Vol. 397: 173–185, 2009
doi: 10.3354/meps08193

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 17

Contribution to the Theme Section 'Conservation and management of deep-sea corals and coral reefs'

OPEN ACCESS

Growth rate and age determination of bamboo corals from the northeastern Pacific Ocean using refined ^{210}Pb dating

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ABSTRACT: Bamboo corals from Davidson Seamount and from the Gulf of Alaska were aged using a refined ^{210}Pb dating technique. The goal was to determine growth rates and age for several bamboo corals with higher precision. Radiometric results for 2 Davidson Seamount corals (*Keratoisis* sp.) converged on a radial growth rate of ~0.055 mm yr^{-1}. One colony was aged at 98 ± 9 yr, with an average axial growth rate of ~0.7 cm yr^{-1}. The age of a large colony was >145 yr with an estimated axial growth rate of 0.14 to 0.28 cm yr^{-1}. Inconsistent rates may indicate nonlinear axial growth. A *Keratoisis* sp. specimen from the Gulf of Alaska was aged at 116 ± 29 yr from a radial growth rate of ~0.056 mm yr^{-1}, which led to an average axial growth rate of ~1.0 cm yr^{-1}. An *Isidella tentaculum* colony was aged at 53 ± 10 yr and grew most rapidly with a radial growth rate of ~0.10 mm yr^{-1} and an average axial growth rate of ~1.4 cm yr^{-1}; however, the ^{210}Pb decay pattern may have provided evidence for either a hiatus in radial growth or environmental changes in ^{210}Pb. Our findings of slow growth and long life compared favorably with other bamboo coral studies and provided age estimates with greater precision. The high longevity of bamboo coral is an indication that recovery from disturbance or removal may take decades to a century. These age data provide a basis for a defensible position on the protection of bamboo coral and essential information for describing other life history characteristics.

KEY WORDS: Lead-210 · Radiometry · Deep sea · Longevity · Isididae

INTRODUCTION

Deep-sea corals can provide high-relief habitat that is ecologically diverse and intrinsically valuable (McDonough & Puglise 2003, Freiwald et al. 2004, Freiwald & Roberts 2005). These coral habitats support diverse assemblages of invertebrates and fishes that are unique (Husebo et al. 2002, Stone 2006, Love et al. 2007, Rogers et al. 2007). Deep-sea habitat created by corals has many ecological benefits including essential fish habitat, but it should also be considered important from a world heritage perspective because these living habitats are very fragile and may not recover within our lifetime (e.g. Willison et al. 2001, Andrews et al. 2002). With many fish stocks on the decline, there is increasing fishing pressure in deep-water habitats worldwide and the impact on deep-sea corals is increasing with devastating results (Auster & Langton 1999, Clark & Koslow 2007). It is essential that these habitats, especially those that remain undisturbed, are

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identified, protected, and studied in more detail before irreversible damage occurs.

Information about the life history of habitat-forming corals, such as age, growth, and longevity, is necessary before their sensitivity to and potential to recover from disturbance can be fully understood. Age determination studies to date have found that deep-sea corals can attain ages in the order of decades to thousands of years (e.g. Druffel et al. 1995, Andrews et al. 2002, Adkins et al. 2004). 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. ^{210}Pb dating), or a combination thereof.

Some deep-sea coral species can be aged by counting growth zones in skeletal structures using axial cross sections, but validating the periodicity of the growth zones is essential for the estimates to be useful in understanding the biology of the organism (Andrews et al. 2002, Risk et al. 2002, Thresher et al. 2004, Roark et al. 2005, Sherwood et al. 2005, Sherwood & Edinger 2009). 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 *Keratoisis* sp. using 2 radiometric schemes and Roark et al. (2005) used bomb radiocarbon (Δ^{14}C) to independently measure growth rates for bamboo corals.

^{210}Pb dating is a technique that uses the radioactive decay of ^{210}Pb as a natural chronometer that can reveal estimates of age and growth. This process begins with the natural incorporation of ^{210}Pb from seawater into the coral skeleton. As the coral grows like a tree, laying down growth rings, the radioactivity of ^{210}Pb decreases from the youngest (outer edge) to the oldest (center) material of the skeleton. The reason ^{210}Pb activity decreases is because it slowly decays away (radioactive decay) at a known rate (half-life of 22.26 yr). 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 ^{210}Pb measurements, the decrease of ^{210}Pb activity can be used to determine the age and growth of the deep-sea coral (Druffel et al. 1990). This approach is useful in samples up to about 100 to 120 yr of age, at which time the activity of ^{210}Pb has decreased asymptotically to levels that approach the activity of ^{226}Ra.

The goal of the present study was to provide more accurate age and growth determinations using a refined ^{210}Pb dating technique of several bamboo corals from 2 regions of the northeastern Pacific Ocean: Davidson Seamount off California and the Gulf of Alaska. To determine more refined age and growth characteristics, ^{210}Pb dating was applied using micromilling and a new approach to radial sampling of the skeletal axis.

MATERIALS AND METHODS

Specimen collection and identification. Corals were collected from Davidson Seamount in 2002 and 2006 using the ROV 'Tiburon' from the RV 'Western Flyer', and Gulf of Alaska corals were collected in 2006 along the continental slope of southeastern Alaska during fisheries stock assessment surveys using long-lines. Two colonies collected from Davidson Seamount were selected for this analysis based on good colony condition and to expand on a previous study (Andrews et al. 2005). The colonies from the Gulf of Alaska were collected at depths of 746 (57.885° N, 137.492° W) and 874 m (55.007° N, 134.435° W), while the Davidson Seamount colonies were deeper, collected at 1425 m (35.728° N, 122.713° W) and 1574 m (35.765° N, 122.702° W). The colonies ranged in height from 70 to 120 cm and the shape of colonies ranged from irregular to relatively symmetrical (Table 1).

All colonies were initially classified superficially based on branching patterns and incomplete species descriptions for the regions, but were later classified

Table 1. *Keratoisis* sp. and *Isidella tentaculum*. Collection location, specimen ID, and original collection reference number are provided with the potential species determinations for the bamboo coral specimens examined in the present study

Location	Year	Colony ID	Colony no.	Depth (m)	Observation height (cm)	Species
Davidson Seamount	2002	D02	T428-A10	1425	Irregular	*Keratoisis* sp. (D grp?)[a]
	2006	D06	T948-A2	1574	70	*Keratoisis* sp. (D1a)[b]
Gulf of Alaska	2006	GOA99	GOA06-99A	746	120	*Keratoisis* sp. (B1c)[c]
	2006	GOA107	GOA06-107BB	874	72	*Isidella tentaculum*[d]

[a]D grp designation based on superficial observations
[b]Genetic identification by S. France, University of Louisiana at Lafayette (haplotype igr4-12/msh1 D1a)
[c]Genetic identification by S. France, University of Louisiana at Lafayette (haplotype igr4-9/msh1 B1c)
[d]Confirmation of genetic identification by S. France (pers. comm.), with the new species subsequently described (Etnoyer 2008)

based on ongoing morphological and genetic studies. Portions of each colony were provided to L. Watling (University of Hawaii, Manoa) and S. France (University of Louisiana, Lafayette) for specific identification (Table 1) and have been preserved in their collections. Colony D06 was confirmed as a member of the genus *Keratoisis* and was placed in genetic clade D1 (haplotype igr4-12/msh1 D1a; Fig. 1a). Colony D02 (collected in 2002) was not analyzed genetically due to a lack of sufficient material, but was assumed to also be a member of the D1 clade (*Keratoisis* sp.) based on morphological similarities (Fig. 1b). Colony GOA99 was also confirmed as a member of the genus *Keratoisis*, but was placed in genetic clade B1 (haplotype igr4-9/msh1 B1c; Fig. 2a). Colony GOA107 was identified as a member of the genus *Isidella* and was recently described as *Isidella tentaculum* sp. nov. (Etnoyer 2008; Fig. 2b).

