

AGE AND GROWTH OF TWO GENERA OF DEEP-SEA BAMBOO CORALS (FAMILY ISIDIDAE) IN NEW ZEALAND WATERS

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ABSTRACT

We provide a detailed description of growth zone counts at two locations in the skeletal structure of four bamboo coral colonies (Family Isididae, sub-family Keratoisidinae, genera *Lepidisis* spp. and *Keratoisid* sp. from New Zealand). Zone counts were made microscopically on skeletal cross-sections of calcareous internodes producing counts of up to 90 for *Lepidisis* spp. and 160 for *Keratoisid* sp. Scanning Electron Microscope (SEM) images taken of cross-sections at the junction of the calcareous internode and gorgonin node revealed clear zone resolution and produced counts that were substantially higher (a maximum 490 zones). Lead-210 dating was applied to the skeletal structure of one specimen of *Lepidisis* sp. to develop an independent estimate of age and growth. Radial micro-sampling of the skeletal carbonate indicated the age of the colony at the largest section (7.4 mm average radius) was 43 yrs old (26–61 yrs 95% CI), with an average radial growth rate of 0.18 mm yr⁻¹ (0.13–0.29 mm yr⁻¹ 95% CI). Comparisons between the three age estimates for *Lepidisis* sp. were made and it was hypothesized that zones observed by light microscope have a bi-annual periodicity and that SEM-observed zones at the nodal juncture may represent an environmental event, such as lunar periodicity.

Bamboo corals (Order Scleractinia: Calcaxonia: Isididae) are sedentary, non-tropical, octocorals with a conspicuously jointed, central skeletal axis comprised of white calcareous segments or internodes alternating with dark gorgonin nodes, often referred to as organic or proteinaceous material. The gorgonin provides a structural framework in the biomineralisation process and is responsible for flexibility of the skeletal axis. The calcite provides skeletal support, facilitating growth in regions with significant current flows. The central axis is covered by a coenenchyme containing calcareous spicules and bearing polyps. Skeletal micro- and ultra-structure of isidid skeletons is described in detail in Noé and Dullo (2006).

Genera within the Isididae can be tentatively identified from their mode of branching, and species can be identified based on the microscopic form of the spicules and their arrangement within the polyps and coenenchyme. The lack of a comprehensive systematic description often makes it difficult to differentiate genera and species.

Bamboo corals are widely distributed in New Zealand's Exclusive Economic Zone occurring on seamounts, as well as in areas of comparatively flat slope topography and deep-sea reef (Grant, 1976; Smith et al., 2004). They are found at water depths in excess of 100 m, with many living well below 1000 m. To date, 14 species of sub-family Keratoisidinae have been identified for the New Zealand region (Grant, 1976; Smith et al., 2004; Sanchez, unpubl. data), some are endemic (Sanchez et al., 2004).

Together with other gorgonian, stony, and encrusting corals, bamboo corals provide an ideal habitat for small invertebrates and shelter for fish species (Auster and Langton, 1999; Fossa et al., 2002; Husebo et al., 2002; Rowden et al., 2005). They also contain invaluable information about the age of deep-water coral communities, as well as about past climate events (Thresher et al., 2004).

New Zealand fisheries for high value commercial species, such as orange roughy (*Hoplostethus atlanticus* Collett, 1889), black oreo (*Allocyttus niger* James, Inada, and Nakamura, 1988), and smooth oreo (*Pseudocyttus maculatus* Gilchrist, 1906), use heavy fishing gear. These trawling activities can impact fragile benthic communities, such as corals (Clark, 1999; Clark and O'Driscoll, 2003). Other fisheries studies, such as those by Koslow et al. (2000), Hall-Spencer et al. (2002), and Morgan et al. (2005), also discuss trawling damage and subsequent implications to coral communities in other regions. Additional threats include impacts from oil and gas exploration and extraction, the laying of cables and telecommunications links, and waste disposal (Glover and Smith, 2003; Kogan et al., 2003). An understanding of deep-sea coral systematics, biology, longevity, and growth rates is essential to appreciate the nature and extent of any impacts, and to mitigate them.

As part of the impact of fishing and biodiversity studies carried out at the National Institute of Water and Atmospheric Research (NIWA), New Zealand, an ageing project was started to obtain estimates of age and growth of the various deep-sea corals. Primarily, the work has focused on developing some understanding of the regeneration potential of these important long-lived and slow growing organisms in order to manage the resource, improve ecosystem management, and prevent population collapse.

For some species of coral, ages can be estimated by counting skeletal growth zones in cross sections of the axial skeleton (Grigg, 1974; Andrews et al., 2002; Risk et al., 2002; Marschal et al., 2004; Thresher et al., 2004; Roark et al., 2005; Sherwood et al., 2005). Unlike other coral groups that have complex growth, such as the branching scleractinian group and bubble-gum corals where sections can display complex and confusing growth structures, the bamboo corals, whose calcareous sections exhibit relatively simple and clear zone structure, provide a good opportunity for coral growth-zone studies. Various validation methods are available to confirm zone counts and age of corals. Thresher et al. (2004) found good agreement between zone counts in *Keratoisis* spp and two radiometric decay schemes. Roark et al. (2005) used the bomb radiocarbon ($\Delta^{14}\text{C}$) marker to determine growth rates for bamboo corals to verify independent age and growth zone count data. Roark et al. (2005) also counted Sr/Ca cycles and assumed monthly lunar growth bands.

