of this it was necessary to move further up the colony to obtain a segment that was cylindrical. The diameter of the first uninterrupted internode was 7.6 to 8.3 mm through the central part of the segment, with slightly enlarged ends (near the nodes), and a length of 47-52 mm (calcified portion only). Because the radius was on the order of 4 mm and getting 8 samples would require an extraction path of ~0.5 mm, the decision was made to cut the center of the internode segment into a series of sections just under 2 mm thick. This allowed for extraction of 8 radial samples from each section that could be added together to increase the sample mass for a given radius. Six of these cross sections, each of which had 8 radial samples removed, resulted in 48 separate micro-samples that ranged in mass from 0.00327 g in the center to 0.02994 g near the edge.

The first set of 8 samples was produced by pooling each radial sample from the first 6 extractions (radius 1-6) from sections A-C (Figure 7). The 2 radial extractions near the center (radius 7 and 8) were very small and it was necessary to pool from all 6 cross sections (A-F) to attain enough mass (greater than ~0.02 g). As a result, there were 8 radial samples from this segment, with a replicate for radial extractions 1-6. Analysis of the 6 replicate samples from the other 3 cross sections (D-F) is still in progress and will be appended at a later date for inclusion in a peer reviewed scientific journal. Reported here are the 8 radial samples completed to date (Table 2).

Radium determinations were similar to the findings of the previous study, but more refined (lower error). Activities were measured with a relatively high degree of uncertainty in Andrews et al. (2005); measured values were 0.190 ± 20 % and 0.266 ± 8.0% at two locations in colony T428-A10 with an average of 0.228 ± 0.054 dpm/g. Measurements for this study were from T948-A2 and were relatively consistent (0.247 ± 0.059 dpm/g; n = 3). The overall average for these samples was 0.239 ± 0.041 dpm/g (n = 5), but the average of the three most recent runs was

used because of the lower margin of error (~3%). As with the replicate lead-210 samples for T948-A2, additional radium-226 samples will be appended at a later date for inclusion in a peer reviewed scientific journal.

Lead-210 dating age and growth

Lead-210 dating provided continued support for the findings of previous studies performed on bamboo corals from Davidson Seamount. Lead-210 data from colony T428-A10 provided fairly well constrained slope that resulted in a radial growth rate of 0.041 mm/yr (0.025 to 0.12 mm/yr 95% CI; Figure 10). The growth rate data for this portion of the colony translated to an age of 180 years (60 to 310 yr 95% CI). This age and growth information was based on a regression of 6 out of 8 data points. Two data points were not included for different reasons. The center sample (D02-8) had an elevated lead-210 activity (0.3250 ± 11%) relative to the steady decline observed in the previous radial samples. This has been observed in other bamboo corals and may be the result of some kind of secondary deposition within the tubular core of the skeleton (Tracey et al. In Press). The other sample (D02-7) was near equilibrium with radium-226 (0.247 ± 0.059 dpm/g), indicating the age of this portion of the section was on the order of 100 years old (samples on the slope or decline of lead-210 activity can be used for determining a growth rate; Appleby and Oldfield 1992). Given this sample, located at an average radius of 5.5 mm, was approximately 100 years old, a limit can be applied to the uncertainty of the calculated growth rate (Figure 11). Rates more rapid than 0.055 mm/yr are unlikely because sample D02-7 would not have been in equilibrium. Hence, the minimum age of this section is near 136 years (Table 4). Given the calculated growth rate, a decay plot revealed the general conformity of the lead-210 activity series to the expected decay curve (Figure 12).

In concert with the findings for T428-A10, colony T948-A2 provided a well-constrained slope that resulted in a radial growth rate of 0.063 mm/yr (0.056 to 0.073 mm/yr 95% CI; Figure 13). The growth rate data for this portion of the colony translated to an age of 70 yr (60 to 79 years 95% CI). This age and growth information was based on a regression of 7 out of 8 data points. The excluded sample was at the outer edge (D06-1) because it included an unknown amount of the mounting medium (Cytoseal®). The result was reduced lead-210 activity (1.2848 ± 12% dpm/g) relative to the next radial sample inward. The sample at the center (D06-8) was not

removed from the analysis because it did not show signs of elevated lead-210 activity from what may be occasional secondary deposition. Given the calculated growth rate, a decay plot revealed good conformity of the lead-210 activity series to the expected decay curve (Figure 14).

Because the sampled portion of colony T948-A2 was up and away from the basal section (broken during collection) by approximately 75 mm, the maximum age of this colony can be estimated from the measured diameter of the base (10.8 – 11.7 mm). Using the calculated growth rate (0.063 mm/yr) and the average radius (5.63 mm) an age of 89 years was calculated for this colony, with a potential age range of 74 to 106 years based on the range of radii and growth rates (Table 4). In addition, use of in situ measurements from lasers separated by 29 cm a maximum height of approximately 70 cm was determined for this colony, which was verified with the intact collected specimen. Based on the age range and this measured height, assuming the longest axis is representative of consistent axial growth though the life of the colony, the linear extension rate of this colony may have been 0.7 to 1.0 cm/yr. This result must be considered a maximum possible rate because of the assumptions stated above.

Discussion

The subfamily Keratoisinae, most commonly encountered in the deep sea, has a global distribution and is in great need of taxonomic revision. Use of the samples from Davidson Seamount in the exploration of morphological and genetic characteristics of this group will provide a greater geographical representation and a broader context for the subfamily revisions and descriptive biogeographical patterns.

The reanalysis of the bamboo coral colony collected in 2002 (T428-A10) provided a temporal context to age and growth estimates made from growth zone counts (Andrews et al. 2005). The basal portion of this colony had a measured radius of 8 to 11 mm, which led to an estimated age for the section of 80 to 220 years. The basis for this determination was using growth rates estimated from growth zone counts that were not well defined (0.05 - 0.11 mm/zone). Based on the refined information presented in this study, the age of this colony had a lower limit of approximately 145 yr based on the growth rate limits provided by the sample in equilibrium

(0.055 mm/yr). The 95% CI for the lead-210 determination provided a colony age of up to 450 yr for the lowest growth rate (0.025 mm/yr; 95% CI).