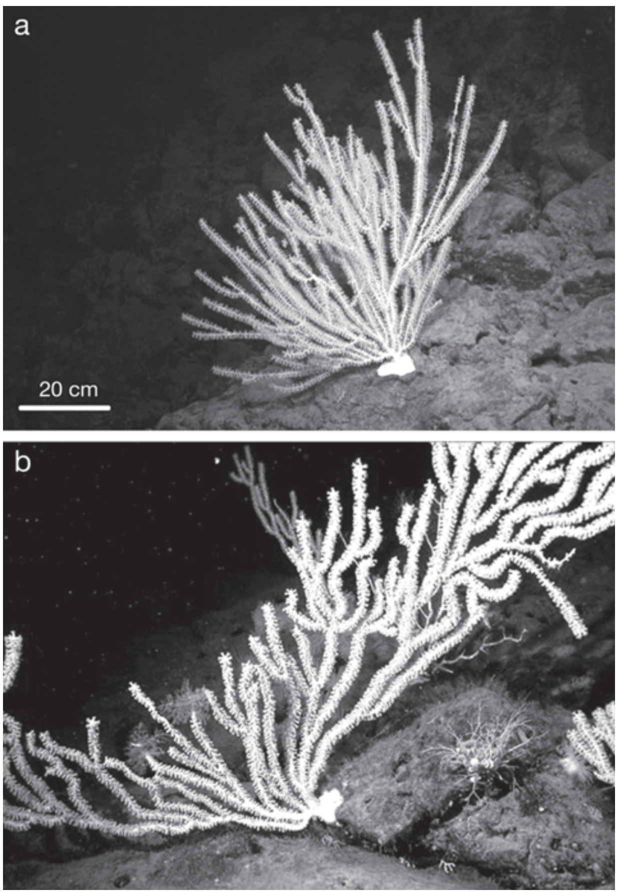

Fig. 1. *Keratoisis* sp. (a) Smaller bamboo coral colony (D06) collected from Davidson Seamount at 1574 m in 2006 (NOAA/MBARI). (b) Larger bamboo coral colony (D02) collected from Davidson Seamount at 1425 m in 2002 (NOAA/MBARI). This colony was reanalyzed in the present study to build on previous ^{210}Pb dating information (Andrews et al. 2005). Each was collected with the ROV 'Tiburon' from aboard the RV 'Western Flyer'

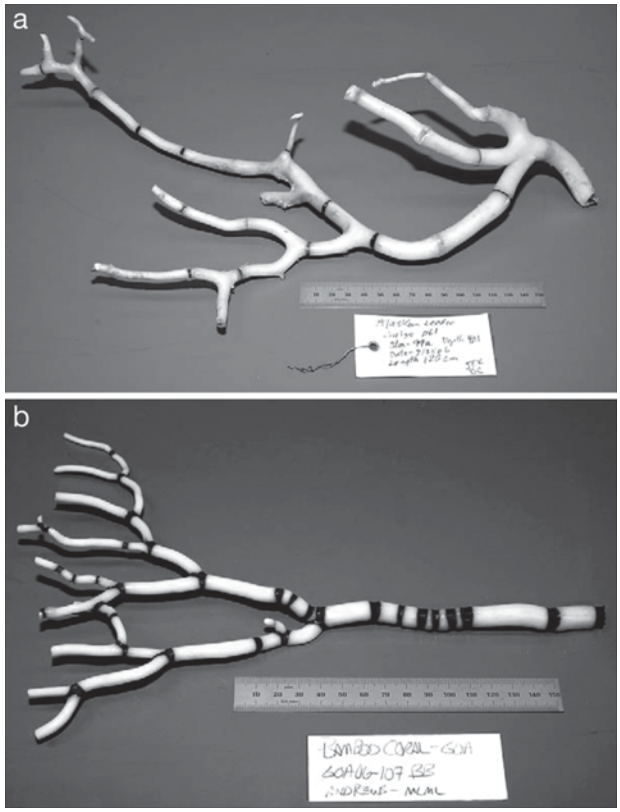

Fig. 2. *Keratoisis* sp. and *Isidella tentaculum*. (a) Lower portion of the *Keratoisis* sp. GOA99 bamboo coral colony after cleaning. (b) Lower portion of the *I. tentaculum* GOA107 bamboo coral colony after cleaning. Sections for each colony were taken from internode segments near the base

^{210}Pb dating. Radial sampling of skeletal cross-sections using a New Wave Research® micromilling machine provided an opportunity to measure ^{210}Pb activity with higher spatial resolution than previously possible. The sections were cut as cross-sections and mounted to glass slides for sample extraction using the micromilling machine. 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. For colonies with a small axial diameter, a refinement was made with successive radial samples to increase the sample size for the same formational period. By sampling 'cylinders' of growth, sample mass was increased, and as a result ^{210}Pb activity increased and could be measured for a narrower period of growth (Fig. 3). Because ^{210}Pb dating relies on determining total ^{210}Pb activity by proxy, using α-spectrometry of ^{210}Po, increasing the sample size was important for making higher precision measurements. To facilitate the sample design, calcified internode segments with a cylindrical shape were chosen and were typically located up the skeletal axis, a short dis-

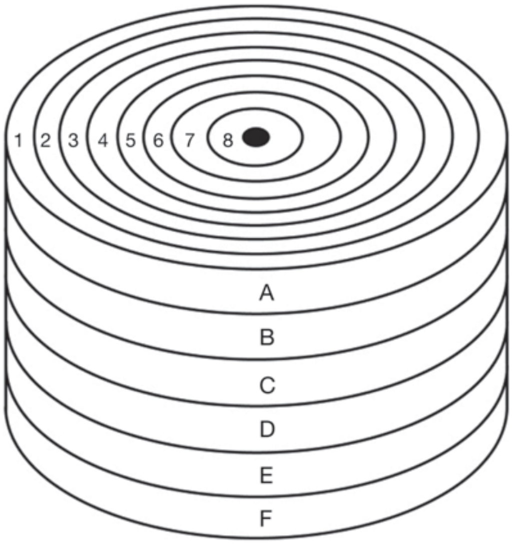

Fig. 3. Diagram of the extraction sample design used to maximize collection of material for a given formational period. This method was applied to colonies D06 and GOA107. The chosen cylindrical segment was cut into 4 to 6 sections (A–F). Each section was sampled successively in a radial manner with the micromill from the edge to the core 1–8. This approach was necessary because of physical limitations on drill bit depth (tapered shank diameter)

tance away from the base. Hence colony age was calculated using the radial growth rate determined from ^{210}Pb dating and measured basal-segment diameter.

