Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California

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Abstract. A recent biological characterization of the Davidson Seamount off central California using a remotely operated vehicle revealed communities rich with deep-sea corals. During this characterization several corals were collected and three colonies were made available for an age and growth study. The colonies examined were identified as bubblegum coral (*Paragorgia* sp.), bamboo coral (*Keratoisis* sp.), and precious coral (*Corallium* sp.). Age was estimated from growth zone counts made in skeletal cross sections. These age estimates were used to estimate growth rates and colony age. Estimated growth rates determined for each species were quite different. The bubblegum coral had a relatively high estimated growth rate, with the precious and bamboo coral estimated as slow growing. These age and growth observations were evaluated relative to published studies on related species and an attempt was made to validate the age and growth estimates with an independent radiometric ageing technique (i.e., lead-210 dating). This approach was not successful for the bubblegum coral, and was successful for the bamboo and precious corals to differing degrees. For the bamboo coral, a minimum colony age of over 200 years was determined. For the precious coral, a linear growth rate of approximately 0.25 cm/yr led to a colony age of about 115 years; however, based on the radial growth rate, an age of up to 200 year is possible.

Keywords. Octocoral, *Paragorgia*, *Corallium*, *Keratoisis*, Davidson Seamount, age, growth, radiometry, lead-210, radium-226

Introduction

Deep-sea corals can provide high relief habitat that is ecologically diverse and intrinsically valuable. The coral habitats are inhabited by assemblages of species of invertebrates and fishes that are often unique, many of which have yet to be discovered and described (Fosså et al. 2002; Krieger and Wing 2002). The value of the deep-sea environment created by corals is often related to some form of benefit to humans, like essential fish habitat, but it should also be considered important from a perspective of world heritage because these living habitats are very fragile. Once these communities are disturbed or removed, many of the corals and the habitat they create may not recover within our lifetime (Andrews et al. 2002b). 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; Koslow et al. 2000). 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. This requirement has been recognized internationally with conservation efforts, such as the preservation of the Darwin Mounds off the United Kingdom and the efforts of nongovernmental agencies like the Ecology Action Center, the Marine Conservation Biology Institute, and Oceana (Breeze et al. 1997; Roberts and Hirshfield 2003; Morgan et al. 2005).

Information about the life history of habitat forming corals, such as age, growth, and longevity, is necessary before their sensitivity and their importance as fisheries habitat can be fully understood. Age determination studies to date have found that deep-sea corals, as well as some of the associated fishes, can attain ages that are on the order of a hundred to perhaps thousands of years (Druffel et al. 1990; Rogers 1999; Cheng et al. 2000; Andrews et al. 2002a, b). Age and growth of deep-sea corals is typically determined from outgrowth studies in the field, growth zone counts in the skeletal structure, a radiometric technique (e.g., lead-210 dating), or a combination of these methodologies.

Lead-210 dating is a radiometric technique that utilizes the radioactive decay of lead-210 that has been isolated from the environment (i.e., incorporated into the skeletal structure of coral) as a natural chronometer (Dodge and Thomson 1974). The approach is analogous to sedimentation rate studies (Lewis et al. 2002). Because the rate of decay for lead-210 is well known (half-life of 22.26 yr), measurements of radioactivity throughout a skeletal structure (young to old) can be used as a natural chronometer. Lead-210 is incorporated into the skeletal matrix at the time of formation; younger growth accretes over the oldest portion of the skeleton and the activity of lead-210 decreases to a point where it is supported by radium-226, a naturally occurring calcium analog. Note that this system is dependent upon the incorporation of lead-210 that is in excess of supported levels from radium-226, this is easily established by measuring lead-210 in the youngest material (i.e., skeleton near the actively growing margin). By taking a series of measurements from near the actively growing margin to parts of the skeleton that are buried deeper by layers of growth, the decrease of lead-210 activity can be used as an independent indicator

of age and growth. This approach is useful to about 100 years of age at which time the activity of lead-210 decreases to a level approaching the activity of radium-226, nearing an equilibrium activity ratio.

The focus of this study was to investigate the age and growth of corals collected from biological characterization surveys of the Davidson Seamount. This seamount is located in the northeastern Pacific Ocean, 120 kilometers to the southwest of Monterey, California. At 42 kilometers in length it is one of the largest seamounts along the western coast of the United States. The Davidson Seamount is 2400 m from base to crest and 1250 m below the sea surface. It has an atypical seamount shape, having northeast-trending ridges created by a type of volcanism only recently described (Davis et al. 2002). At least 20 different corals were identified at this location (DeVogelaere et al. 2005). Three coral colonies typical of the faunal diversity of the surveyed region were collected, the bubblegum coral (*Paragorgia* sp.), bamboo coral (*Keratoisis* sp.), and precious coral (*Corallium* sp.). The first goal was to verify the initial taxonomic identifications of the specimens and determine if specific identifications could be made. The second goal was to investigate age estimation using quantification of growth zones visible in skeletal cross sections from each species. These age and growth observations were evaluated relative to other studies on similar species and an attempt was made to validate the age and growth estimates with an independent radiometric ageing technique (i.e., lead-210 dating).

Materials and methods

Specimen habitat, collection and identification

Coral specimens were collected from the Davidson Seamount during a collaborative survey led by the Monterey Bay National Marine Sanctuary on May 17-24, 2002. Three of the coral species collected were made available for age and growth analyses: 1) bubblegum coral (*Paragorgia* sp.) collected from 1313 m, 2) bamboo coral (*Keratoisis* sp.) collected from 1425 m, and 3) precious coral (*Corallium* sp.) collected from 1482 m. Each coral resided on rocky outcrops and were collected using the Monterey Bay Aquarium Research Institute ROV *Tiburon* from the Davidson Seamount (near 35º45'N/122º42'W) in water that was about 2.5ºC with a salinity of about 34.5 ppt. Specimens were stored frozen until used in the age determinations. The bubblegum coral was a fully intact colony that measured 80 cm from base to the furthest tip along the main axis. The bamboo coral was very fragmented and only sections of the colony were intact. The precious coral was very brittle and in excellent condition, measuring 29 cm in length along the primary axis to the furthest point on the colony from the base. Coral specimens were identified to genus, with a qualified identification to species, by three cnidarian taxonomists.