Based on the findings of this study, a linear growth rate calculated for the colony collected in 2002 (T428-A10) could also be reanalyzed (Andrews et al. 2005). The estimated age for a second section (5.6 - 6.5 mm radius) taken from the colony, that was at a distance of 24.5 cm from the basal section, was 56 to 131 years, based once again on growth rates from growth zone counts. Translating the extremes of estimated ages to a linear growth rate resulted in an estimate of 0.19 to 0.44 cm/year. The results from the range of growth rates presented here (0.025 – 0.055 mm/yr) provided a linear growth rate that was similar (0.24 cm/yr) to much lower (0.093 cm/yr) than initially calculated from growth zone counts. As stated previously, however, linear extension rates were more subjective than radial growth because losses or changes in colony growth cannot be accounted for.

Because both colonies (T428-A10 and T948-A2) are presumably the same species, it is possible to consider the growth rates for each colony together as either a way to hone in on a more accurate growth rate for these colonies or as a representation of the potential range of growth rates. When considering the growth of the larger colony collected in 2002 (T428-A10) relative to the growth of the smaller colony collected in 2006 (T948-A2), it is possible that the average growth rate was greater for the smaller colony. The difference in growth rates could be due to a slowing of growth with age. In support of this was the calculated linear extension growth rate of 0.7 to 1.0 cm/yr for the smaller colony (T428-A10); however, the height of the colony was highly variable and any loss of branches, changes in growth direction, and addition of branches by the colony cannot be accounted for. Roarke et al. (2005) provided data that suggest the contrary in that growth may have been greater for larger colonies, presumably because larger colonies are more efficient at collecting food. Alternatively, the data provided in this study could indicate radial growth is consistent throughout the life of this species and is approximately 0.055 mm/yr (based on the convergence of growth rate limits for the two colonies studied here).

Relative to other studies on bamboo corals, the findings presented here are similar and continue to provide support for extreme longevity in this group of corals. Although species were not

specifically known (deemed members of Family Isididae), bamboo corals studied from Warwick Seamount in the Gulf of Alaska using bomb radiocarbon dating revealed ages from 64 ± 4 yr to 208 ± 42 yr for samples that had a cross section radius of 5.7 to 20.1 mm (Roarke et al. 2005). Radial growth from that study was 0.05 ± 0.01 to 0.16 ± 0.01 mm/yr. For a bamboo coral taken off New Zealand (*Lepidisis* sp.), lead-210 dating resulted in a measured a growth rate of 0.18 ± 0.02 mm/yr (Tracey et al. In Press). In a unique study, a fossil bamboo coral skeleton (Family Isididae) was collected off of New Zealand that provided a colony age of 305 ± 30 years using the difference between radiocarbon dates determined for the interior and exterior. The estimated radial growth rate of this colony was on the order of 10 times higher at 0.4 mm/yr (0.23–0.64 mm/yr; Noé and Dullo 2006).

Specific to *Keratoisis* spp., an analysis using lead-210 dating on a specimen collected off SE Tasmania in approximately 1000 m of water provided data that could be used to determine a radial growth rate (Thresher et al. 2004). Based on lead-210 attaining equilibrium for the inner 12 mm of a section that had a radius of approximately 19 mm (calculated from figure 1 in Thresher et al. (2004)) a growth rate of approximately 0.05 mm/yr was determined for the cross section. This determination roughly implied that the overall age of the section was on the order of 400 years and that lead-210 had reached equilibrium just prior to the last 7 mm of growth. In the present study, colony T428-A10 provided similar evidence for such an age; lead-210 had attained equilibrium at approximately 5.5 mm from the edge and provided a growth estimate of approximately 0.055 mm/yr. This growth rate was convergent between the colonies analyzed in this study and is supported by the results from the specimen taken off Tasmania; hence, a colony age estimate, based on the radius of the basal portion of the colonies and a radial growth rate of 0.055 mm/yr, of 98 to 106 years for the smallest colony (T948-A2) and 145 to 200 years for the largest colony (T428-A10) was supported.

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References

Adkins, J.F., G.M. Henderson, S.-L. Wang, S. O'Shea, and F. Mokadem. 2004. Growth rates of the deep-sea scleractinia *Desmophyllum cristagalli* and *Enallopsammia rostrata*. Earth and Planetary Science Letters 227: 481-490.

Andrews, A.H., K.H. Coale, J.L. Nowicki, C. Lundstrom, Z. Palacz, E.J. Burton, and G.M. Cailliet. 1999. Application of an ion-exchange separation technique and thermal ionization mass spectrometry to ^{226}Ra determination in otoliths for radiometric age determination of long-lived fishes. Can. J. Fish. Aquat. Sci. 56: 1329-1338.

Andrews, A.H., E. Cordes, M.M. Mahoney, K. Munk, K.H. Coale, G.M. Cailliet, and J. Heifetz. 2002. Age and growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. *In*: Biology of cold water corals. L. Watling and M. Risk. (Eds.) Hydrobiologia. 471: 101-110.

Andrews, A.H., G.M. Cailliet, L.A. Kerr, K.H. Coale, C. Lundstrom, and A. DeVogleare. 2005. Investigations of age and growth for three species of deep-sea coral from the Davidson Seamount off central California. *In*: Cold-water Corals and Ecosystems. A. Freiwald and J.M. Roberts. (Eds.) Proceedings of the Second International Symposium on Deep Sea Corals. Erlangen, Germany. September 8 - 13, 2003. pp. 965-982.

Appleby, P.G. and F. Oldfield. 1992. Application of lead-210 to sedimentation studies. *In*: M. Ivanovich and R. S. Harmon. (Eds.) Uranium-series disequilibrium: Applications to earth, marine, and environmental sciences. Claredon Press, Oxford, pp. 731-778.

Auster, P.J. and R.W. Langton. 1999. The effects of fishing on fish habitat. *In*: Fish Habitat: Essential fish habitat and rehabilitation. American Fisheries Society Symposium 22: 150-187.

Clark, M.R. and J.A. Koslow. Impacts of fisheries on seamount. *In*: Seamounts: Ecology, fisheries, and conservation. pp. 413-441. T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N.

Haggen, R.S. Santos. (Eds.) Fish and Aquatic Resources Series 12. Blackwell Publishing Ltd. Oxford, UK. 527 p.

Druffel, E.R.M., L.L. King, R.A. Belastock, and K.O. Buesseler. 1990. Growth rate of a deep-sea coral using ^{210}Pb and other isotopes. Geochim. Cosmochim. Acta 54: 1493-1500.

Freiwald, A., J.H. Fossa, A. Grehan, T. Koslow. 2004. Cold water coral reefs: Out of sight – no longer out of mind. UNEP-WCMC Biodiversity Series no. 22. 84 p.