In the present study we applied lead-210 (^{210}Pb) dating as a tool for determining estimates of age and growth and to provide support for the interpretation of observed growth zone counts. This radiometric technique utilizes the radioactive decay of ^{210}Pb that has been isolated from the environment (i.e., incorporated into the skeletal structure of coral) as a natural chronometer (Dodge and Thomson, 1974; Andrews et al., 2002; Adkins et al., 2004). 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 the encapsulated ^{210}Pb decreases to a point where it is supported by radium-226 (^{226}Ra). By taking a series of measurements from near the actively growing margin to parts of the skeleton that were formed earlier, the decrease of ^{210}Pb activity can be used as a measure of age and growth. Lead-210 has a half-life of 22.26 yrs; hence, this approach is useful to about 100 yrs of age, at which time the activity of ^{210}Pb decreases to a level approaching the activity of ^{226}Ra (nearing an equilibrium activity ratio of 1.0). Use of this technique is based on the assumption there is little variation in uptake of ^{210}Pb over time, which is supported in the literature (Appleby and Oldfield, 1992).

METHODS

SAMPLE SELECTION.—Samples were taken from four bamboo coral partial colonies. All four colonies had been collected opportunistically from within the New Zealand Exclusive Economic Zone between 1998 and 2002 by Ministry of Fisheries observers on commercial fishing vessels and were stored dry in the NIWA invertebrate collection. Selection criteria ensured the bamboo coral colonies were sourced from diverse geographic locations and environments, from the flat bottom slope as well as from seamount features, to enable comparisons of growth by region. The colonies appeared to be reasonably complete and were the most intact we could source from the NIWA collection. Some growing tips were broken, but the base region that was sectioned appeared reasonably close to what the actual base region would be in the natural habitat and we therefore assumed the main growth axis for each colony was being studied. Date of sampling was known and the three *Lepidisis* spp. and one *Keratoisis* sp. were live when sampled. *Lepidisis* spp. samples were from the East Cape region in 690–800 m water depth (colony 1), Wanganella Bank, West Norfolk Ridge region sampled in 874–1030 m (colony 2), and from a seamount in the “Graveyard Complex”, Northwest Chatham Rise region in 638–840 m (colony 3; Fig. 1). The *Keratoisis* sp. (colony 4) represents the most southern of the bamboo coral samples sites and was collected from the Snares Shelf, Campbell Plateau region in 935 m (Fig. 1).

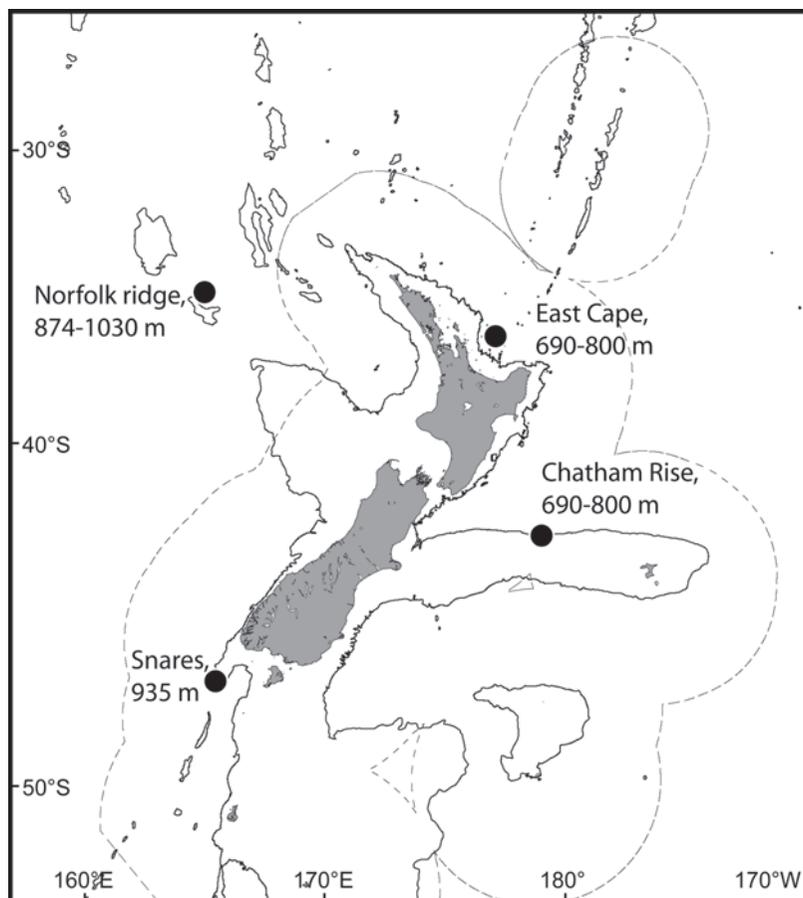


Figure. 1. Map of New Zealand region showing the locations of the four bamboo coral colonies examined.