The Davidson Seamount corals were prepared for examination differently because of differences in colony size and morphology. Colony D02 had a relatively large diameter (15 mm) for the section analyzed and sufficient sample material was extracted from 8 concentric samples in a single thick section. Each radial sample was numbered sequentially from D02-1 (outer sample toward the edge) to D02-8 (inner sample toward the center). A series of thin sections were necessary for colony D06 because of its small diameter (~8 mm) and it was with this colony that a full application of the improved radial sampling design was applied. Eight radial samples from a series of 6 thin sections (~2 mm thick) were extracted to provide sufficient sample from each radial path (Fig. 3). A total of 48 microsamples were extracted from this set of sections, of which many were combined from the same radius to increase size of sample. Each sample consisted of 3 to 6 radial microsamples and was numbered D06-1 (outer microsamples toward the edge) through D06-8 (inner microsamples toward the center). The target sample weight was at least 0.02 g per sample to increase the activity of ^{210}Po and, consequently, reduce the count time and the counting statistics error from α-spectrometry. This minimum was estimated based on previous activity observations (Andrews et al. 2005). In addition, double the amount of material was extracted from some samples to allow for replicate analyses at a given radius to allow better estimates of precision for the growth rate determination.

The scenario was similar for the corals from the Gulf of Alaska because of the differences in diameter for the chosen segments. Because GOA99 was larger, 7 concentric paths were taken from a single section that was 7.5 mm in radius. More concentric extractions covering a finer radius could have been taken, but the number of samples processed for this analysis was limited by the resources available. Colony GOA107 was chosen arbitrarily for an application of the finer sampling design. Greater resolution was targeted with the extraction of 10 concentric paths from each of 4 sections with a 5.5 mm in radius. Target sample weight was once again no less than 0.02 g per sample.

The decay of exogenous ^{210}Pb across the radius of the skeletal structure, which was unsupported by ^{226}Ra, was used to determine a radial growth rate. For samples with ages that exceeded the utility of this method (~100 yr), the ^{210}Pb:^{226}Ra secular equilibrium was used to establish limits to the calculated growth rate uncertainty. ^{210}Pb was measured indirectly using α-spectrometry on its daughter product, ^{210}Po. The specifics of determining ^{210}Pb activity were based on a previously established protocol that was described elsewhere (Andrews et al. 2002).

A detailed protocol describing sample preparation, chromatographic separation of radium from barium and calcium, and analysis of ^{226}Ra using mass spectrometry was presented in Andrews et al. (1999). The procedures were similar in the present study, except for 2 aspects of the analysis: (1) radium recovery was improved by shifting the collection interval on the final chromatography column to begin after elution of the first 200 µl (as opposed to after 250 µl), and (2) purified radium samples were analyzed using multi-collector inductively coupled plasma mass spectrometry (MC-ICPMS) in place of thermal ionization mass spectrometry (TIMS). While equal levels of purification are needed, MC-ICPMS avoids issues of ionization suppression, which can limit precision on this kind of carbonate sample.

^{226}Ra analyses were performed using an MC-ICPMS. The improved analysis took place on a Nu Plasma™ HR instrument located in the Department of Geology at the University of Illinois, Urbana-Champagne. The analysis introduced the chemically purified radium as a 2% HNO_3 solution into a desolvating nebulizer. The sample was converted into dry aerosols which were swept into the argon plasma and into the mass spectrometer. Sensitivity during radium analysis corresponds to approximately 25 counts per second (cps) radium at an uptake rate of 70 µl min^{-1}. Once in the spectrometer, isotope ratios were measured by switching the magnet back and forth between atomic mass units (amu) 226 and 228 after a 1 min background taken at amu 225.5 or 227.5. An individual sample analysis consisted of 10 measured ratios representing 10 s integrations on each amu peak. After each analysis, the system was washed successively with 5% HNO_3 and 2% HNO_3 for 10 min until no residual radium signal could be observed. Count rates on samples in the present study were usually >1000 cps for each radium isotope, compared to the nominal background on clean acid, which was <1 cps. The strongest runs were used in the final determinations of the baseline-supported levels.

Because ^{210}Pb levels were much greater than ^{226}Ra levels, individual sample analyses of ^{226}Ra was attempted, but resulted in low recovery and a margin of uncertainty that made the determination of ^{226}Ra activity questionable. Based on this finding, the remaining samples from the series were pooled in order to provide a single, well-determined value, resulting in an average ^{226}Ra activity across the section. This value was used to estimate equilibrium for Pb-Ra activities and is represented as a horizontal line in the ^{210}Pb decay plots. It is possible that ^{226}Ra uptake varied by as much as ~10% across the section based on the initial sample series, but greater masses would be required to verify this determination.

Because exogenous ^{210}Pb was present in high quantities, a technique was employed that was analogous to the determination of sediment accumulation rates (Appleby & Oldfield 1992). Measured ^{210}Pb activities in the series of extractions, ranging from the edge (youngest) to near the center (oldest), were used to determine the radial growth rate of the colony based on the exponential decay of ^{210}Pb in accordance with the radioactive decay law. Average sample ^{226}Ra activities were determined across the radial series and subtracted from the measured ^{210}Pb activity, assuming ^{210}Pb was in secular equilibrium with ^{226}Ra, as in previous studies (e.g. Druffel et al. 1990), resulting in estimates of the unsupported or exogenous ^{210}Pb and a determination of growth rates (e.g. Andrews et al. 2002). Radial growth rates were used to determine colony age, and age determinations were subsequently used to estimate axial growth rates (growth along the axis that can represent height in some cases). Colony age estimate uncertainty was based on the regression uncertainty (2 SE).

RESULTS

Davidson corals

^{210}Pb-^{226}Ra determinations

The segment selected from D02 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. Sample mass ranged from 0.0151 to 0.0652 g and the activity of ^{210}Pb decreased as expected from 0.684 ± 7.4 to 0.256 ± 11% dpm g^{-1}, but with an elevated value near the center (0.325 ± 5.5% dpm g^{-1}).

Colony D06 had a small base that was fractured as a consequence of collection and it was necessary to move further up the colony to obtain a cylindrical segment that was 7.6 to 8.3 mm in diameter. Because the radius was ~4 mm, 8 samples would require an extraction path of ~0.5 mm. Hence the center of the segment was cut into a series of sections just under 2 mm thick. This allowed for the extraction of 8 radial samples from each section, and each could be added together to increase the sample mass for a given radius. Six cross sections, each with 8 radial samples, resulted in 48 separate microsamples that ranged in mass from 0.00327 g at the center to 0.02994 g near the edge.

The first set of 8 samples from D06 was produced by pooling each radial sample from the first 6 extractions (radii 1 to 6) from sections A to C (Fig. 3). The 2 radial extractions near the center (radii 7 and 8) were very small and it was necessary to pool all 6 cross sections (A to F) to obtain enough mass (≳0.02 g). As a result, there were 8 radial samples from this segment, with a replicate for radial extractions 1 to 6. Analysis of 4 of the 6 replicate samples from the other cross sections (D to F) provided additional support for the observed decay trend. Sample mass for the full series ranged from 0.0274 to 0.0685 g and the activity of ^{210}Pb decreased as expected from 1.412 ± 4.8% near the edge to 0.434 ± 9.3% dpm g^{-1} near the center (Table 3).