Freiwald, A. and J.M. Roberts. (Eds.) 2005. Cold-water Corals and Ecosystems. Erlangen Earth Science Series. Springer-Verlag Berlin Heidelberg. 1243 p.

Grigg, R.W. 1974. Growth rings: annual periodicity in two gorgonian corals. Ecology 55(4): 876-881.

Heifetz, J. 2002. Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia. 471: 19-28.

Husebo, A., L. Nottestad, J.H. Fossa, D.M. Furevik, and S.B. Jorgensen. 2002. Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia. 471: 91-99.

Love, M.S., M.M. Yoklavich, B.A. Black, and A.H. Andrews. 2007. Age of black coral (*Antipathes dendrochristos*) colonies, with notes on associated invertebrate species. 2007. Bulletin of Marine Science. 80(2): 391–400.

Lundstrom, C.C., J. Glessner, Z. Zhang, F. Huang, C. Bopp, and Ianno. In Prep. Rapid, accurate and precise measurement of U-series nuclides by multicollector ICP-MS. To be submitted to Journal of Mass Spectrometry and Ion Processes.

Marschal, C., J. Garrabou, J.G. Harmelin, M. Pichon. 2004. A new method for measuring growth and age in the precious red coral *Corallium rubrum*. Coral Reefs 23: 423–432.

McDonough, J.J. and K.A. Puglise. 2003. Summary: Deep-sea corals workshop. International planning and collaboration workshop for the Gulf of New Mexico and the North Atlantic Ocean. Galway, Ireland, January 16-17, 2003. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-60, 51 p.

Neil, H., D.M. Tracey, P. Marriott, R. Thresher, A.H. Andrews, and J. Sanchez. In Press. Preliminary evidence of oceanic climate change around New Zealand over the last century: the pole-equator seesaw. Proceedings of the Third International Symposium on Deep-Sea Corals: Science and Management. University of Miami, Florida. November 28 – December 2, 2005.

NOAA. 2007. State of deep coral ecosystems of the United States: 2007. NOAA Technical Memorandum CRCP-3.

Noé, S.U., W.–Chr. Dullo. 2006. Skeletal morphogenesis and growth mode of modern and fossil deep-water isidid gorgonians (Octocorallia) in the West Pacific (New Zealand and Sea of Okhotsk). Coral Reefs 25: 303-320.

Risk, M.J., J.M. Heikoop, M.G. Snow, and R. Beukens. 2002. Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia 471: 125-131.

Roark, B.E., T.P. Guilderson, S. Flood-Page, D.B. Dunbar, L.B. Ingram, S.J. Fallon, and M. McMulloch. 2005. Radiocarbon based ages and growth rates of bamboo corals from the Gulf of Alaska. Geophysical Research Letters, LO4606 Vol. 32. 1–5 p.

Rogers, A.D., A. Baco, H. Griffins, T. Hart, and J.M. Hall-Spencer. Corals on Seamounts. *In*: Seamounts: Ecology, fisheries, and conservation. pp. 141-169. T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N. Haggen, R.S. Santos. (Eds.) Fish and Aquatic Resources Series 12. Blackwell Publishing Ltd. Oxford, UK. 527 p.

Sherwood, O.A., D.B Scott, M.J. Risk, and T.P Guilderson. 2005. Radiocarbon evidence for annual growth rings in the deep-sea octocoral *Primnoa resedaeformis*. Mar. Ecol. Prog. Ser. 301: 120-134.

Thresher, R., S.R. Rintoul, J.A. Koslow, C. Weidman, J. Adkins, and C. Proctor. 2004. Oceanic evidence of climate change in southern Australia over the last three centuries. Geophys. Res. Letter, Vol. 31, 4 p.

Tracey, D.M., J.A. Sanchez, H. Neil, P. Marriott, A.H. Andrews, and G.M. Cailliet. In Press. Age and growth of two genera of deep-sea bamboo corals (Family Isididae) in New Zealand. Proceedings of the Third International Symposium on Deep-Sea Corals: Science and Management. University of Miami, Florida. November 28 – December 2, 2005.

Willison, J.H., J. Hall, S.E. Gass, E.L.R. Kenchington, M. Butler, and P. Dougherty. (Eds.) 2001. Proceedings of the first international symposium on deep-sea corals. Ecology Action Center and Nova Scotia Museum of Natural History, Halifax, Nova Scotia. 231 p.

Table 1. Data for specimens collected and used in this study.

Specimen (year)	Depth (m)	Location	Water temp (ºC)	Salinity (ppt)	Oxygen (mL/L)	Colony mass (kg)	Observed height & width (cm)
T948-A2 (2005)	1574	35.728º N 122.713º W	2.6	34.54	1.15	0.58	70 x 50
T950-A10 (2005)	1628	35.775º N 122.669º W	2.4	34.55	1.30	1.3	43 x 30
T428-A10 (2002)	1455	35.765º N 122.702ºW	2.5	34.53	n.a.	n.a.	n.a.

Table 2. Radiometric data from the large *Keratoisis* sp. colony (T428-A10) collected in 2002 and reanalyzed in this study. Listed is the extracted sample mass and measured total lead-210 activity. Activity was determined as disintegrations per minute per gram (dpm/g) with propagated error given as a percentage (2 standard errors).

Sample number	Sample mass (g)	Lead-210 activity (dpm/g) ± 2SE
D02-1	0.0446	0.6843 ± 15%
D02-2	0.0270	0.5954 ± 8.8%
D02-3	0.0556	0.3810 ± 37%
D02-4	0.0151	0.3113 ± 10%
D02-5	0.0652	0.2950 ± 21%
D02-6	0.0260	0.2879 ± 9.1%
D02-7	0.0381	0.2555 ± 22%
D02-8	0.0306	0.3250 ± 11%

Table 3. Radiometric data from the small *Keratoisis* sp. colony (T948-A2) collected in 2006. Listed is the extracted sample mass and measured total lead-210 activity. Activity was determined as disintegrations per minute per gram (dpm/g) with propagated error given as a percentage (2 standard errors).

Sample number	Sample mass (g)	Lead-210 activity (dpm/g) ± 2SE
D06-1*	0.0361	1.2848 ± 12%
D06-2*	0.0685	1.4283 ± 9.6%
D06-3*	0.0560	1.0270 ± 17%
D06-4*	0.0549	0.8194 ± 11%
D06-5*	0.0398	0.6575 ± 13%
D06-6*	0.0304	0.5901 ± 15%
D06-7	0.0423	0.5082 ± 15%
D06-8	0.0274	0.4776 ± 17%

* Replicate sample currently being processed.