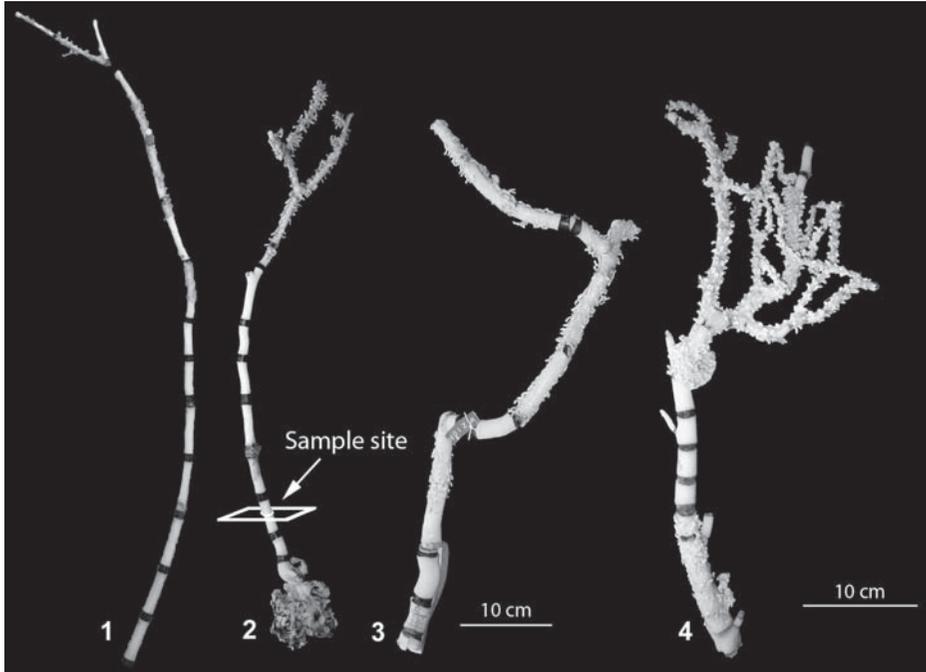


Figure 2. Study species, left to right, *Lepidisis* spp. 1, 2, and 3, and *Keratoisis* sp. 4. Thin section sampling site shown in spp. 2.

The specimens selected for the study were identified using genetic (Smith et al., 2004) as well as taxonomic (Sanchez, unpubl. data) information. Spicule morphology provided the identification to only genus level and the final selection comprised partial colonies of the bamboo coral subfamily Keratoisidinae, species: *Lepidisis* spp. (3 colonies) and *Keratoisis* sp. (1 colony) (Fig. 2).

Colony 1 *Lepidisis* sp. was sectioned at four locations along the axial skeleton ranging from near the base (oldest portion) to near the tip (youngest portion) of the colony (Fig. 3). Thin transverse sections were prepared for growth zone counts. Sections for Scanning Electron Microscope (SEM) imaging were taken at the junction of the gorgonin nodes and calcareous internodes (Fig. 3), adjacent to the thin section sites. The remaining colonies were only sampled at one site close to the base. Radial and linear section measurements for all colonies are provided in Table 1. Mean colony radii were obtained from minimum and maximum

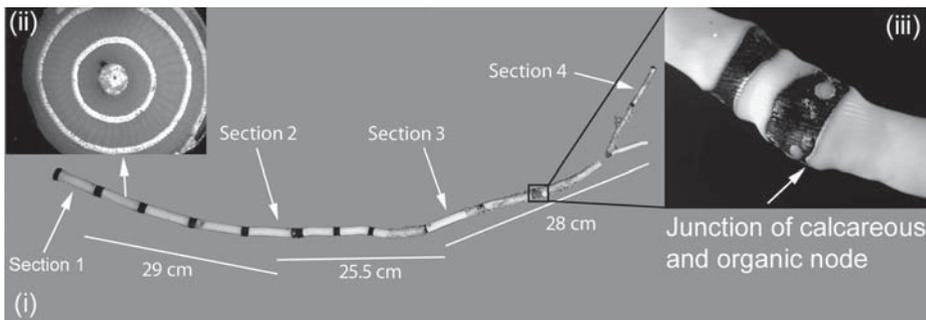


Figure 3. (A) Section sites for radial and linear samples from base region to near tip, on *Lepidisis* sp. colony 1. (B) Radial micro-mill drilling sites on colony 1. (C) Site of the junction or interface between the calcareous and gorgonin node prepared for SEM imaging.

measurements taken from the outer margin to the edge of the inner hollow core on the thin section preparations.

THIN SECTIONING.—The internode was sectioned with a diamond-edged wafering blade. Sections were ground and polished with a lapidary wheel, mounted with epoxy resin on glass slides, and viewed with either reflected or transmitted light to elucidate any growth zones visible in the sections. Counts of alternating light and dark zone couplets were made from the core region to the edge using a binocular microscope with illumination by transmitted light at 40–80× magnification. The structure of the surface was described and photographs obtained to aid zone counting and resolution. An index of average percentage error APE (Beamish and Fournier, 1981) was applied to zone counts by reader two readers.

SCANNING ELECTRON MICROSCOPY (SEM).—Due to the braided appearance and difficulty in counting zones along the axis from the core to the edge of the *Lepidisis* spp. sections, use of SEM was investigated with the intention of providing a better resolution of the zones. The end surfaces of the calcareous internodes of bamboo corals form a platform of elevated rings that seem to serve as an anchor point for gorgonin node. After slow digestion of the gorgonin material using a dilute hypochlorous acid (commercial bleach), growth zones at this interface were discrete and easily counted. Sections were prepared for SEM imaging adjacent to the sample sites on the calcite internode, at the junction of the internode and node (Fig. 3). Additional longitudinal SEM images were made at the branch tip to investigate the hollow core structure.

LEAD-210 DATING.—Age and growth estimates were made using lead-210 dating on colony 1 (*Lepidisis* sp.). Microsamples from the skeletal carbonate were extracted from a series of sampling locations in the colony adjacent to the thin section cuts. Extracted material came from the basal section at four sites across the radius. In addition, material was drilled from three sections adjacent to the thin section sites up the main growth axis, from the base to the growing tip region, to investigate linear growth in the colony.

The extracted samples were then assayed for ^{210}Pb activity and an exogenous level was determined for each sample from measured levels of ^{226}Ra . The exogenous ^{210}Pb ($^{210}\text{Pb}_{\text{ex}}$), and its decay relative to section radius was used to determine a growth rate and age. The details of radiometric analyses were given elsewhere (Andrews et al., 2002).