Table 2. *Keratoisis* sp. Radiometric data from the largest *Keratoisis* sp. colony (D02) collected from Davidson Seamount in 2002. Listed are the extracted sample mass and measured total ^{210}Pb activity. Activity was determined as disintegrations per minute per gram (dpm g^{-1}) with propagated error given as a percentage (2 SE). Sample masses were mistakenly transposed and 2 SE erroneously reported as twice the actual value in the original report (Andrews et al. 2007)

Sample number	Sample mass (g)	^{210}Pb activity (dpm g^{-1}, ±2 SE[%])
D02-1	0.0270	0.684 ± 7.4
D02-2	0.0446	0.595 ± 4.4
D02-3	0.0151	0.381 ± 19
D02-4	0.0556	0.311 ± 5.1
D02-5	0.0260	0.295 ± 11
D02-6	0.0652	0.288 ± 4.5
D02-7	0.0306	0.256 ± 11
D02-8	0.0381	0.325 ± 5.5

Table 3. *Keratoisis* sp. Radiometric data from the smaller *Keratoisis* sp. colony (D06) collected from Davidson Seamount in 2006. Listed are the extracted sample mass and measured total ^{210}Pb activity. Activity was determined as disintegrations per minute per gram (dpm g^{-1}) with propagated error given as a percentage (2 SE; erroneously reported 2 times actual value in the original report, Andrews et al. 2007)

Sample number	Sample mass (g)	^{210}Pb activity (dpm g^{-1}, ±2 SE[%])
D06-1[a]	0.0361	1.245 ± 5.9
D06-2a	0.0685	1.412 ± 4.8
D06-2b	0.0384	1.193 ± 4.9
D06-3a	0.0560	1.002 ± 8.8
D06-3b	0.0352	0.914 ± 5.2
D06-4	0.0549	0.798 ± 5.6
D06-5a	0.0398	0.622 ± 7.0
D06-5b	0.0350	0.677 ± 5.9
D06-6a	0.0304	0.552 ± 7.8
D06-6b	0.0318	0.515 ± 7.1
D06-7	0.0423	0.474 ± 7.9
D06-8	0.0274	0.434 ± 9.3

[a]Lower activity per unit mass may be due to inclusion of mounting medium and/or young material (<2 yr old) that is not in equilibrium (^{210}Po:^{210}Pb)

^{226}Ra determinations for D02 in the present study were similar to the findings of a previous study (Andrews et al. 2005) and had greater precision. In Andrews et al. (2005), the ^{226}Ra activities had a relatively high degree of uncertainty and measured values were 0.190 ± 20 and 0.266 ± 8.0 % dpm g^{-1} at 2 locations in the colony, with an average of 0.228 ± 0.054 dpm g^{-1}. The most reliable measurements for the colony in the present study were relatively consistent with these findings and were used as an estimate of supported levels (0.247 ± 0.059 dpm g^{-1}; n = 3). Radium for D06 (0.251 ± 0.032 dpm g^{-1}) was determined from a series of 6 samples across the section and the baseline supported level was similar and more consistent relative to D02.

^{210}Pb dating

^{210}Pb data from colony D02 provided a fairly well constrained radial growth rate of 0.051 mm yr^{-1} (0.039 to 0.074 mm yr^{-1}, 2 SE). The growth rate data for this portion of the colony translated to an age of 148 yr (102 to 195 yr, 2 SE). 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 ^{210}Pb activity (0.325 ± 5.5 dpm g^{-1}) 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. 2007). The other sample (D02-7) was near equilibrium with ^{226}Ra (0.247 ± 0.059 dpm g^{-1}), indicating the age of this portion of the section was in the order of 100 yr old (samples on the slope or decline of ^{210}Pb activity can be used for determining a growth rate; Appleby & Oldfield 1992). Given this sample, located at an average radius of 5.5 mm, was approximately 100 yr old, a limit can be applied to the uncertainty of the calculated growth rate. Rates more rapid than 0.055 mm yr^{-1} were unlikely because sample D02-7 would not have been in equilibrium. Hence the minimum age of this segment was near 136 yr, leading to an age range of 145 to 282 yr for the colony based on the radius range in the basal segment (8 to 11 mm; Table 4). Given the calculated growth rate, a decay plot revealed the general conformity of the ^{210}Pb activity series to the expected decay curve (Fig. 4).

In concert with the findings for D02, colony D06 provided a well-constrained slope that resulted in a radial growth rate of 0.057 mm yr^{-1} (0.052 to 0.064 mm yr^{-1}, 2 SE). The growth rate data for this portion of the colony translated to an age of 98 yr (89 to 107 yr, 2 SE). This age and growth information was based on a regression of 11 out of 12 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 ^{210}Pb activity (1.245 ± 5.9 % dpm g^{-1}) 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 ^{210}Pb activity from what may be occasional secondary deposition. Given the calculated growth rate, a decay plot revealed good conformity of the ^{210}Pb activity series to the expected decay curve (Fig. 5).

Table 4. *Keratoisis* sp. Growth rates and estimated ages calculated for bamboo coral segments and full colonies based on ^{210}Pb data and constrained by another factor. ^{210}Pb data calculations for D02 did not take into consideration a minimum age determined based on ^{210}Pb-^{226}Ra equilibrium. 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 (range = 2 SE). Axial rate was calculated assuming constant growth

Colony	Species	Radial rate (mm yr^{-1})	Segment age (yr)	Colony age (yr)	Axial rate (cm yr^{-1})
D02	*Keratoisis* sp.	0.051	148	–	–
	(D grp?)	(0.074–0.039)	(102–195)		
		0.055[a]–0.039	136–195	145–282	0.28–0.14
D06	*Keratoisis* sp.	0.057	77	98	0.74–0.67
	(D grp)	(0.054–0.059)	(69–84)	(89–107)	

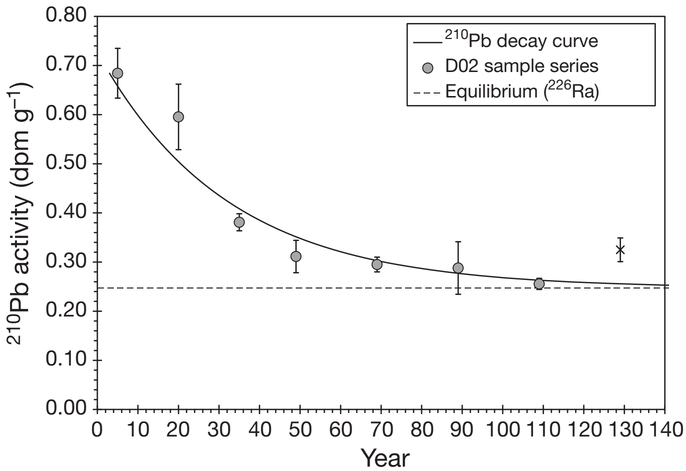

Fig. 4. The general conformity of ^{210}Pb activities to the decay curve for colony D02 based on the fitted regression to the ln-transformed data. ^{210}Pb:^{226}Ra equilibrium was based on the average measured ^{226}Ra (0.247 ± 0.059 dpm g^{-1}). Calculated radial growth rate for this colony was 0.051 mm yr^{-1} (0.039 to 0.074 mm yr^{-1}, 2 SE). Note that the center sample (×) was elevated relative to the pattern of ^{210}Pb decline and the innermost samples were excluded from this relationship because: (1) one was in equilibrium with ^{226}Ra and provided an unrealistic representation of exogenous ^{210}Pb; and (2) the other was elevated in ^{210}Pb activity relative to the decay series, likely due to incorporation of younger material within the axial pore