Age estimation

Each skeletal structure was sectioned with a hacksaw, razor blade, or Dremel® tool. The bubblegum coral had a soft axial skeleton that was cut initially with

either a hacksaw (thick sections of the trunk) or a utility razor blade. Sections from the bamboo and precious coral were extracted with a Dremel® tool or hacksaw (thick base on bamboo coral) and were smoothed with a lapidary wheel. Sections were air dried and mounted to glass with Cytoseal® for viewing with a dissecting microscope. Sections were taken from several locations along the axial skeleton ranging from near the base to near the tip of each colony. To investigate internal structure and growth zones in the bamboo coral, the organic nodes were also thinned and mounted to glass slides. Magnification was varied from low to high to cover all possibilities of growth zone size and resolution for each species. Estimates of age were made from any quantifiable growth zones seen in the sections and an estimated growth rate and colony age was made based on this information. Magnification ranged from the unaided eye to 40 times, depending on the specimen, using an Olympus dissecting microscope.

Lead-210 dating

Adjacent to each section, a small core (center of the skeletal structure) was removed for lead-210 and radium-226 analyses. The decay of exogenous (unsupported) lead-210 over the length of the skeletal structures was used in an attempt to determine an independent growth rate with the possibility of validating age estimation from growth zone counts. For samples with age estimates that exceeded the utility of this method (about 100 years), the use of lead-210:radium-226 equilibrium was used to establish a minimum colony age. This process involved the measurement of lead-210 *via* alpha-spectrometry and radium-226 *via* thermal ionization mass spectrometry (TIMS). For each species, the first assay involved analyzing two sections for growth zone counts and two core samples to evaluate lead-210 and radium-226 levels. Based on the findings for each species, additional sections and core samples were taken to better establish possible trends. The determination of lead-210 and radium-226 were based on previously established protocol (Andrews et al. 1999; Andrews et al. 2002b).

Bubblegum coral

Six segments, 2 cm in length, were extracted adjacent to each location where aged sections were taken (Fig. 1). These segments were cored with a razor blade to a 4-5 mm center portion. These cores were cleaned, dried, weighed, and dissolved for radiochemical analyses.

Bamboo coral

The core material of two segments, adjacent to the first two aged sections near the base of the colony was extracted using a milling machine. The powdered sample was dried, weighed, and dissolved for radiochemical analyses. In a younger section, toward the upper part of the colony (Fig. 2), three additional segments were analyzed whole (not cored); coring was not possible in these thin, tubular segments. Because of these constraints a general pattern of decreasing overall lead-210 was targeted to determine if lead-210 dating would be possible and if a method could be developed to extract core material. The youngest sample consisted of two

skeletal tips that were separated from the colony. These segments were measured in diameter, cleaned, dried, weighed, and dissolved for radiochemical analyses.
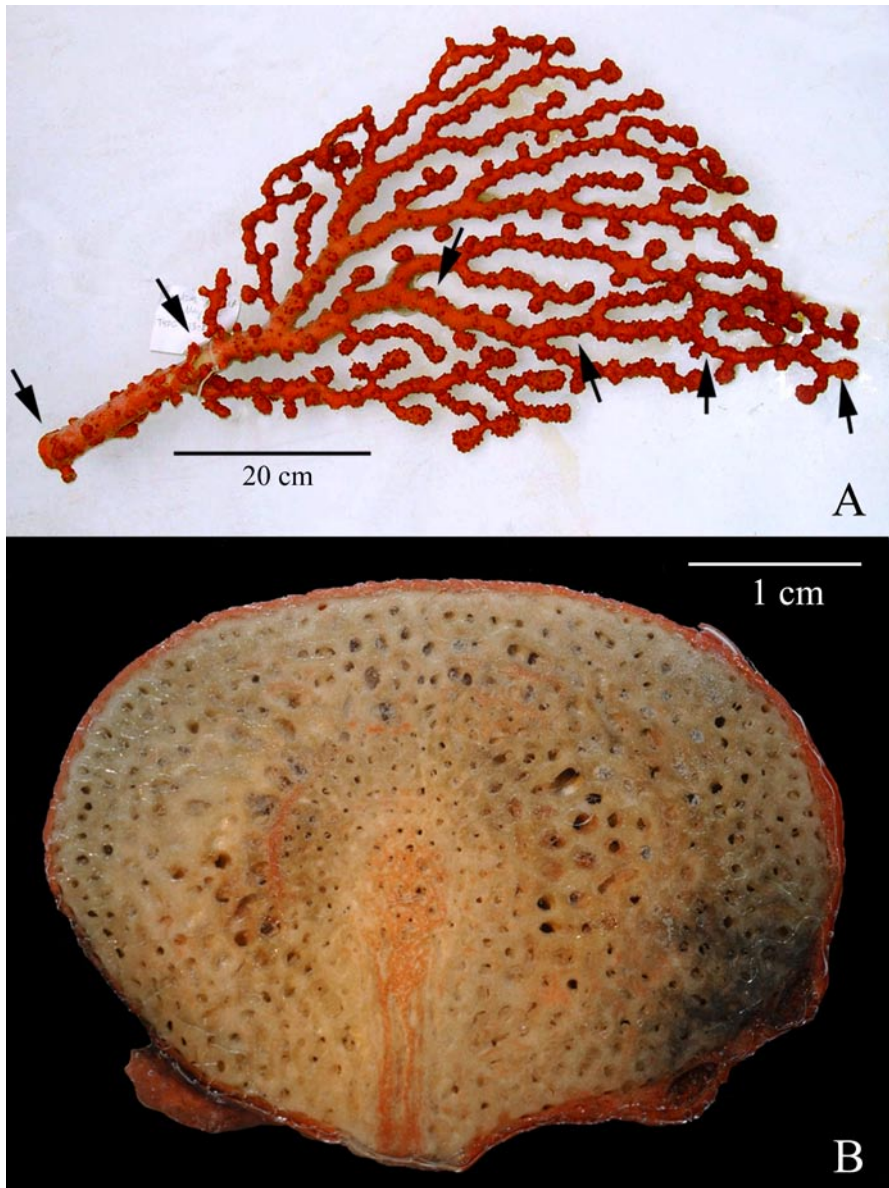