RESULTS

On microscopic examination, the polished thin sections of the calcareous axis were somewhat crystalline and blurry, and while there were areas of fine regular zones visible in some regions, a rope-like or braided spiral pattern appeared to be super-imposed over parts of the sections (Fig. 4). The occurrence of this braiding pattern was most obviously displayed on colony 2, the most northern *Lepidisis* sp. sample, but was visible in all *Lepidisis* spp. colonies and made zone counting difficult along parts of the radial axis.

The fine regular zone formation seen in some regions of the *Lepidisis* spp. thin sections related well to the clear zone structure of fine regularly spaced light and dark banding exhibited along the entire radial growth axis in the *Keratoisis* sp. thin section (sample 4, Fig. 5). This clear zone deposition pattern in *Keratoisis* sp. made zone counting relatively easy for this species. During examination of the coral sections, clear “event” marks were visible on the thin section and SEM images (Figs. 4, 5).

Zone counts and growth rates for radial and linear growth in skeletal sections of *Lepidisis* spp. and *Keratoisis* sp. from both the thin sections and SEM images (Table 1) were based on the mean counts of two readers of concentric bands from core to edge. Although confidence in the thin section counts for *Lepidisis* spp. was affected

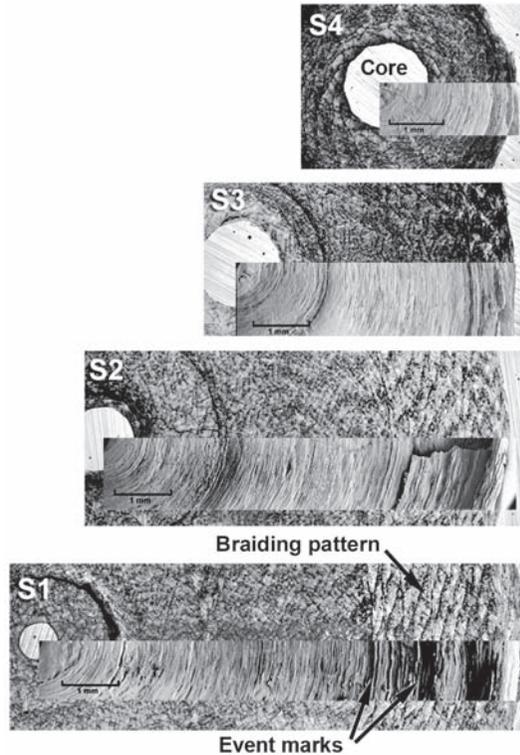


Figure 4. Light microscope transverse thin sections of the linear samples S1–S4 of *Lepidisis* sp. colony 1 (see Fig. 3), overlaid with SEM images of adjacent sections from the junction of the gorgonin node of the same colony. The thin section image shows regular concentric zones in some regions, but these are hard to discern across the whole section due to the rope-like or braiding pattern of microfabrics. The SEM images produced clear resolution zones, higher counts, and also enabled counts to be made within the core region. Mean radial zone counts from the thin section images were from base (S1) to tip (S4), 86, 72, 58, and 32, and from the adjacent SEM images were 426, 370, 242, and 150.

by the braiding pattern observed on the thin sections, estimates with a low APE were obtained and zone counts were presented for the three colonies.

AXIAL CORE.—In the transverse cross-sections, the axial core of the bamboo corals is hollow and shrinks with increasing overall diameter (Fig. 4). A considerable amount of secondary in-growth could be taking place in this region of the colony. This would imply that if zone counts were made from within the core there would be an overestimate of age. Thin section counts were made to the edge of the core. Counts on the SEM images could be made in 80% of the core region. To ensure that the age and growth estimates would be directly comparable, the zone counts made between the first radial micromilled site for ^{210}Pb analysis and the center of the core (Fig. 4) were subtracted from the thin section and SEM total counts for both the radial and linear samples on colony sample 1.

COUNTS FROM THIN SECTIONS.—For the three *Lepidisis* spp. colonies, all of which had a similar radial measurement, zone counts for the base thin sections ranged from 69–116 (Table 1). *Keratoisis* sp. had a mean zone count of 157. For *Lepidisis* sp. colony 1, thin radial section zone counts from base to tip sections ranged from 86 to 31.5 zones and radial growth was estimated at the base to be $0.084 \text{ mm zone}^{-1}$. Linear growth along the axis of colony 1 (Fig. 3) was estimated from the measured distance

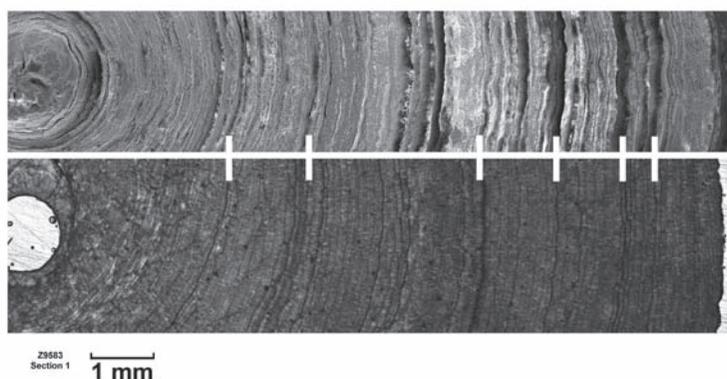


Figure 5. Light microscope transverse thin section image (top) and SEM image (bottom) of *Keratoisis* sp. colony 4. Clear concentric zone deposition is visible on both images. Counts from the thin section was 157 zones, and from the SEM image, 490 zones. Note major event marks are visible with both techniques.

between section sites divided by the difference in mean zone count from each thin section. The growth estimates for the distance between S1 and S2, S2 and S3, and S3 to S4 were 20.7, 17.9, and 10.6 mm zone⁻¹. Growth from these 3 data points appears more curvilinear than linear in structure.