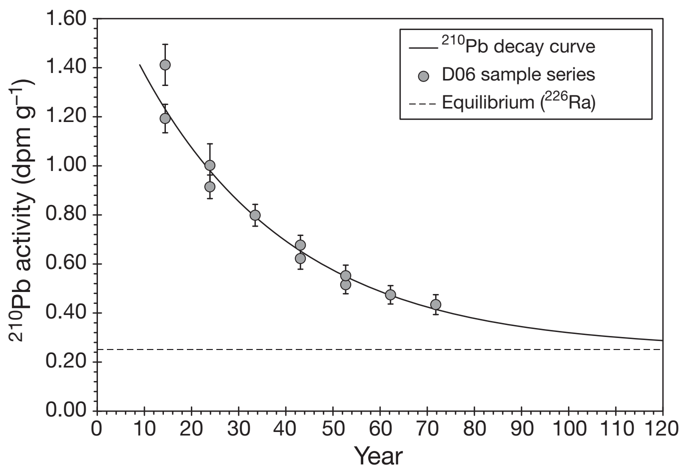

Fig. 5. The relatively tight conformity of ^{210}Pb activities to the decay curve for colony D06 based on the fitted regression to the ln-transformed data. ^{210}Pb:^{226}Ra equilibrium was based on the average measured ^{226}Ra (0.251 ± 0.032 dpm g^{-1}). Calculated radial growth rate for this colony was 0.057 mm yr^{-1} (0.052 to 0.064 mm yr^{-1}, 2 SE)

Because the sampled portion of colony D06 was up the axis and away from the basal section (broken during collection) by approximately 7.5 cm, the maximum age of this colony can be estimated from the measured diameter of the base (10.8 to 11.7 mm). Using the calculated growth rate (0.057 mm yr^{-1}) and the average radius (5.63 mm), an age of 98 yr was calculated for this colony, with a potential age range of 89 to 107 yr (Table 4). In addition, through the 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 axial growth rate of this colony may have been 0.67 to 0.74 cm yr^{-1}.

Radiometric results for both of the Davidson Seamount corals (*Keratoisis* sp., D02 and D06) converged on a radial growth rate of approximately 0.055 mm yr^{-1}, and calculated axial growth rates were variable. For the smaller of the 2 colonies (~70 cm tall), the age was 98 yr with an average axial growth rate of approximately 0.7 cm yr^{-1}. A minimum age of 145 yr (upper limit of 282 yr) was determined for the largest colony; an irregular shape and height made it difficult to determine an axial growth rate. Based on one major branch length (~40.5 cm) that could be followed through to the base, the axial growth rate was lower than that of the younger colony, and ranged between 0.14 and 0.28 cm yr^{-1}. Differences in the axial growth rates between the 2 colonies may indicate nonlinear growth with increasing colony height.

Alaska corals

^{210}Pb-^{226}Ra determinations

The *Keratoisis* sp. specimen (GOA99) provided 7 radial samples that ranged in weight from 0.0252 g toward the middle of the section to 0.0402 g at the edge (Table 5). Measured ^{210}Pb activity decreased as expected from near the edge to near the middle and ranged from 0.435 ± 4.8 to 0.133 ± 13.2 % dpm g^{-1}. The extracted exterior was not analyzed for ^{210}Pb because of the unavoidable inclusion of adhesive material, and the potential for ^{210}Po (proxy for ^{210}Pb) to not attain secular equilibrium in the youngest material (collected <2 yr prior to analysis).

The *Isidella tentaculum* specimen (GOA107) provided 10 radial samples (pooled radial samples from 4 contiguous sections) which ranged in weight from 0.0273 g toward the middle of the section to 0.0709 g near the edge (Table 6). Measured ^{210}Pb activity decreased as expected from near the edge to near the middle and ranged from 1.202 ± 4.6 to 0.509 ± 7.1 % dpm g^{-1} near the middle; the middle sample was slightly elevated (0.557 ± 7.7 % dpm g^{-1}). The extracted exterior was not analyzed for ^{210}Pb because of the potential inclusion of adhesive material.

Table 5. *Keratoisis* sp. Radiometric data from the *Keratoisis* sp. specimen (GOA99) collected from the Gulf of Alaska. Listed is the extracted sample mass and measured total ^{210}Pb activity. Activity was determined as disintegrations per minute per gram (dpm g^{-1}) with propagated error given as a percentage (2 SE). nm: not measured because of included adhesive

Sample number	Sample mass (g)	^{210}Pb activity (dpm g^{-1}, ±2 SE [%])
GOA99-1	0.0402	nm
GOA99-2	0.0629	0.435 ± 4.8
GOA99-3	0.0626	0.285 ± 5.6
GOA99-4	0.0512	0.223 ± 6.8
GOA99-5	0.0374	0.214 ± 8.3
GOA99-6	0.0342	0.204 ± 9.2
GOA99-7	0.0252	0.133 ± 13.2

Table 6. *Isidella tentaculum*. Radiometric data from the *I. tentaculum* specimen (GOA107) collected from the Gulf of Alaska. Listed is the extracted sample mass and measured total ^{210}Pb activity. Activity was determined as disintegrations per minute per gram (dpm g^{-1}) with propagated error given as a percentage (2 SE). nm: not measured because of included adhesive

Sample number	Sample mass (g)	^{210}Pb activity (dpm g^{-1}, ±2 SE [%])
GOA107-1	0.0453	nm
GOA107-2	0.0709	1.202 ± 4.6
GOA107-3	0.0736	1.128 ± 4.7
GOA107-4	0.0636	1.021 ± 4.9
GOA107-5	0.0645	0.918 ± 4.9
GOA107-6	0.0580	0.877 ± 5.1
GOA107-7	0.0457	0.651 ± 5.8
GOA107-8	0.0396	0.632 ± 6.1
GOA107-9	0.0352	0.509 ± 7.1
GOA107-10	0.0273	0.557 ± 7.7

Radium determinations were made from pooled samples in the radial series. For *Keratoisis*. sp., the average ^{226}Ra activity from a combined sample weight of 0.1885 g (from GOA99-1, 2, 4, and 6) was 0.177 ± 7.8% (2 SE) dpm g^{-1}, lower than all of the ^{210}Pb activities except for the most central sample (0.133 ± 13.2% [2 SE] dpm g^{-1}). For *Isidella tentaculum*, the average ^{226}Ra activity from a combined sample weight of 0.2156 g (from GOA107-3, 5, 7, and 9) was 0.211 ± 6.2% (2 SE), lower than all of the ^{210}Pb activities in the sample series by at least a factor of 2. Each of these radium runs was very good, with 16 to 23% of the ^{226}Ra signal from the sample. These values were used to determine the baseline acivity levels and to properly approximate exogenous ^{210}Pb activities.