Fig. 1 Photograph of the bubblegum coral (*Paragorgia* sp.) used in this study with the locations of the six segments (used for radiochemical analyses) and sections (used to estimate age from growth zones) marked with arrows (**A**). The length of the colony on its longest axis was 80 cm. The section taken at the colony base (**B**) was estimated for age from what appears to be a concentric orientation of the pores radiating from the center

Precious coral

Five segments of the precious coral colony were analyzed; two from older and thicker parts of the skeleton, two from a thin branch (Fig. 3), and one sample consisting of a collection of tips from all over the colony. All were cored to a 1-2 mm diameter segment, except for the tips, which remained whole. Tips, the most recent growth of the skeletal structure, were collected from various branches in the colony to obtain enough material for the analysis. Because new branches can
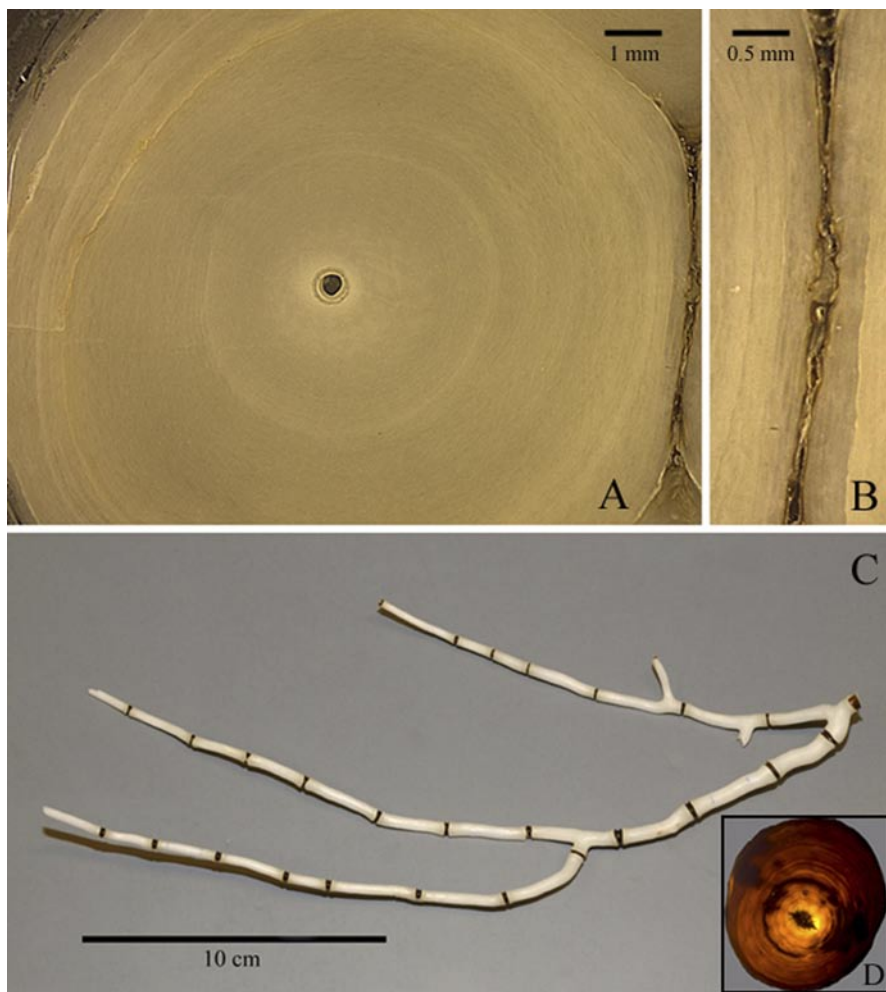