The zone count for *Lepidisis* sp. colony 2 was 69 and radial growth 0.08 mm zone⁻¹. For *Lepidisis* sp. colony 3, 116 zones were counted and radial growth was 0.09 mm zone⁻¹. For the *Keratoisis* sp. colony 4, clear zone structure of fine regularly spaced light and dark banding was exhibited along the entire radial growth axis from the core to edge in the base radial thin section and produced a zone count of 157 (Fig. 5). The radial growth rate was 0.05 mm zone⁻¹.

COUNTS FROM SEM IMAGES.—SEM methodology revealed that both *Lepidisis* spp. and *Keratoisis* sp. had clearly visible and regularly spaced concentric growth zones in this region of the colony (Figs. 4, 5) and eliminated the problem of zone discrimination caused by braiding patterns in the comparable thin sections for *Lepidisis* spp. SEM images revealed elevated ridge-like structures defining the zones in bamboo corals. However, the APE estimates were higher between readers for the SEM image zone counts than they were for the thin section counts.

Counts from the SEM images were high. *Lepidisis* sp. colonies 1–3 had zone counts of 426, 345, and 397, respectively. *Keratoisis* sp. had a radial zone count of 490. Mean radial zone counts of the SEM images from the internodes adjacent to the base to tip thin section sites of colony 1 were 426, 370, 242, and 150.

From the SEM counts, *Lepidisis* spp. colonies 1 and 2 both had a radial growth of 0.02 mm zone⁻¹ and colony 3, 0.03 mm zone⁻¹. Growth for *Lepidisis* sp colony 1 was curvilinear from base to tip (5.2, 2.0, and approximately 3.0 mm zone⁻¹), as initial longitudinal growth at the base of the colony seems to be a lot faster than longitudinal growth farther up the colony. Growth for the sample taken between S3 and S4 is indicative as the total distance between S3 and S4 was estimated due to a section missing from the specimen near the tip region. *Keratoisis* sp. SEM section counts for the base region were 490 zones giving a radial growth rate of 0.02 mm zone⁻¹.

LEAD-210 DATING.—Extracted sample weight was low, but the activities of lead-210 and radium-226 were relatively high. Sample weights ranged from 0.0368 g to

Table 1. Radial and linear growth rates, thin section and SEM zone counts, and age data (assumed), for *Lepidisis* spp. and *Keratoisis* spp. colonies 1–4. For the *Lepidisis* spp. colonies, assumed ages for the thin section samples were based on bi-annual zone deposition and assumed ages for the SEM preparations were based on monthly lunar zone deposition. S1–S4 are the samples from base to near the tip of colony 1. (see Fig. 3). *Biannual deposition was not assumed for *Keratoisis* spp.

| Colony number and section type | Section radius (mm) | Thin sections | | | SEM | | |
|--------------------------------|---------------------|----------------------|-------------------|------------------------------------|----------------------|-------------------|------------------------------------|
| | | Zone count \pm APE | Assumed age (yrs) | Growth rate (mm yr ⁻¹) | Zone count \pm APE | Assumed age (yrs) | Growth rate (mm yr ⁻¹) |
| <i>Lepidisis</i> spp. | | | | | | | |
| 1 – Radial S1 | 7.2 | 86 \pm 4.7 | 43 | 0.17 | 426 \pm 5.5 | 33 | 0.22 |
| 1 – Radial S2 | 5.9 | 72 \pm 2.8 | 36 | 0.16 | 370 \pm 0.4 | 28 | 0.21 |
| 1 – Radial S3 | 4.6 | 58 \pm 3.4 | 29 | 0.16 | 242 \pm -0.6 | 19 | 0.24 |
| 1 – Radial S4 | 1.9 | 32 \pm 4.8 | 16 | 0.11 | 150 \pm 11.0 | 12 | 0.14 |
| 1 – Linear S1 | | | 43 | | | 33 | |
| | | | | 41.4 | | | 57.0 |
| 1 – Linear S2 | | | 36 | | | 28 | |
| | | | | 36.0 | | | 22.2 |
| 1 – Linear S3 | | | 29 | | | 19 | |
| | | | | 21.5 | | | 33.6 |
| 1 – Linear S4 | | | 16 | | | 12 | |
| 2 – Radial | 5.3 | 69 \pm 10.1 | 35 | 0.15 | 345 \pm 1.0 | 27 | 0.2 |
| 3 – Radial | 9.9 | 116 \pm 0.9 | 58 | 0.17 | 397 \pm 6.4 | 31 | 0.32 |
| <i>Keratoisis</i> spp. | | | | | | | |
| 4 – Radial | 8.5 | 157 \pm 10.8 | n/a | 0.05* | 490 \pm 0.3 | 38 | 0.22 |

0.1178 g (Table 2). Lead-210 activities decreased as expected from younger to older material, except for the center sample (R1). The elevated value for this sample was attributed to the accretion of younger material within the axial core. All measured ²¹⁰Pb:²²⁶Ra activity ratios exceeded 1.0, indicating the presence of ²¹⁰Pb_{ex}, a requirement for the use of lead-210 dating. A radial growth rate was determined from the four concentric samples taken from section S1 (R2–5) via natural log transformation of the respective ²¹⁰Pb_{ex} activities relative to the distance from the edge (Fig. 6). A regression of these data indicated the age of the largest section was 43 yrs old (26–61 yrs 95% CI), with an average radial growth rate (S), of 0.18 mm yr⁻¹ (0.13–0.29 mm yr⁻¹ 95% CI). The results from the three linear milled samples in this colony were problematic with high variability and one sample result falling outside the expected decay series. When considering the 95% CI for linear lead-210 dating, the growth rate range became inconclusive (1.5 cm yr⁻¹ to infinity). Because of this large degree of statistical uncertainty the linear radiometric results are not presented in this paper.