^{210}Pb dating

^{210}Pb data for GOA99 provided a well-constrained slope that resulted in a radial growth rate of 0.056 mm yr^{-1} (0.044 to 0.075 mm yr^{-1}, 2 SE). One sample could not be taken into consideration because its measured value was below the average ^{226}Ra value. It is uncertain why this was the case, but it may have been close to equilibrium and within a natural variation that could not be accounted for with such a small sample size. Given the lowest ^{210}Pb value and its proximity to secular equilibrium with ^{226}Ra, an age of approximately 90 yr can be determined for the near center radial sample. Given the calculated growth rate and the radius of the sample (minus the central axis pore), these data can be translated to a colony age of 116 yr (87 to 146 yr, 2 SE; Table 7). Based on the calculated growth rate, a decay plot revealed good conformity of the ^{210}Pb activity series to the expected decay curve (Fig. 6). Based on the age and approximate height of the colony, an average axial growth rate of 1.03 cm yr^{-1} (0.82 to 1.38 cm yr^{-1}) was determined.

^{210}Pb data for GOA107 provided a good slope, with some irregularities that are discussed below, that resulted in a radial growth rate of 0.10 mm yr^{-1} (0.084 to 0.12 mm yr^{-1}, 2 SE; Fig. 7). Given the calculated growth rate and the radius of the sample (minus the central axis pore), these data can be translated to a colony age of 53 yr (43 to 63 yr, 2 SE; Table 7). An average axial growth rate of 1.36 cm yr^{-1} (1.14 to 1.67 cm yr^{-1}) was determined from the age and approximate height of the colony. Given the calculated growth rate, a decay plot revealed good conformity of the ^{210}Pb activity series to the expected decay curve (Fig. 8). This species grew most rapidly with a radial growth rate of 0.10 mm yr^{-1}, nearly twice the rate of the *Keratoisis* spp. in the present study.

Closer investigation of the ln-transformation and decay plots provided an indication of what appeared to be 2 periods of interrupted radial growth (Figs. 9 & 10). This offset can be seen between the 5th and 6th, 7th and 8th, and perhaps the 8th and 9th data points in

Table 7. *Keratoisis* sp. and *Isidella tentaculum*. Growth rates and estimated age calculated for bamboo corals based on ^{210}Pb data. Axial rates were an average for the life of the colony, assuming constant growth. Ranges are given in parentheses

Colony	Species	Radial rate (mm yr^{-1})	Colony age (yr)	Axial rate (cm yr^{-1})
GOA99	*Keratoisis* sp. (B grp)	0.056 (0.044– 0.075)	116 (87–146)	1.03 (0.82–1.38)
GOA107	*I. tentaculum*	0.10 (0.084– 0.12)	53 (43–63)	1.36 (1.14–1.67)

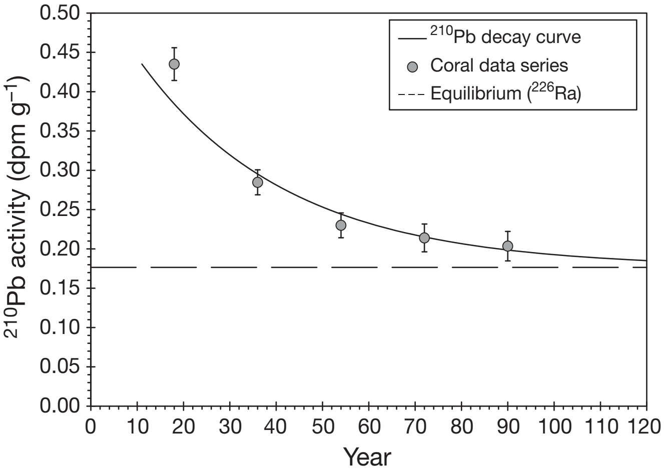

Fig. 6. The general conformity of ^{210}Pb activities to the decay curve for colony GOA99 based on the fitted regression to the ln-transformed data. ^{210}Pb:^{226}Ra equilibrium was based on the average measured ^{226}Ra (0.177 ± 7.8% dpm g^{-1}). Calculated radial growth rate for this colony was 0.056 mm yr^{-1} (0.044 to 0.075 mm yr^{-1}, 2 SE)

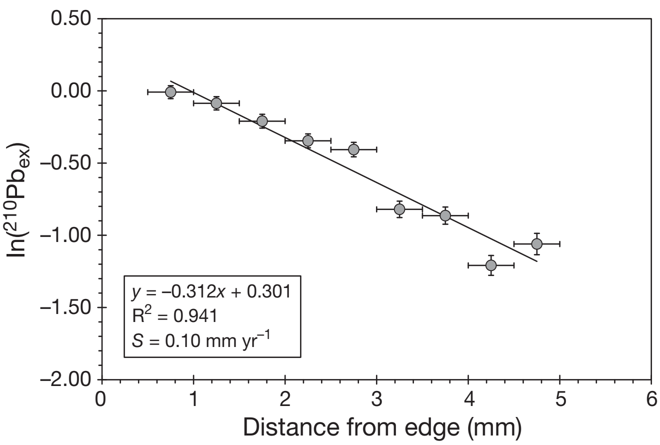

Fig. 7. ln-transformed exogenous ^{210}Pb ($^{210}Pb_{ex}$) relative to the distance from the edge for GOA107. Linear regression revealed a radial growth rate (S) of 0.10 mm yr^{-1} (0.092 to 0.11 mm yr^{-1}) for this colony

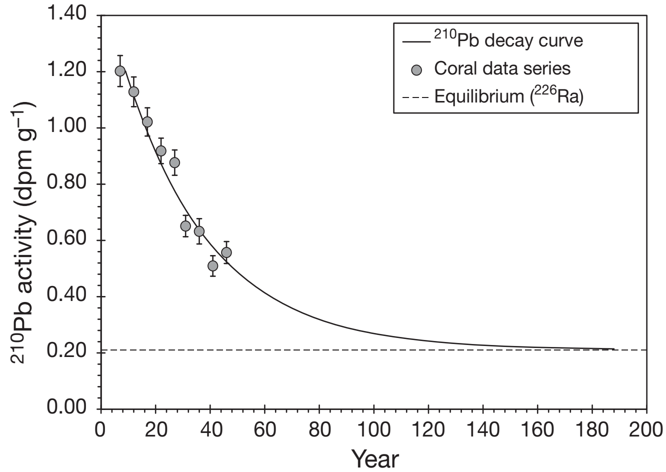

Fig. 8. The general conformity of ^{210}Pb activities to the decay curve for colony GOA107 based on the fitted regression to the ln-transformed data. ^{210}Pb:^{226}Ra equilibrium was based on the average measured ^{226}Ra (0.211 ± 6.2% dpm g^{-1})