Fig. 2 A composite of images for the bamboo coral (*Keratoisis* sp.) used in this study. A section near the base of the colony (**A**) was very difficult to interpret, having a woven or braided appearance to most of the visible zones. Small regions of this section (**B**) that were clearer than most were used to estimate age. The upper portion of the colony (**C**) was used to investigate other approaches to age estimation and validation. The organic node (**D**) seemed to show the most promise for age estimation from growth zone counts. The diameter of this section was 3 mm
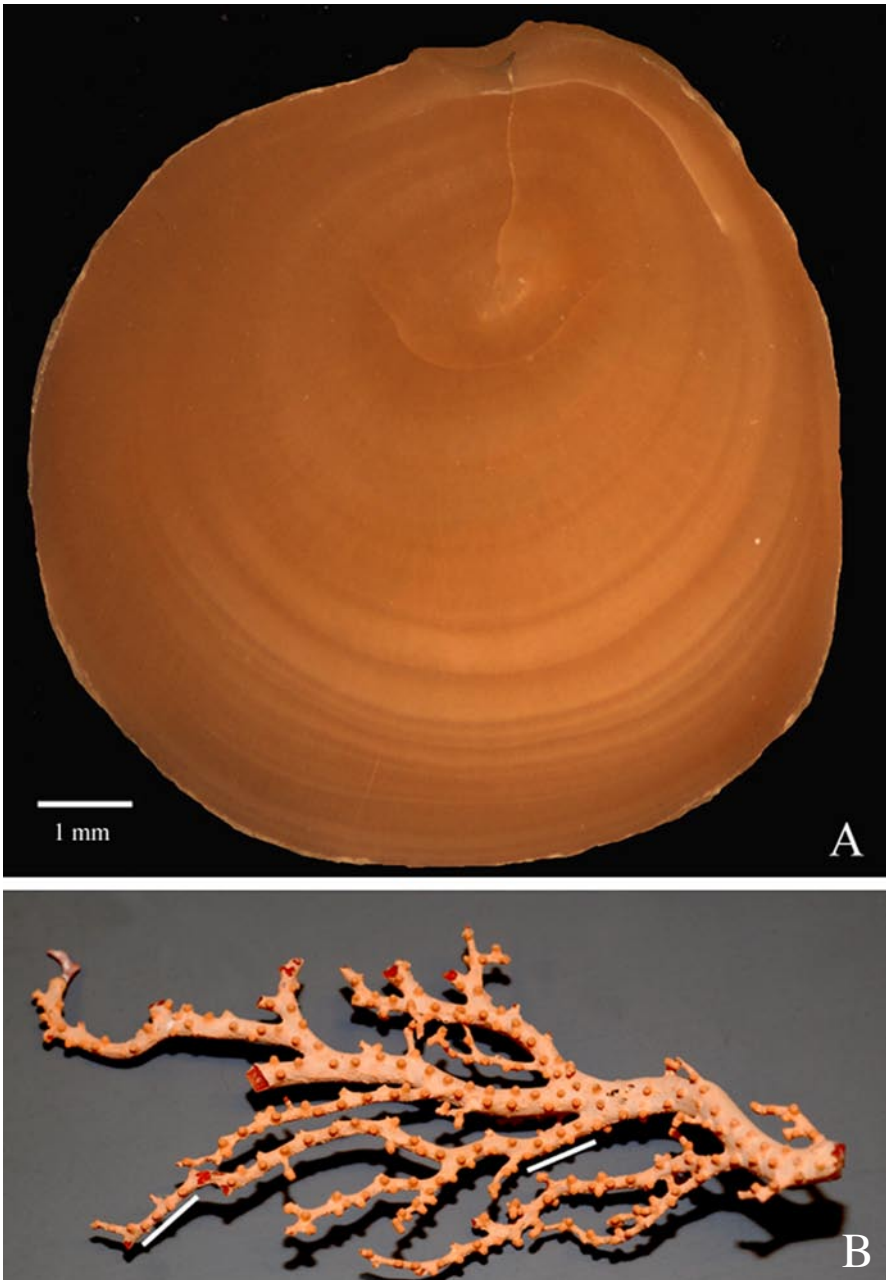
Fig. 3 The growth zones visible in cross sections of the precious coral (*Corallium* sp.) were variable in thickness and counts were subjective (**A**). Based on the radiometric results for the segments near the base (samples 4 and 5), a thinner branch was selected (**B**) from part of the colony for further analyses and age validation with lead-210 dating. Samples 2 and 3 are delineated with a white bar

start on older segments, a relationship between segment diameter and colony length between the segments (slope = 5.97) was used to determine the approximate distance the tips would have been from the younger of the two older segments (~8.9 cm). This necessitated the assumption that once a segment begins growing it continues to grow and that there is a linear relationship between skeletal diameter and colony length (analogous to tree growth). These samples were cleaned, dried, weighed, and dissolved for radiochemical analyses.

Results

Species identification

Coral specimens were identified to genus, with a qualified identification to species, by three cnidarian taxonomists. The determination of deep-water corals to species is not well defined and is a work-in-progress for all experts in the field. Initial identification of each species at the time of collection was 1) gorgonian coral (*Paragorgia* sp.), 2) bamboo coral and, 3) precious coral. Taxonomists confirmed the genus of the gorgonian coral as *Paragorgia*, and indicated that it might be *Paragorgia pacifica* based on branch size (Bruce Wing, Curator at Auke Bay Laboratory, NMFS, Juneau, AK, pers. comm.), but could be a smaller colony of *P. arborea*. In general, the literature is poor for the west coast fauna and revisions in coral taxonomy are required (Gary Williams, Curator at the California Academy of Sciences, San Francisco, CA, pers. comm.). The bamboo coral was identified as a *Keratoisis* sp., possibly *Keratoisis profunda*, the only species listed for the northeastern Pacific Ocean (Bruce Wing and Dr. Gary Williams, pers. comms.). The precious coral was identified as a member of the genus *Corallium* (Stephen Cairns, Curator at Smithsonian Institution, Washington D.C., pers. comm.). Several species have been identified from the Pacific Ocean (Bayer 1996) and this specimen might be *C. regale*; however, the taxonomy of this genus is a work-in-progress and needs a re-evaluation considering two additional species, *C. imperiale* and *C. sulcatum* (Frederick Bayer, Smithsonian Institution, Washington D.C., pers. comm.). Most *Corallium* sp. have been described from latitudes further south than the location on the Davidson Seamount (35º45'N); however, recent collection of a *Corallium imperiale* was made at the Patton Seamount (54ºN, 1750-1850 m; Amy Baco-Taylor, Biology Department, Wood's Hole Oceanographic Institution, Wood's Hole, MA, pers. comm.). Samples from each colony have been accessioned to the California Academy of Sciences, Department of Invertebrate Zoology and Geology, Golden Gate Park, San Francisco, CA 94118 and the Smithsonian Institution, National Museum of Natural History, Department of Systematic Biology - Invertebrate Zoology, Washington D.C. 20013.

Age estimation

Bubblegum coral

Of the six skeletal cross sections taken along the main axis, spanning the tip to the base of the 80 cm colony (Fig. 1A), growth zones were visible at low or

no magnification. The porous nature of the skeleton made what appeared to be concentric zones of pores. Age was estimated from these concentric zones, which were more visible when viewed slightly out of focus. Estimated age at the base of the colony was 9 to 14 years (Fig. 1B). Based on these age estimates and the distance along the axis to the tip, a growth rate of 6 to 9 cm/year was estimated. Additional sections taken between the base and tip supported this finding; however, the counting of these growth zones was very subjective and should be interpreted with caution.