DISCUSSION

ZONE COUNTS.—Prior to this study it was assumed that the growth zones from bamboo corals would be annual; but some of the colonies with trunks with reasonably small radii had high zone counts suggesting higher than expected longevity. Zone counts from the thin section of the internode ranged from 69–157. A different result was obtained from the interface with the node (SEM image) where zone counts were even higher, ranging from 345–490. Even with reasonable between-reader vari-

Table 2. Summary of radial sampling details and the radiometric results for *Lepidisis* sp. (colony 1). Radial samples were taken from the center to near the edge of the thickest coral section (S1). Samples R1 and R3 were combined into one run for TIMS (Thermal Ionization Mass Spectrometry) analysis to increase sample size. Activity of ^{226}Ra used for R2 was an average of all radium values ($n = 5$; including some values from other parts of the skeleton not presented here). Two SE expressed as percentage for activities.

| Sample number | Radius (mm) | Sample weight (g) | ^{210}Pb activity (dpm g^{-1}) | ^{226}Ra activity (dpm g^{-1}) | ^{210}Pb : ^{226}Ra | $^{210}\text{Pb}_{\text{ex}}$ activity (dpm g^{-1}) | Age range (yrs) | Growth rate (mm yr^{-1}) |
|---------------|-------------|-------------------|--|--|---------------------------------------|--|-----------------|-------------------------------------|
| R1 | Center | 0.0368 | $0.264 \pm 13.0\%$ | 0.115 ± 3.0 | 2.30 | N.A. | | |
| R2 | 2.3 | 0.0563 | $0.189 \pm 15.6\%$ | $0.112 \pm 14\%$ | 1.69 | $0.077 \pm 15.6\%$ | 20–45 | 0.18 (0.13–0.29) |
| R3 | 3.3 | 0.0811 | $0.197 \pm 9.6\%$ | $0.115 \pm 3.0\%$ | 1.71 | $0.082 \pm 8.4\%$ | 16–35 | 0.18 (0.13–0.29) |
| R4 | 6.0 | 0.1178 | $0.254 \pm 7.4\%$ | $0.101 \pm 8.2\%$ | 2.51 | $0.153 \pm 9.4\%$ | 7–15 | 0.18 (0.13–0.29) |
| R5 | 7.5 | 0.1013 | $0.293 \pm 7.2\%$ | $0.110 \pm 2.6\%$ | 2.66 | $0.183 \pm 13.2\%$ | | |

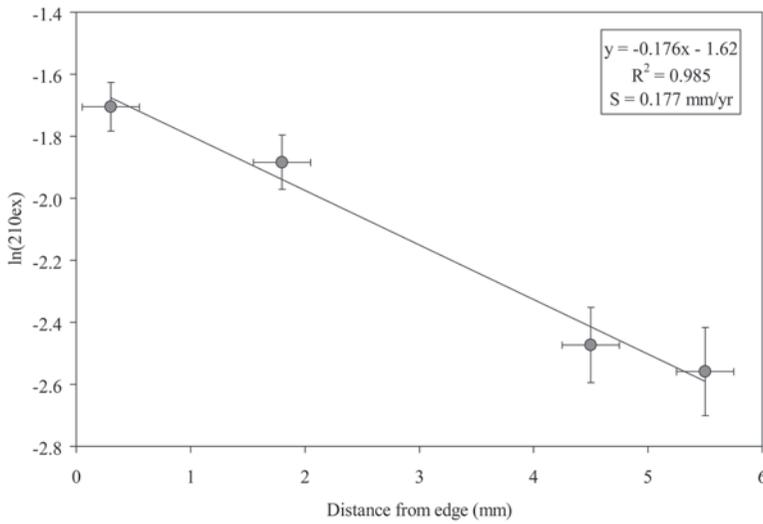


Figure 6. Plot of the \ln -transformed $^{210}\text{Pb}_{\text{ex}}$ data from the radial sampling with respect to the distance from the edge. The sample taken at the center was removed from consideration because the elevated activity was evidence the material was younger. Transformation of the slope in this plot indicated the radial growth rate (S), was 0.18 mm yr^{-1} (2 SE uncertainty from regression was $0.13\text{--}0.29 \text{ mm yr}^{-1}$). Horizontal bars represent the width of the sample extraction along the radius (drill bit used was $500 \mu\text{m}$ diameter). Vertical bars represent 2 SE for ^{210}Pb measurements.

ability, both zone count methods are subjective and the difference in zone counts from the two preparation techniques highlighted the need to apply an independent age estimation method.

RADIOMETRIC AGE ESTIMATION.—Lead-210 dating provided support for the age estimated from growth zone counts and evidence for some other environmental marker seen in SEM images that was not annual. The primary complication in the radial experimental design was suspected growth in the axial tube of the colony. It is likely that this occurs because of the reduction in tube diameter with increasing section thickness and the abrupt increase in ^{210}Pb activity in the center radial sample. Noé and Dullo (2006) describe in detail the organo-mineralic component of *Isididae*, and state that the core is organic rich, a factor which may affect core ^{210}Pb results. The analysis of radial samples first allowed for an alteration of the linear sampling design to avoid possible axial tube ingrowth. By measuring the change in diameter of the axial tube with colony length and making microscopic observations of the growth patterns in the cross sections, we concluded that a radius of about 2.3 mm would avoid potential newer (i.e., younger) material. Because sampling near the center was close to incorporating younger material, it is possible that variability calculated in the linear growth rate can be attributed to unseen flaws in sample extraction; however, the downward trend of $^{210}\text{Pb}_{\text{ex}}$ in this series does provide general support for the more robust findings from the radial sample design. The method does work well under closed conditions, as was the case with a number of other deep-water corals (e.g., Andrews et al., 2002; Adkins et al., 2004).