Table 4. Growth rates and estimated ages calculated for bamboo coral segments and full colonies based on lead-210 data and constrained by another factor. Lead-210 data calculations for T428-A10 did not take into consideration a minimum age determined based on lead-radium equilibrium (Figure 11). Segment age is less than colony age because the portion analyzed was located away from the base of each colony. Colony age was estimated based on the basal diameter. Linear rate (extension rate) was calculated assuming constant growth.

Colony	Calculation	Radial rate (mm/yr)	Segment age (yr)	Colony age (yr)	Linear rate (cm/yr)
T428-A10	Lead-210 data	0.041 (0.025 - 0.12)	180 (60 - 310)	-	-
	Constrained	0.055 – 0.12	136 - 310	145 - 450	0.093 – 0.24
T948-A2	Lead-210 data	0.063 (0.056 – 0.073)	70 (60 - 79)	89 (74 – 106)	0.7 – 1.0

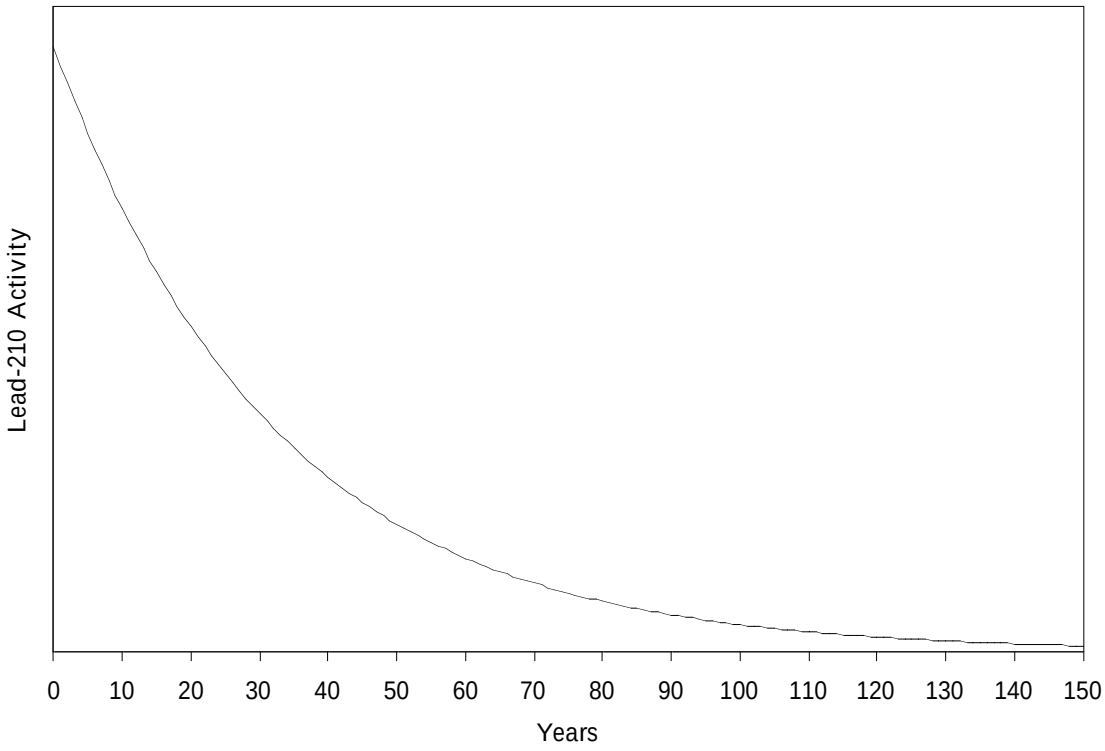

Figure 1. Diagrammatic representation of lead-210 activity from youngest to oldest material in something that may have been 150 years old. Note that lead-210 activity decays by 50% in 22.26 years (known as the half-life) and that the activity has reached a level approaching zero (if unsupported by radium-226), or some measured radium-226 activity level, at about 100-150 years.