Bamboo coral

The growth zones visible throughout the bamboo coral section were too complex and low in contrast to be enumerated, typically having a woven or braided appearance (Fig. 2A). Therefore, growth zones visible in parts of the section near the base of the colony were used to extrapolate an age for the section and colony. Better-defined portions of the skeleton at the joint between two branches and in another location were used to determine a growth zone width of 0.05-0.11 mm/zone (Fig. 2B). The measured radius of the basal section was 8 to 11 mm, leading to an estimated age for the section of 80 to 220 years, assuming the zones are formed annually and that the pattern or rate is similar throughout. The other portion of the basal section was near the edge of the colony where 16 zones were visible in 1 mm of radius. Based on the calculated radial growth, the estimated age of the second section taken in the colony (5.6-6.5 mm radius) was 56 to 131 years. With a distance of 24.5 cm between sections, a linear growth rate of 0.19 to 0.44 cm/year was estimated.

Additional sections were taken toward the tip of the colony because of the high estimated age of the older sections and the radiometric findings, which are discussed later (Fig. 2C). Estimating age at the nodes looked the most promising. Growth zones were clearly visible, but variable in width. Age estimates from the cleanest section were about 60 years; however, age estimates varied considerably and depended on magnification and growth zone interpretation (Fig. 2D). Based on the calculated radial growth rate from the basal section, the age for these sections would be between 30 and 60 years old. The findings from the node supported the slower growth rate.

Precious coral

Two skeletal cross sections were extracted from the precious coral colony, separated by 15.7 cm. Each section was aged, but growth zones were poorly defined and variable in width. Age was subjectively assigned to both sections. The thickest section was aged at 20 to 21 years (Fig. 3A). The smaller section was aged at 3 to 7 years. Based on the separation between these sections and the extremes of age the estimated growth rate was 0.9 to 1.1 cm/yr. Given this estimate is accurate and we assume a constant growth rate for the 29 cm colony, the overall age of the colony age would be about 30 yr.

Lead-210 dating

For each species the radiochemical analyses and results varied considerably (Table 1). In most cases a small core (center of the skeletal structure) was removed

for lead-210 and radium-226 analyses, with the intent of using either exogenous (unsupported) lead-210 over the length of the skeletal structures to determine a growth rate or the use of lead-210:radium-226 equilibrium as an indicator of a minimum colony or segment age (approximately 100 years).

Bubblegum coral

The activity of lead-210 tended to increase slightly from near the tip to the base for the six segments (range of 1.12 ± 6.5 % to 1.61 ± 3.9 % dpm/g; Table 1). Radium-226, however, was not consistent between the base and tip and differed by a factor of about two (0.649 ± 1.7 % to 1.33 ± 1.4 % dpm/g). The resultant lead-210: radium-226 ratios ranged from 1.2 to 1.9, hence exogenous lead-210 was present in the skeletal system of this species. Because of the inconsistent pattern of lead-210 and radium-226 activity, however, it was not possible to determine a growth rate from the decay of exogenous lead-210.

Bamboo coral

Measurement of lead-210 and radium-226 in the first two aged sections, near the base of the colony (sample numbers 4 and 5), resulted in activity ratios that were near equilibrium (Table 1). Lead-210 levels were similar (0.248 ± 6.3 % and

Table 1 Radiometric data for three corals organized by sample number from the tip to near the base of each colony. Activity for lead-210 and radium-226 was expressed as disintegrations per minute per gram of sample material

Coral	Sample number	Lead-210 (dpm/g) activity ± % error[1]	Radium-226 (dpm/g) activity ± % error[1]	210/226 ratio (error range)
Bubblegum	1 (tip)	1.26 ± 4.1	0.649 ± 1.7	1.9 (1.8-2.1)
(*Paragorgia* sp.)	2	1.12 ± 6.5	n/m[2]	n/a
	3	1.27 ± 6.9	n/m[2]	n/a
	4	1.57 ± 6.7	n/m[2]	n/a
	5	1.51 ± 7.1	n/m[2]	n/a
	6 (basal)	1.61 ± 3.9	1.33 ± 1.4	1.2 (1.1-1.3)
Bamboo	1 (tip)	0.560 ± 10.4	0.228[3]	2.5
(*Keratoisis* sp.)	2	0.533 ± 6.1	0.228[3]	2.3
	3	0.517 ± 5.2	0.228[3]	2.3
	4	0.248 ± 6.3	0.266 ± 8.0	0.9 (0.8-1.1)
	5 (basal)	0.267 ± 10.4	0.190 ± 20[4]	1.4 (1.0-1.9)
Precious	1 (tip)	0.566 ± 5.6	0.273[3]	2.1
(*Corallium* sp.)	2	0.429 ± 11.4	0.273[3]	1.6
	3	0.361 ± 7.7	0.273[3]	1.3
	4	0.248 ± 4.5	0.278 ± 8.8	0.9 (0.8-1.0)
	5 (basal)	0.288 ± 4.2	0.268 ± 7.2	1.1 (1.0-1.2)

[1] Sigma (SD) expressed as a percentage.
[2] Not measured or calculated.
[3] Average of samples 4 and 5 for each respective species.
[4] High error associated with low radium recovery; may be an unreliable run.