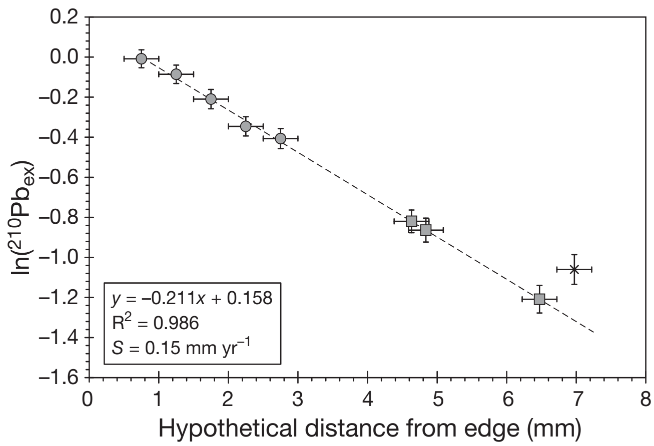

Fig. 9. Investigation of a possible hiatus in growth for GOA107 that was based on the linear relationship established by the first 5 samples. The line best fit was used to determine the potential position of the measured values, given growth was not halted for period (hypothetical distance from edge). The hiatus period was determined based on the growth rate (S, 0.15 mm yr^{-1}) and each break in growth may have been ~11 to 13 yr in duration (interpolated samples denoted with a grey square). The axial center value (×) was not considered in this calculation because it deviated from the expected trend

each plotted series. Assuming ^{210}Pb uptake was consistent for the entire radial series, relative to the first 5 data points in the series (where no apparent interruptions occurred), a regression could provide a prediction of missing growth in terms of radius and time (Fig. 9). The calculated missing radial growth for the 2 sections of the plot were approximately 1.9 and 1.6 mm, which translated into periods of interrupted growth with durations of approximately 13 and 11 yr (±3 yr), respectively. This finding also required an increase in the calculated radial growth rate from 0.010 mm yr^{-1} (average overall rate) to 0.15 mm yr^{-1} during periods of growth; the age of the colony does not change because the decay of ^{210}Pb dictates the time between end points (near edge to near center). Given these were actually periods of arrested development, no radial growth would have occurred in this basal section from approximately 1961 to 1973 and 1975 to 1987 (±3 yr). It is interesting to note, however, that there were no apparent microscopic rings in the cross sections as visible evidence for such periods of interrupted growth, which points to another possibility. Environmental ^{210}Pb may have changed during these periods (Fig. 10), but would require significant changes to account for the observed differences in

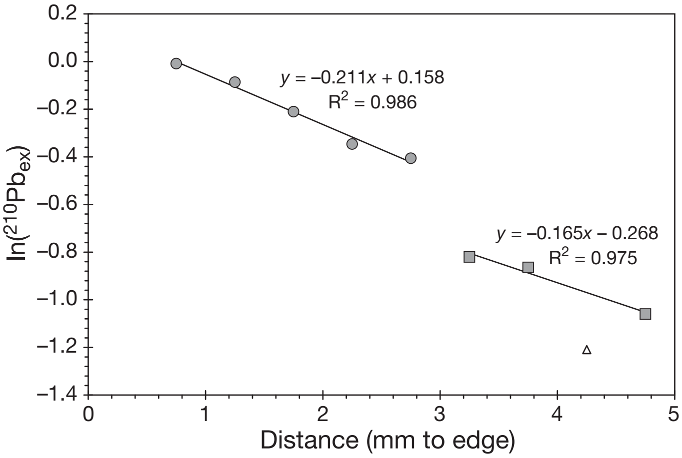

Fig. 10. To further investigate an alternate interpretation of the apparent offset in ^{210}Pb activities, changes in environmental ^{210}Pb were considered. Assuming consistent growth, sample series that appeared to run in parallel were considered representative of consistent environmental ^{210}Pb after changes took place. A regression of the each series indicated there was some consistency to the growth rates between the 2 hypothetical periods (average = 0.17 ± 0.02 mm yr^{-1}). One sample (mid-series and toward the middle of the axial section, △) appears to indicate a drop in ^{210}Pb to even lower levels

measured activity (~20 to 50% based on the back-calculation of initial-uptake activities).

Possible changes in environmental ^{210}Pb are perhaps the only caveat to the age determination and could increase the age uncertainty for the colony. However, if the latest growth (the first 5 data points) is used as an indication of growth rate during a time of consistent ^{210}Pb uptake, it is not unreasonable to assume the radial growth rate would be the same for earlier sections of the radius (0.15 mm yr^{-1}). In support of this approach, 3 additional data points that run nearly parallel, but at an initial activity level 20% lower, provided an estimate of 0.19 mm yr^{-1}. Given this scenario, when growth was continuous and uptake of ^{210}Pb was variable, an average radial growth rate of 0.17 provides a colony age closer to 32 yr.

DISCUSSION

Refined ^{210}Pb dating provided well-constrained estimates of age and growth for bamboo corals of the northeastern Pacific Ocean, but also revealed complexities associated with either interrupted radial growth or changes in the environmental availability of ^{210}Pb. Growth rates determined in the present study compared favorably with rates determined for the group elsewhere, which will be dicussed later. *Isidella tentaculum* has the greatest recovery potential of the 3 species studied, growing to 72 cm in ~50 yr post-recruitment and possibly faster at ~30 yr, if the observed differences in ^{210}Pb activity were due to environmental changes. In general, *Keratoisis* spp. seems to be slower growing and longer-lived, and recovery time for this group might be in the order of a century or more. Our findings of slow growth and long life compare favorably to those made for bamboo corals from other regions of both the Pacific and North Atlantic Oceans, the details of which are discussed in the following paragraphs, and highlight the need for immediate conservation measures to protect known concentrations of these large, and particularly fragile, habitat-forming members of deep-sea ecosystems.

The analysis of the bamboo coral colony collected in 2002 (D02) was refined by adding more samples to the ^{210}Pb dating series and a more accurate measure of age and growth than those made previously (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 roughly 80 to 220 yr (Andrews et al. 2005). The basis for this determination was from growth zone counts in small regions of the cross section that were not well defined (0.05 to 0.11 mm per zone), which were extrapolated to the full section radius. Based on the refined ^{210}Pb dating in the present study, the age of this colony had a lower limit of 145 yr with a maximum of 282 yr from the lowest growth rate (0.039 mm yr^{-1}).

Based on the findings of the present study, the axial growth rate for D02 could also be reassessed. The estimated growth rate from zone counting translated to an axial growth rate of 0.19 to 0.44 cm yr^{-1} (Andrews et al. 2005). The present study provided a more refined axial growth rate of 0.14 to 0.28 cm yr^{-1}; however, losses or changes in the growth of branches cannot be accounted for and as a result axial growth rates are not certain. At best, these determinations are an average over the life of the colony and the actual time for a colony to reach a given height could be highly variable.

Because both Davidson Seamount colonies (D02 and D06) were 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 (D02) relative to the growth of the smaller colony collected in 2006 (D06), 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 axial growth rate of ~0.7 cm yr^{-1} for D02; however, the height of the colony was variable and any loss or addition of branches and changes in growth direction by the colony cannot be accounted for. Roark et al. (2005) provided data that suggested growth may have been greater for larger colonies, presumably because larger colonies are more efficient at feeding. In terms of radial growth, however, the present study provides an indication that growth may be consistent throughout the life of this species and was approximately 0.055 mm yr^{-1} based on the convergence of growth rates between the colonies.