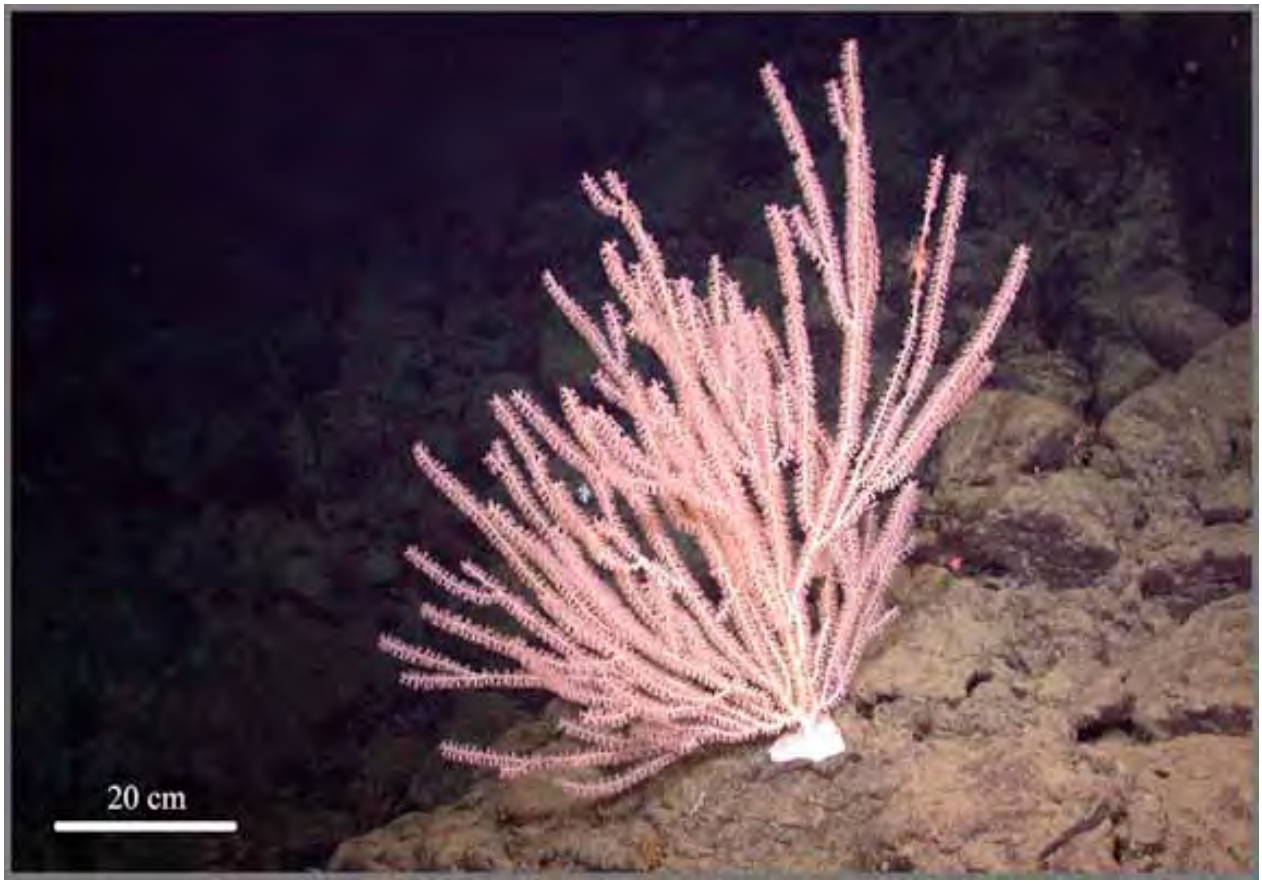

Figure 2. Bamboo coral colony (T948-A2) at 1574 m on Davidson Seamount prior to collection with the ROV *Tiburon*.

Figure 3. Bamboo coral colony (T948-A2) after collection and prior to lead-210 dating analysis.

Figure 4. Bamboo coral colony (T950-A10) at 1684 m on Davidson Seamount prior to collection with the ROV *Tiburon*.

Figure 5. Bamboo coral colony (T428-A10) at 1455 m collected during the 2002 Davidson Seamount surveys was reanalyzed in this study to build on previous lead-210 dating information (Andrews et al. 2005).

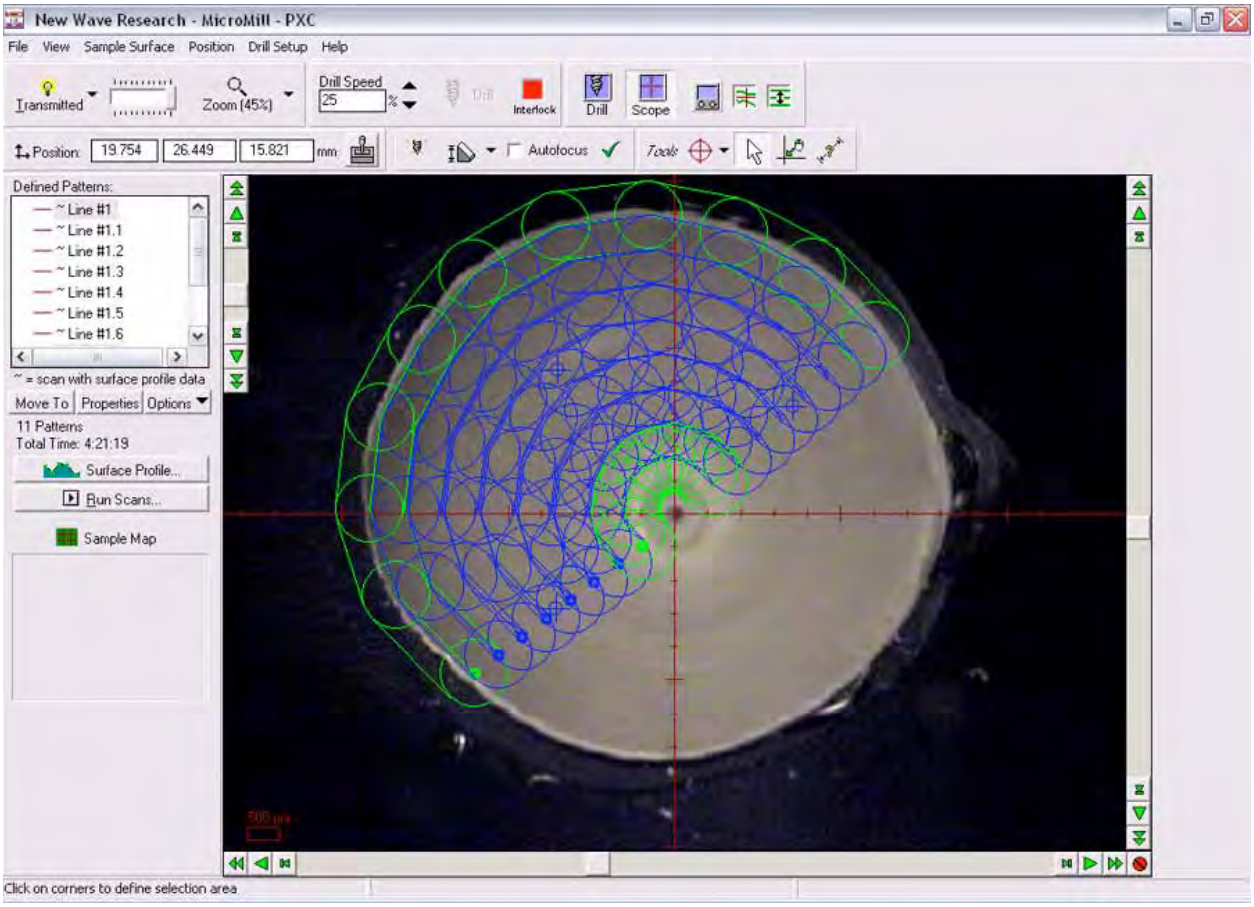

Figure 6. Bamboo coral cross section from T948-A2 that was mounted for sample extraction with the New Wave Research micromill. This computer frame grab illustrates how the software was used to delineate the extraction paths (1-8) along the radius, beginning with the edge and ending at the core. This extraction routine was performed on each section (A-F).