0.267 ± 10.4 % dpm/g), with radium-226 differing slightly (0.190 ± 20 % and 0.266 ± 8 % dpm/g). The resultant lead-210:radium-226 ratios ranged from 0.9 to 1.4 with a margin of error that encompassed a ratio of one (equilibrium). Hence, these segments were in or near equilibrium. For sample number 5, low recovery of radium-226 made the assumption of equilibrium more subjective (1.0 to 1.9). Presumably the value of radium-226 was closer to the measured value of sample number 4 (0.266 ± 8.0 %). This is supported by the position of the sample in an older portion of the colony, constrained by the finding of equilibrium for sample 4. Hence, we subjectively conclude that this section of the colony was more than 100 years old. Based on this finding, the decision was made to sample in a thinner, presumably younger, limb of the colony (Fig. 2C).

In the younger limb (sample numbers 1-3), the measured lead-210 activity was highest in the tip segment and decreased in the older segments (0.560 ± 10.4 %, 0.533 ± 6.1 %, 0.517 ± 5.2 % dpm/g; Table 1). These levels were considerably higher than the core material in the basal segments (sample numbers 4 and 5) and the calculated activity ratios (average radium-226 = 0.228 ± 0.054 dpm/g) exceeded 2.0. Hence, exogenous lead-210 was present in the skeletal system of this species. These results indicate lead-210 dating could work for this species, given a method to extract cores from the fragile, tubular segments could be developed. No growth rate was determined for these samples because the samples were whole sections (not cores) and it would require the development of a mass growth rate model with circular reasoning with respect to age.

Precious coral

Results for the two segments near the base of the colony (sample numbers 4 and 5) were similar to that of the basal segments of the bamboo coral (Table 1). Measurement of lead-210 and radium-226 in the core material of these segments resulted in activity ratios that were near equilibrium. Lead-210 levels were similar (0.248 ± 4.5 % and 0.288 ± 4.2 % dpm/g), with radium-226 being very similar (0.268 ± 7.2 % and 0.278 ± 8.8 % dpm/g). The resultant lead-210:radium-226 ratios were 0.9 to 1.1 with a narrow margin of error that encompassed a ratio of one (equilibrium). Hence, these segments were more than 100 years old and the decision was made to collect three samples from thinner, presumably younger, segments of the colony. Two segments were extracted from a thinner limb, and one sample was a collection of the thinnest tips from all over the colony.

For the thinner segments and the tips (sample numbers 1-3), the measured lead-210 activity was highest in the tips and decreased for the segments (0.566 ± 4.6 %, 0.429 ± 11.4 %, 0.361 ± 7.7 % dpm/g; Table 1). These levels were considerably higher than the core material in the basal segments and the calculated activity ratios (average radium-226 = 0.273 ± 0.008 dpm/g) were 2.1, 1.6, and 1.3. Hence, exogenous lead-210 was present in the skeletal system of this species and lead-210 dating was possible and a linear growth model could be applied. Given the distances between samples (measured between the segments and calculated for the tips) relative to the decay of exogenous lead-210, the growth rate of the colony was approximately 0.43 cm/yr (95 % range = 0.25-1.7 cm/yr; Fig. 4). Given this
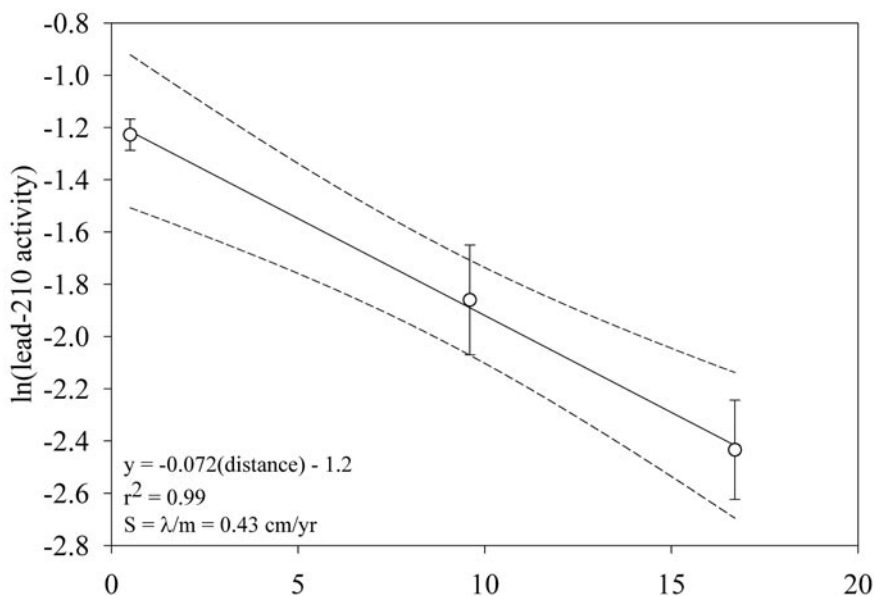
Fig. 4 Plot of exogenous lead-210 activities (total lead-210 activity minus average radium-226 activity) that have been natural log transformed to provide a linear relationship. This relationship was used to determine a growth rate based on the decay of lead-210 over the length on the precious coral colony. Three data points are all that can be plotted because the activities measured in the two segments toward the base (samples 4 and 5) were in equilibrium (lead-210:radium-226 = 1.0)

estimate, and we assume a constant growth rate along the main axis for the 29 cm colony, the overall age of the colony age was about 67 yr (95 % range = 17-116 yr). This presents a possible contradiction relative to the findings in the two older segments because an age of more than 100 years is required to attain lead-210:radium-226 equilibrium. For the oldest of the three thin limb segments (sample number 3), the highest age estimate for the growth rate range (0.25-1.7 cm/yr) from the linear growth model was 63 yr.