The findings from the radial sampling were well constrained because the decay of $^{210}\text{Pb}_{\text{ex}}$ from near the edge to near the center had a strong concordance to what would be expected from the law of radioactive decay. This sampling design has been

successfully applied to other deep-water bamboo corals and was pioneered for deep-water corals by work performed on the precious coral (*Corallium niobe* Bayer, 1964; Druffel et al., 1990). A study on a similar bamboo coral (*Acanella* sp.) collected off the northern Californian coast of the U.S.A. indicated the activity of ^{210}Pb was constant, assuming lead-210 and radium-226 were in equilibrium, near the center), suggesting the age of the colony was over 100 yrs (H. Spero, Department of Geology, University of California, Davis, pers. comm.). Recent carbon-14 work on coral specimens in the same family (Isididae), collected from the Gulf of Alaska at about 700 m, indicated colony age could range from about 75 yrs to over 200 yrs (Roark et al., 2005). This observation was based on the detection of bomb-produced carbon-14 and its use as a time specific marker. The extrapolated radial growth rates ranged from 0.05 to 0.16 mm yr⁻¹, similar to the rate estimated in the present study. In a recent study of *Keratoisis* sp. specimens taken from about 1000 m water off southern Australia, a well constrained growth rate was determined using three radiometric techniques (ca. 0.056 and 0.074 mm yr⁻¹; Thresher et al., 2004).

INTERPRETATION OF ZONE COUNTS.—The age estimate from the ^{210}Pb dating indicated that ages were about half that taken from thin section growth zone counts for the *Lepidisis* sp. Colony 1. The ^{210}Pb dating technique produced ages that did not match the zone counts but the ^{210}Pb age estimates, enabled us to theorize on some of the probable cues for zone deposition. Based on the ^{210}Pb age estimates (Table 2), growth zone counts from the internode suggest that, in the case of *Lepidisis* spp., zone deposition may be bi-annual, with two light and dark zone couplets deposited per annum. Applying this assumption the three *Lepidisis* spp. thin section mean colony ages would be 35–58 yrs (Table 1). As the ^{210}Pb growth estimate was produced only for a *Lepidisis* spp. colony, the growth estimates presented by Thresher et al. (2004) for *Keratoisis* sp. were used to assume annual, not bi-annual, zone deposition for the *Keratoisis* sp. colony in this study. Zone counts for the *Keratoisis* sp. colony were 490.

Where the internode abuts the gorgonin region, SEM counts were much higher and zone deposition could be influenced by either monthly lunar modulated events such as carbon or nitrate flux, or, in particular areas of the New Zealand region, may represent downward transport of material potentially sourced from organic blooms (Nodder and Northcote, 2001). Roark et al. (2005) also speculated that band deposition reflects lunar (monthly) time-scales linked to changes in zooplankton biomass and particulate organic carbon (POC) flux. An analysis of our zone counts was carried out to estimate additional age and growth data for colonies based on lunar deposition.

Mean zone counts from the base section SEM images for the four colonies, and for the linear section images from colony 1, were divided by 13 (assumed lunar cycle) to provide an age estimate. The assumed age range from the SEM zone counts for *Lepidisis* spp. from this scaling were 27–33 yrs and an estimated age of 38 yrs for *Keratoisis* sp. (Table 1). SEM linear samples along *Lepidisis* sp. colony 1, from base to tip, would be 33, 28, 19, and 12 yrs. These ages correspond reasonably well with the thin section annual age estimates (43, 36, 29, and 16 yrs). Growth is estimated to be slow and appears curvilinear, slowing as the colony ages.

We also hypothesized that SEM zone counts from the Snares *Keratoisis* sp. colony 4 may not reflect monthly lunar events but more the occurrences of export of particulate matter (e.g., spring blooms). Several studies discuss the effects and influ-

ences of nutrient flux on the formation of growth zones in octocorals (Druffel, 1989; Sherwood et al., 2005; Noe and Dullo, 2006). Around 3–7 per sedimentation events have been recorded per annum in the sub-tropical convergence waters around New Zealand (Nodder and Northcote, 2001).

GROWTH RATES.—Assuming bi-annual zone deposition, the radial growth rate for the base area of the three *Lepidisis* spp. colonies from thin section counts would range from 0.15 to 0.17 mm yr⁻¹. For *Lepidisis* sp. colony 1 annual radial growth would be 0.17 mm yr⁻¹ at the base, reducing towards the tip to 0.11 mm yr⁻¹ (Fig. 3). Linear annual growth estimated from thin section counts between the three sites had a mean of 33 mm yr⁻¹ (Table 1).

Scaled SEM growth data provided higher estimates but were generally similar to the radiometric and scaled thin section results. *Lepidisis* spp. radial growth for colonies 1 and 2 were very close to the radiometric result of 0.18 mm yr⁻¹. (colony 1, 0.22 mm yr⁻¹ and colony 2, 0.20 mm yr⁻¹. For colony 3 on the Chatham Rise, radial growth was higher at 0.32 mm yr⁻¹.