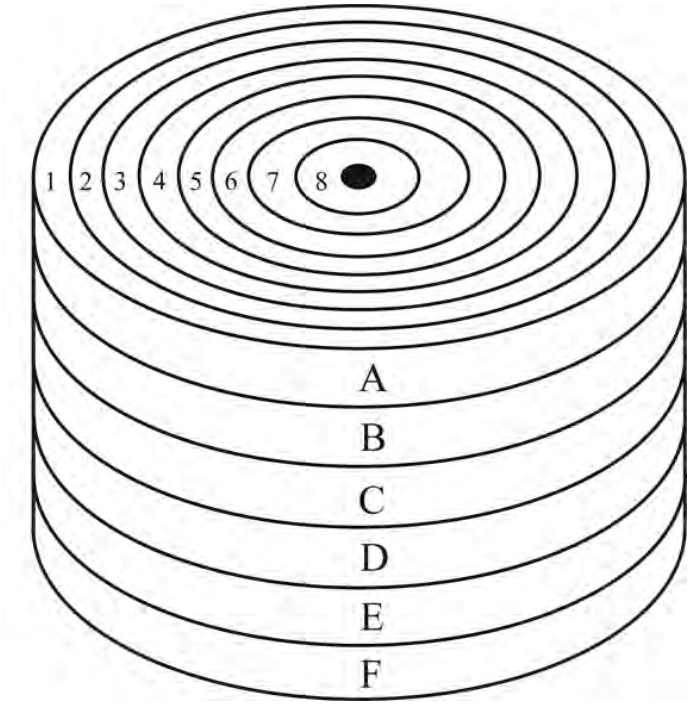

Figure 7. Diagram of the extraction sample series for bamboo coral colony T948-A10. The segment was cut into six sections (A-F). Each section was sampled successively in a radial manner with the micromill from the edge to the core. This approach was necessary because of limitations on drill bit depth.

Figure 8. Two bamboo corals collected from Davidson Seamount during the 2006 surveys. The two specimens were thought to be the same species, but based on closer examination were not. Specimen T950-A10 (on left) had a much more robust morphology when compared with specimen T948-A2 (on right). Samples from these colonies are now part of a larger study being conducted to monograph the subfamily Keratoisidinae.

Figure 9. Base and middle axial region of bamboo coral colony (T950-A10) after cleaning. The left portion was basal and attached to the rock. The portion on the right was attached to the skeletal axis of the upper part of the basal structure, creating a gnarled and knotted configuration. The configuration of this coral is evidence that this colony had been broken in many places, yet survived and grew over the fragments. Lead-210 dating was not possible because of the skeletal condition.

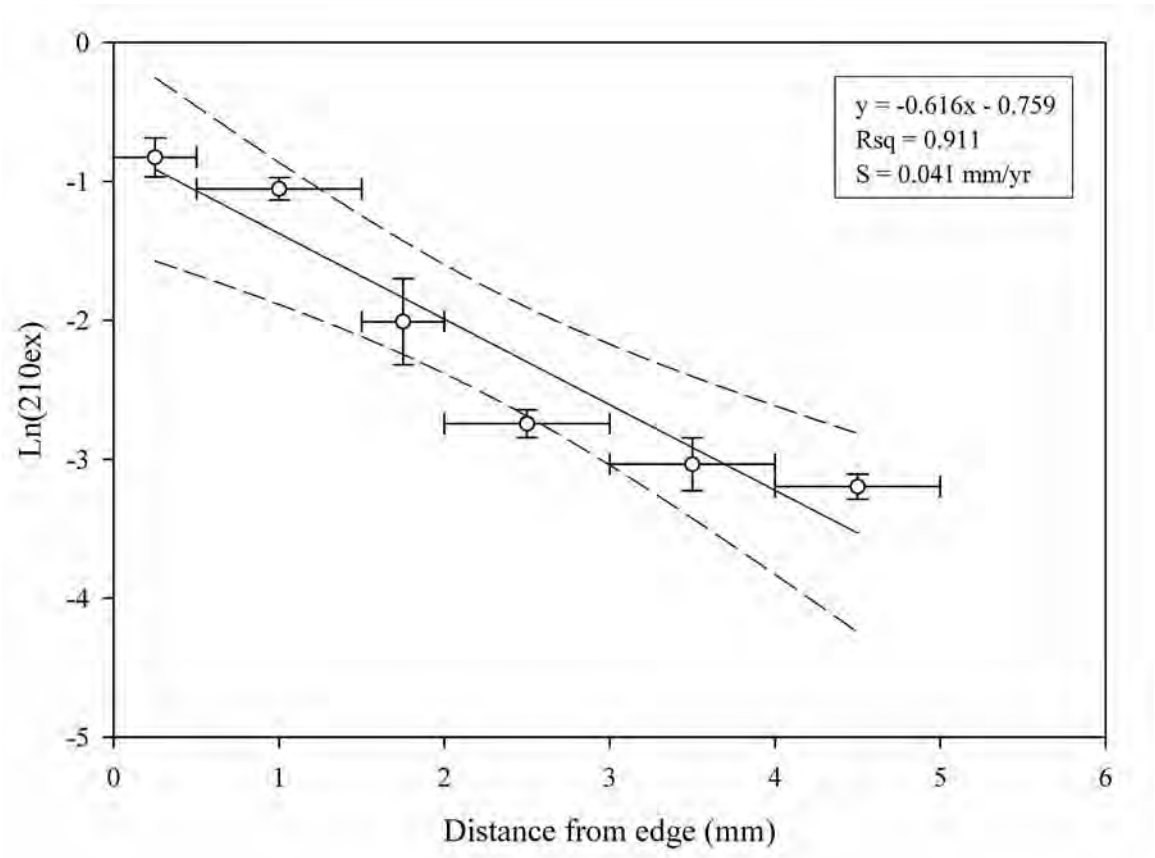

Figure 10. Plot of ln-transformed exogenous lead-210 relative to the distance from the edge for the larger colony T428-A10 collected in 2002. These data indicate the growth rate of this colony was 0.041 mm/yr (95% CI range of 0.025 – 0.12 mm/yr).