To approach the problem from a different perspective, segment diameter was used as an indicator of age. Assuming the second segment from the base was 100 years old (sample number 3), age was related to diameter (4.27 mm) as 23 times the diameter; hence, age was determined for each segment using this relationship and the decay of lead-210 was plotted with these data (Fig. 5). This relationship indicated the colony might have been more than 200 years old.
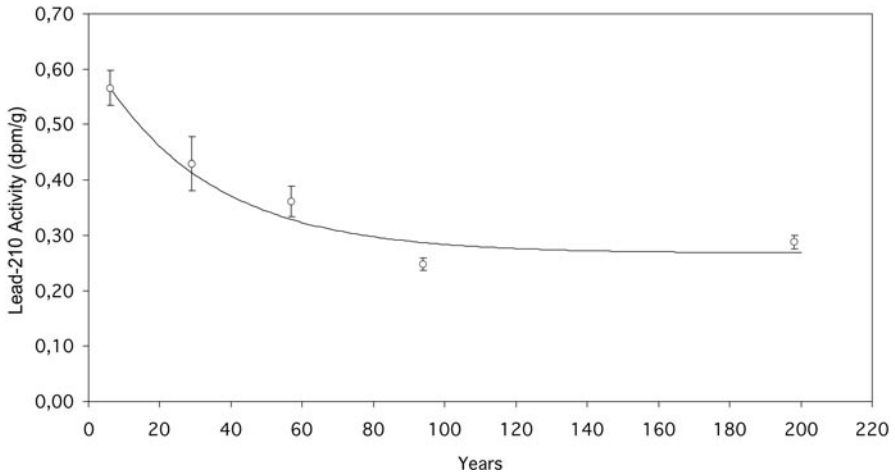
Fig. 5 Plot of age estimated from segment diameter (minus estimated average age of the core material = 6 yr; based on average diameter of 0.5 mm) *versus* the measured total lead-210 activity from all precious coral samples, tips on the right to base on the left. The decay function was driven by initial activity measured in the tips (0.566 dpm/g) with an asymptotic approach to the average lead-210 activity in the two basal segments (samples 4 and 5). The progression of lead-210 decay follows the expected trend, but based on segment diameter the estimated age of the colony could be closer to 200 yr

Discussion

Bubblegum coral

The estimation of age from the growth zones seen in the sections of the bubble gum coral was dubious at best. The pattern of growth used to define growth zones, a series of pores forming concentric arcs, was very different relative to the usual ring pattern identified in calcified structures. When quantified and translated to a linear growth rate, the estimate is relatively high (6-9 cm/yr) compared to other gorgonian species (Andrews et al. 2002b). In some cases, growth rates can be estimated from outgrowth of colonies that settled on a structure of known age. An observation was made for bubblegum coral colonies up to 20 cm in length attached to a telegraph cable known to be 44 years at depth (Davis et al. 2000). Assuming the colony settled shortly after the structure appeared, the growth rate could have been about 0.5 cm/yr, but the rate could be much higher if the timing of settlement occurred later. According to preliminary ^{14}C-dating results, massive colonies collected off New Zealand may have grown at a rate comparable to that calculated here (Dianne Tracy, National Institute of Water and Atmospheric Research Ltd., Wellington, New Zealand, pers. comm.).

The skeletal structure of bubblegum coral is a spongy matrix that is highly organic and may have a cellular component. The presence of tissue throughout the skeleton, and concentrated in the core, that was the same color of the exterior tissue could

mean that the skeleton is not a conserved structure with time. It is possible that the skeletal matrix is regularly reworked, like the cancellous bone of most animals, making the system open to the migration of elements (e.g., lead-210 and radium-226). This is evidenced by the observation that the radiochemical results had no systematic pattern that could be related to growth. Hence, the approach used here did not work for this species and may not work for this kind of skeletal matrix in general. These findings are similar to the results found for the cancellous fin rays of Atlantic sturgeon (*Acipenser oxyrinchus*; Burton et al. 1999) and shark cartilage (Welden et al. 1987).

One avenue that could be pursued to estimate age and growth is the use of the time specific marker produced by bomb radiocarbon (Kalish 1995). Studies have indicated that shark vertebrae are an open system to lead-210 (Welden et al. 1987); however, the organic matrix is evidently conserved in some species. In a study of porbeagle and mako sharks, the determination of bomb radiocarbon in vertebrae successfully validated the annual formation of growth zones in vertebrae of the porbeagle shark and showed promise of validating age estimates for the mako (Campana et al. 2002). It is possible that the organic portion of the bubblegum coral matrix is conserved in the same manner and that the time specific bomb radiocarbon marker could be used to estimate age, given there are no problems with depth and a phase shift in the timing of bomb radiocarbon signal to the deep-water environment (Kalish 2001).

Bamboo coral

Initial growth estimates from growth zone counts in the sections taken near the base revealed a possible age range of 80 to 220 years. This estimate, however, was based on an extrapolation of a radial growth rate (0.05-0.11 mm/zone) to the full radius of the section. Because the lead-210:radium-226 activities of the two core samples near the base were in equilibrium, the age of the colony likely exceeded 100 years. This supports the lower growth rate (approximately 0.05 mm/zone) and higher estimated age (131 years) of the second section up from the base. Therefore, the section near the base would be closer to the estimate of 220 years based on the lower growth rate, giving the colony an age of over 200 years. This is similar to the findings of a study on a similar bamboo coral (*Acanella* sp.) collected off San Francisco, California. In that study, the activity of lead-210 was linear (assuming lead-210 and radium-226 were in equilibrium), suggesting the age of the colony was over 100 years (Howard Spero, Department of Geology, University of California, Davis, pers. comm.). In addition, recent carbon-14 work on a coral specimen in the same family (Isididae), collected from the Gulf of Alaska at about 800 m, indicated the age of the colony was about 50 yr. This observation was based on the detection of bomb-produced carbon-14 and its use as a time specific marker. The extrapolated radial growth rate of 0.1 mm/yr was similar to the rate estimated in this study (Roark et al. 2003). In a recent study of *Keratoisis* sp. specimens taken from 1000 m water off southern Australia, the growth rate was 0.05 mm/yr and in agreement with our conclusions, where lead-210 excess and equilibrium values were about half that

recorded in our study (Ron Thresher, CSIRO Marine Research, GPO Box 1538, Hobart, Tasmania 7001 Australia, pers. comm.).