Keratoisis sp. SEM section counts for the base region comprised 490 zones, providing an assumed annual radial growth based on monthly lunar counts of 0.22 mm yr⁻¹. Growth for this colony from the Snares is similar to the northern *Lepidisis* spp., but slower than the Chatham Rise colony. For studies of *Keratoisis* sp. in other regions, Roark et al. (2005) obtained radial growth of 0.05–0.16 mm yr⁻¹ and Andrews et al. (2005), radial and linear growth of 0.05 mm yr⁻¹ and 1.9–4.4 mm yr⁻¹, respectively. Using lead-radium Thresher et al. (2004) reported growth of 0.05 mm yr⁻¹ in a Tasmanian *Keratoisis* sp. colony aged 400y. Recently the growth rate for the Tasmanian *Keratoisis* sp. has been revised to 0.10 mm yr⁻¹ (Thresher et al., 2007), and is consistent with the radiometric age estimate in this study. All age data presented in this study are significantly lower than those estimated from ¹⁴C ages found for a similar sized *Keratoisis* sp. specimen (Tracey et al., 2003).

A regional difference in bamboo coral growth rate is to be expected for organisms sampled from the dynamic and often complex oceanic region around New Zealand (Chiswell, 2002). Significant differences in annual cycles of water temperature and salinity occur in the region, producing a diverse and complex physical environment. For the two northern samples (colonies 1 and 2), growth was estimated to be slightly higher for the East Cape (colony 1) than for the more northern Norfolk Ridge/Wanganella Bank colony 2. This could be explained by the fact that colony 1 was collected from shallower (690–800 m) warmer waters, and colony 2 from deeper colder waters (874–1030 m). Overall, the Chatham Rise sample appeared to display the fastest growth. This colony (3) was sampled at depths similar to the East Cape colony 1, (638–840 m). A particulate organic carbon influx of 7.5 g m⁻² yr⁻¹ at 1000 m water depth has been recorded for the north Chatham Rise, four times the value measured to the south (Nodder and Northcote, 2001). This suggests there is a pronounced spatial difference in particulate flux across this region, although this rate of flux is considered to be moderately low in comparison to global rates. Labile food sources within sinking particulate matter are available to support faster growth in this region. Export events observed for this region, sometimes occur 3–7 times per annum, and detrital rain reaching deep water from these surface events would contribute significantly to growth. Annual cycles of temperature or salinity, weak and strong tides, and food availability, would also affect skeletal deposition.

Reproduction may also influence zone formation. These corals produce large oocytes, of about 0.5–1.5 mm in diameter, and the energy to produce the eggs would likely influence elemental composition and subsequent zone deposition. This could also account for the theorized bi-annual zone deposition in the internode thin sections.

The Snares *Keratoisis* sp. (colony 4), was collected from an area also influenced by a subtropical frontal zone. However the *Keratoisis* specimen displayed substantially slower growth than the three other *Lepidisis* spp. colonies. Differences in growth could be caused by natural variation, species effect, lower occurrence of organic blooms, or as a result of the cold and deeper (935 m) waters from which this colony had been collected.

MORPHOLOGY.—The observation of fine regular zone formation and absence of braiding in one of the two study genera could be used as a morphological tool to differentiate between species or genera within the family Isididae. Thin sections of Isidids were also examined under reflected light by Noé and Dullo (2006) whose images revealed similar microfabrics as shown in Figure 4. They found fabric changes along a cross-section to be caused by alternating radial and tangential arrangement of calcite fascicles towards the growth plane. The former causes a regular parallel dark-light colour banding, the latter a zig-zag or braided pattern cutting through the concentric macrostructure (S. Noé, Leibniz Institute of Marine Sciences, pers. comm.). During the examination of the coral thin sections and SEM images, clear “event” marks were visible, indicating the presence of a possible environmental, natural climate, grazing, or even biological (e.g., reproductive) events.

AXIAL CORE.—Core size changed as the coral colony grew, with the core becoming wider at the tip on the younger part of colony. It is not known why the diameter of the axial tube increases towards the tip of these corals. Accretion may not occur in the hollow core and this arrangement provides support to the colony as it grows tall and upright, enabling it to sway in the current and seek feed; however, the ^{210}Pb was elevated in the core, so there must be some carbonate exchange with the external environment or accretion occurring on the inner surface of the axial tube. Lateral SEM images of the bamboo coral stem tip show the hollow stem is separated by numerous septa, and multiple chambers appear to be created at the growing tip (Fig. 7).

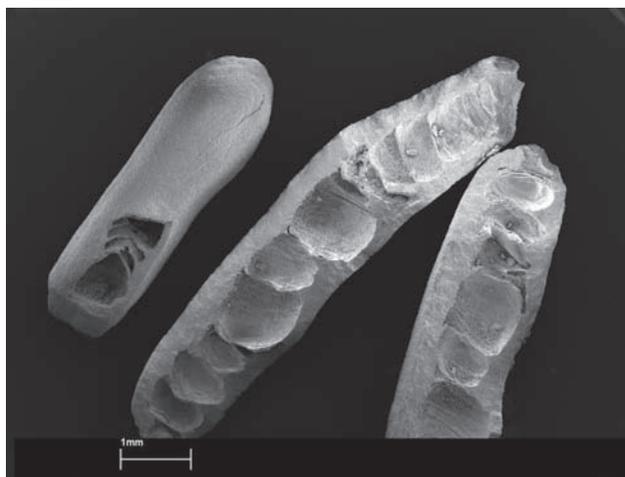


Figure 7. Chamber structure seen in SEM sections of coral stem tip.

The estimates of age and growth for the bamboo corals obtained from this study provide some insight into the regeneration potential of these important long-lived and slow growing organisms and will help in improving ecosystem management. Our success in determining an age estimate of 43 yrs from the ^{210}Pb dating technique for one colony aided in the interpretation of growth zone counts for all colonies and enabled interpretation of zone deposition hypotheses for this deep-sea coral family.

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