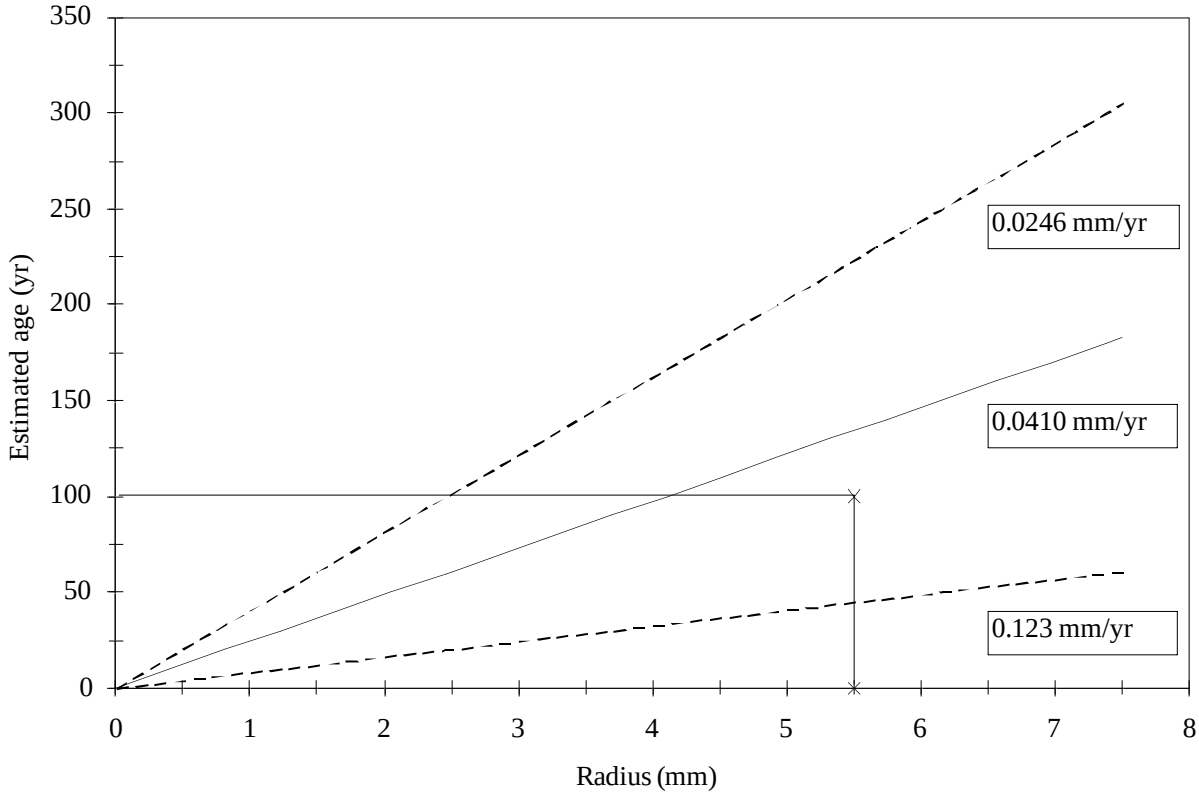

Figure 11. Range of growth rates possible for colony T948-A2 based on 95% CI from regression of ln-transformed exogenous lead-210. Based on the sample that was in equilibrium at a radius of 5.5 mm, more rapid rates can be eliminated with a maximum rate of approximately 0.055 mm/yr, assuming this sample was at least 100 years old.

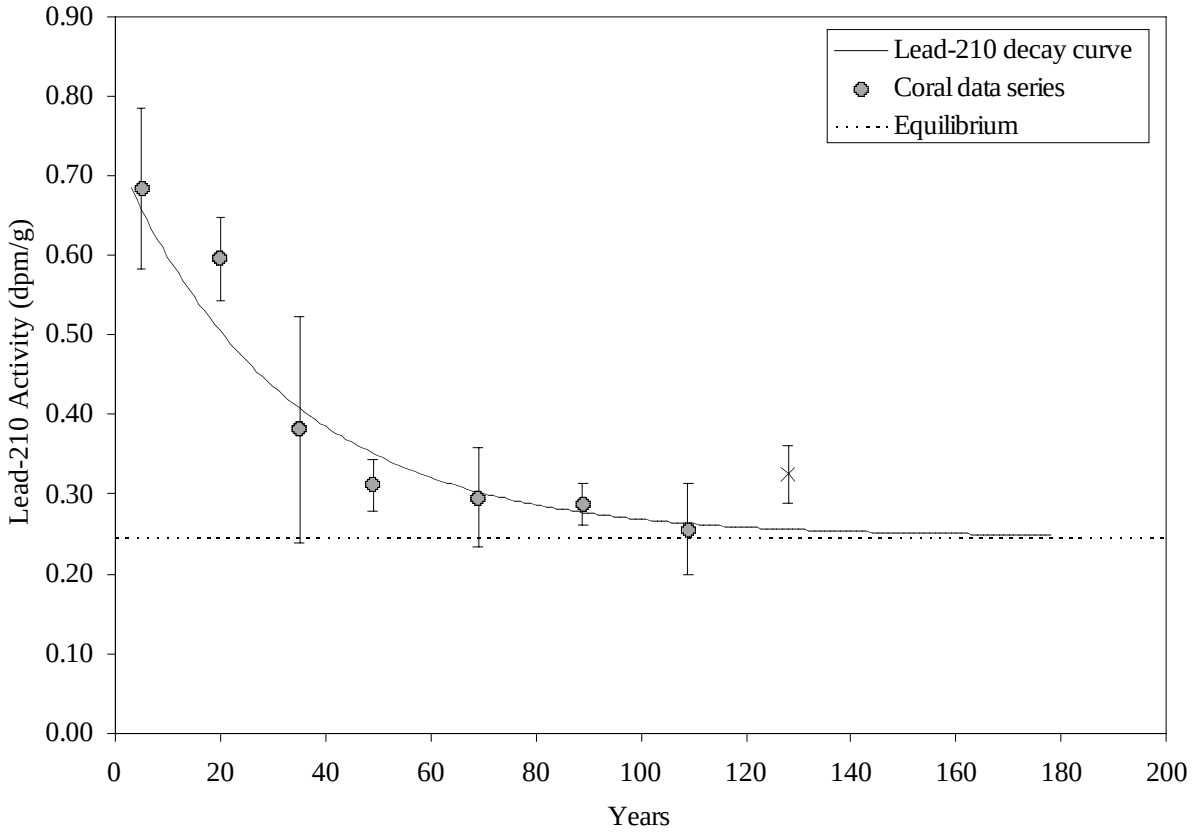

Figure 12. Plot showing the general conformity of lead-210 activities to the decay curve for T428-A10 based on the fitted regression to the ln-transformed data. Lead-210:radium-226 equilibrium was based on the average measured radium-226 (0.247 ± 0.059 dpm/g). Note that the center sample (×) was elevated relative to the pattern of lead-210 decline and was therefore eliminated from the analysis.