Although age validation of this species using lead-210 dating was not entirely conclusive, this study provides guidance for future studies. Further examination of growth zones in the nodes of this species is necessary. This region seems promising for growth zone counts because zonation patterns were clearly visible and estimated ages were close to expected ages, if the age estimate exceeding 200 years for the colony is correct. It is also apparent that a full study using extracted core material from younger sections (estimated to be less that 100 years old) could prove successful based on the regular decay of total lead-210 in the youngest segments. Because sampling core material proved difficult in this study, an alternative would be to sample along a radial path, as was the case with the precious coral, *Corallium niobe* (Druffel et al. 1990), and *Keratoisis* sp. from off Australia (Ron Thresher, CSIRO Marine Research, GPO Box 1538, Hobart, Tasmania 7001 Australia, pers. comm.).

Precious coral

The estimated linear growth rate from growth zone counts (0.9-1.1 cm/yr), making the colony about 30 years old, falls within the uncertainty associated with the lead-210 dating estimate (0.25-1.7 cm/yr). The existence of segments for which measured lead-210:radium-226 was in equilibrium, however, indicated the age of the colony was over 100 years. In the middle of these estimations was the lead-210 dating results making the colony age approximately 67 years with a range of uncertainty from 17 to 115 yr. These results indicated no conclusion could be made about growth; however, these observations can be explained by discontinuous growth manifested as either halted growth, delayed branching, or both. In this case we assumed that the segments from the younger branch were from a branch that had a delayed start and continuous growth between segments. In addition, we had to assume that the tips collected represented actively growing portions of the colony and that the extrapolated distance to the missing tip for that branch was accurate. The decay of lead-210 in this series of three samples seems to support these assumptions, but age and growth estimates can be further constrained by interrelating the segments in equilibrium with the segments coming into equilibrium *via* cross sectional diameter.

If delayed branching is a problem for the linear growth assumption, then branch diameter should be a better predictor of age. An age of 39 years (range of 9 to 63 years) can be assigned to the younger branch based on the growth rate of 0.43 cm/yr (range of 0.25 to 1.7 cm/yr). Given the younger of the two segments in equilibrium was 4.3 mm in diameter and was at least 100 years old, the age of the younger branch (2.7 mm diameter at its thickest) would necessarily be 64 years old, within the range predicted from the decay of lead-210 (growth rate of 0.25 cm/yr). This implies that delayed branching, as opposed to halted growth, is the explanation for the discrepancy between the two findings (decay *vs*. equilibrium). Note that it is the convergence of 1) a minimum age of about 100 years for equilibrium to

be attained for a given diameter and 2) a maximum age that explains the decay of lead-210 that constrains the calculated growth rates. In conclusion for the precious coral, the findings of this study indicate that 1) the growth zones identified in the cross sections were not formed annually and should not be used as an indicator of age, 2) the linear growth rate of this colony was approximately 0.25 cm/yr with delayed branching, and 3) a diameter growth rate of 0.043 mm/yr. Given constant linear growth along the longest axis, this colony was approximately 115 years old; if however, the growth based on diameter is used to determine age, the age of the colony was in excess of 200 years old.

In further support of the lower growth rate is the potential problem of coring accuracy. Because lead-210 results indicate that the age of the colony is much greater than initially estimated from growth zone counts, the target core of the first few years of growth may have included more recent growth, on the order of a decade or more. Incorporation of younger material would raise the apparent lead-210 activity in segments of the young branch, effectively decreasing the measured decay of lead-210 and artificially increasing the estimated growth rate. Therefore, the lower growth rate estimate would be more accurate. This finding is reflected in the plot of estimated age from branch diameter relative to lead-210 activity where the predicted pattern of lead-210 decay is observed (Fig. 5).

These findings are similar to other studies on precious corals (*Corallium* sp.). In an outgrowth study of *Corallium japonicum* the linear growth rate was measured at about 0.3 cm/yr (Grigg 1974). A more recent age and growth study of the much larger growing *Corallium niobe* was validated using lead-210 dating with a calculated radial growth rate of 0.11 mm/yr (Druffel et al. 1990), higher than the radial growth rate determined in this study (0.043 mm/yr). A calculated linear growth rate for *C. niobe* was 0.45-0.71 cm/yr based on the 1 m height of the colony and its estimated age of 180 ± 40 yr, slightly higher than the linear growth rate estimated here (0.25 cm/yr). In a recent carbon-14 study on a *Corallium* sp. collected from Hawaiian waters at a depth of about 400 m, the radial growth rate was approximately 0.15 mm/yr, leading to an estimated age of about 80 yr for the colony (Roark et al. 2003).

It is apparent from the literature, and this study, that deep-sea corals are typically slow growing with a longevity potential on the order of 100s of years, and that one of the most fundamental and pressing requirements in this field is the development of accurate deep-sea coral taxonomy. The determination of age and growth for bubblegum corals (*Paragorgia* spp.) is inconclusive in this study, as well as in the literature. This group of corals may be one of the fastest growing deep-sea corals, but this is based on subjective observations. Bamboo coral has a unique jointed growth structure that has promising attributes for a full age and growth investigation. The well-calcified segments appear to be conserved with time and contain exogenous lead-210. In addition, the organic nodes appear to have well developed growth zones that may be an accurate indicator of age. The findings for the bamboo coral provide a strong basis for concluding that this species is slow growing and that the colony studied here was over 200 years old. The precious coral provided the most successful results for the lead-210 dating technique in this study. Based of the decay

of lead-210, the colony was about 115 yr (linear growth), but may be as old as 200 yr (radial growth). However, before information in this and any other study can be applied to other deep-sea corals, species identification is necessary. Those working to develop future deep-sea research projects should be mindful of this necessity by incorporating funding for taxonomy as part of the project.

Acknowledgements

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