For bamboo coral studies in general, the findings presented here were similar and continue to provide support for relatively slow growth rates and extreme longevity for the group, but also highlight the requirement for better growth rate and age precision. The bamboo corals from Warwick Seamount had a radial growth rate of 0.05 ± 0.01 to 0.16 ± 0.01 mm yr^{-1}, as was determined from bomb radiocarbon ages of 64 ± 4 to 208 ± 42 yr (Roark et al. 2005). ^{210}Pb dating of a bamboo coral (possibly *Lepidisis* sp.) collected near New Zealand revealed a radial growth rate similar to the maximum estimated from Warwick Seamount at 0.18 ± 0.02 mm yr^{-1} (Tracey et al. 2007), and most similar to the *Isidella tentaculum* rate determined here. In a unique study, Noé & Dullo (2006) collected a fossil bamboo coral skeleton (Family Isididae) off New Zealand and, using the difference between radiocarbon ages determined for the interior and exterior of the skeleton, estimated the colony age at 305 ± 30 yr. The estimated radial growth rate of this colony was much greater than most other bamboo coral studies at 0.4 mm yr^{-1} (range = 0.23 to 0.64 mm yr^{-1}; Noé & Dullo 2006).

Specific to *Keratoisis* spp., an analysis using ^{210}Pb dating on a specimen collected off southeastern 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 ^{210}Pb attaining equilibrium just prior to the last 7 mm of growth for a section with a radius of approximately 19 mm (calculated from Fig. 1 of Thresher et al. 2004), a growth rate of approximately 0.05 mm yr^{-1} was determined. This determination roughly implied that the overall age of the section was approximately 400 yr. The Northwest Atlantic Ocean, *Keratoisis ornata* was aged 3 ways (bomb radiocarbon dating, radiocarbon aging, and ^{210}Pb dating), obtaining a range of radial growth rates (0.053 ± 0.009 to 0.075 ± 0.011 mm yr^{-1}) that were also similar to previous studies of *Keratoisis* spp. (Sherwood et al. 2008, Sherwood & Edinger 2009). This genus seems to cluster around a radial growth rate of approximately 0.05 to 0.07 mm yr^{-1} and centenarian colonies are likely a common occurrence in long-standing populations.

Use of micromilling and a replicated radial sampling design made the application of ^{210}Pb dating possible from a series of narrow growth periods in small coral sections. Low sample mass was one of the primary limitations for ^{210}Pb dating of bamboo corals. Increasing the sample mass extracted for a given formational period not only increased measureable ^{210}Pb for better precision, but also provided an opportunity for replicate sampling of a given growth period. For the application to the smaller *Keratoisis* sp. colony (D06), determination of a radial growth rate led to a well-refined result of 0.057 mm yr^{-1} (0.052 to 0.064 mm yr^{-1}). Replicate samples added to the sample series (4 of 11 samples), which covered a radius of <5 mm, increased the precision of the age determination to within 10% (98 ± 9 yr).

The increase in measureable ^{210}Pb using this approach provided an unexpected result with the *Isidella tentaculum* colony (GOA107). Averaging the decay over time led to a reasonable estimate of 53 ± 10 yr; however, the pattern of ^{210}Pb decay provided evidence for either a hiatus in growth or variable uptake of ^{210}Pb from the environment over time. This pattern would not have been differentiable if the precision of measured ^{210}Pb through the sample series was lower, as would have been the case with lower sample mass or wider sampling of growth periods (greater radius per extraction). It is uncertain what the causes were for the observed changes in ^{210}Pb with time.

A hiatus in radial growth for 2 periods of approximately 10 yr each seems unlikely because there was no microscopic evidence visible as a discontinuity in the section; however, this does not preclude the possibility of discontinuous growth. Changes in environmental ^{210}Pb, and as a consequence uptake of ^{210}Pb to the skeletal matrix, may be supported by what appears to be consistent radial growth (0.17 ± 0.02 mm yr^{-1}) during periods of relatively consistent ^{210}Pb. Given a constant growth rate, the observed changes in environmental ^{210}Pb may have been in the order of 20 to 30% and within a period of ~5 yr for each occurrence. The most recent period of formation (15 to 20 yr) was the most consistent and apparently the highest for environmental ^{210}Pb.

The differences between ^{210}Pb uptake consistencies for these corals may be related to location. The *Isidella tentaculum* colony was collected from a shallower continental slope location, which could be influenced by more coastal and continental processes. The *Keratoisis* sp. colonies were collected much deeper and well offshore on the slopes of Davidson Seamount, a region more influenced by oceanic processes and unlikely to change rapidly in terms of environmental ^{210}Pb.

Application of a refined ^{210}Pb dating technique has shown promise for making relatively high-precision growth rate and age determinations for bamboo corals. While there is some question about constant radial growth or the consistency of ^{210}Pb uptake for the *Isidella tentaculum* colony, the application of this refined method provided an opportunity to critically evaluate growth rate and age determinations derived from the assumption of consistent ^{210}Pb uptake. In this light, caution must be taken when applying bomb radiocarbon dating as a tool for extrapolating age because there is no way to account for a hiatus of radial growth. It is recommended that future applications of bomb radiocarbon dating provide support for extrapolated ages by applying ^{210}Pb dating (e.g. Sherwood et al. 2008) or other radiometric methods (e.g. Thresher et al. 2004).

Bamboo corals are common deep-water inhabitants of continental slopes and seamounts of the northeastern Pacific Ocean, regions that are now receiving more attention from fishing activity in search of new resources. The findings presented in the present study, along with previous accounts, clearly indicate that bamboo coral would require decades or more to recover from disturbance. However, to fully understand recovery potential more information is needed in terms of other life history characteristics, and an accurate determination of age and growth is the foundation of understanding long-term population dynamics. Characteristics such as age-specific patterns of fecundity, in terms of both colony and polyp age, and recruitment potential, in terms of lifetime egg production, are just two important factors in understanding population dynamics and potential recovery that remain undescribed. The goal for resource managers should be to identify the location of bamboo coral patches or populations and implement appropriate measures to study and preserve their ecological function.

Acknowledgements. The research on Davidson Seamount corals was made possible by the Monterey Bay National Marine Sanctuary (MBNMS) in a collaborative effort with Monterey Bay Aquarium Research Institute (MBARI). Special thanks to E. Burton at MBNMS for recommending this line of work to Moss Landing Marine Laboratories and for editorial assistance. Thanks to M. Conway (MBARI) for developing ROV 'Tiburon' collection boxes for segregation of collected coral samples. Thanks to the crew of the RV 'Western Flyer' for excellent navigation and food. Thanks to the pilots of the ROV 'Tiburon' (D. French, B. Schaefer, R. Reynolds, C. Scott, and R. Prickett) for careful collection of the fragile coral colonies. The research on Gulf of Alaska corals was made possible by NOAA Fisheries and the collections of J. Karinen and D. Csepp. Thanks to G. M. Cailliet (Moss Landing Marine Laboratories [MLML]) for continued support in this line of coral research, and C. Brooks (MLML) and H. Hawk (MLML) for assistance with sample processing. Thanks to L. Watling (University of Hawaii, Manoa) and S. France (University of Louisiana, Lafayette) for specimen identifications and for including the specimens in a study to monograph the subfamily Keratoisidinae, which is extremely important work. The Davidson Seamount portion of the study was funded by a contract from NOAA's MBNMS with funds from NOAA's Office of Ocean Exploration (reference no. NCND6022-5-00061). The Gulf of Alaska portion of this study was funded by a contract from NOAA Fisheries, Alaska Region, under requisition no. NFFS7400-7-21504.

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Submitted: May 16, 2009; Accepted: July 6, 2009

Proofs received from author(s): October 28, 2009