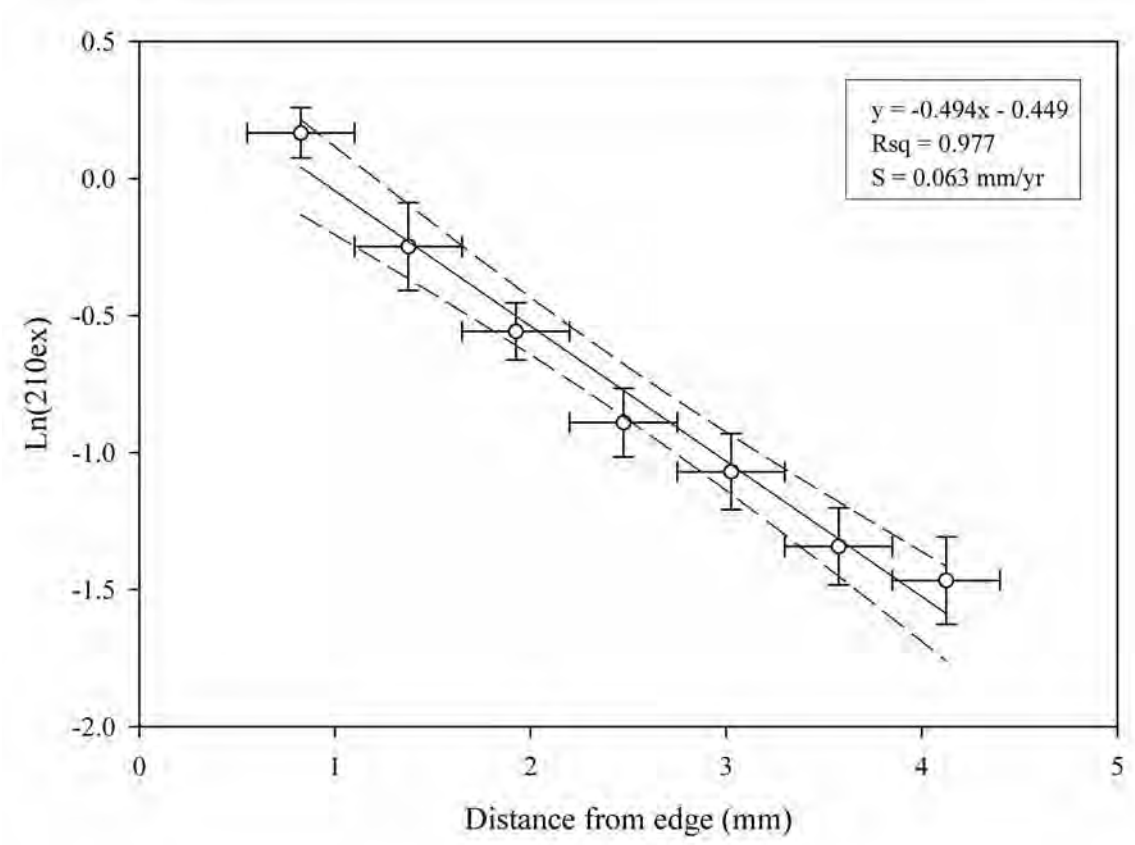

Figure 13. Plot of ln-transformed exogenous lead-210 relative to the distance from the edge for the smaller colony T948-A2 collected in 2006. These data indicate the growth rate of this colony was 0.063 mm/yr (95% CI range of 0.056 – 0.073 mm/yr).

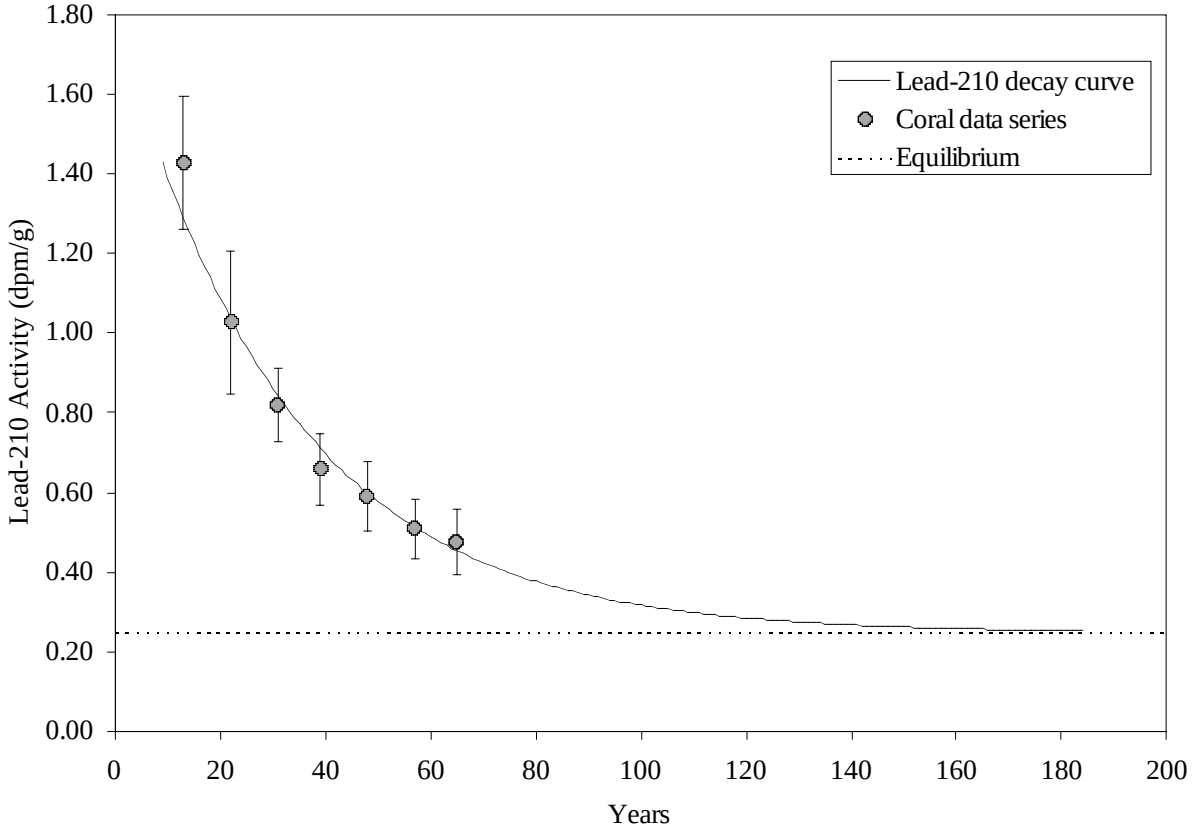

Figure 14. Plot showing the relatively tight conformity of lead-210 activities to the decay curve for colony T948-A2 based on the fitted regression to the ln-transformed data. Lead-210:radium-226 equilibrium was based on the average measured radium-226 (0.247 ± 0.059 dpm/g). Note that the center sample was not elevated relative to the pattern of lead-210 decline and was therefore included in the analysis.