Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska

Allen H. Andrews[1], Erik E. Cordes[1], Melissa M. Mahoney[1], Kristen Munk[2],
Kenneth H. Coale[1], Gregor M. Cailliet[1] & Jonathan Heifetz[3]
[1]*Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039-9647, U.S.A.*
Tel: (831)632-4400; Fax: (831)632-4403; E-mail: andrews@mlml.calstate.edu
[2]*Alaska Department of Fish and Game, CWT and Otolith Lab, Box 25526, Juneau, AK 99802, U.S.A.*
[3]*Auke Bay Laboratory, NMFS, NOAA, 11305 Glacier Highway, Juneau, AK 99801, U.S.A.*

Abstract

Sustainable fisheries require (1) viable stock populations with appropriate harvest limits and (2) appropriate habitat for fish to survive, forage, seek refuge, grow and reproduce. Some deep-water habitats, such as those formed by deep-water stands of coral, may be vulnerable to fishing disturbance. The rate at which habitat can be restored is a critical aspect of fishery management. The purpose of this study was to characterize growth rates for a habitat-forming deep-sea coral. Two nearly complete colonies of red tree coral (*Primnoa resedaeformis*) collected from waters off southeast Alaska were used for an analysis of age and growth characteristics. CAT scans revealed that colonies consisted of multiple settlement events, where older basal structures provided for settlement of new colonies. The decay of ^{210}Pb over the length of the colony was used to validate age estimates from growth ring counts. Age estimates were over 100 yr for sections near the heavily calcified base. Based on validated growth ring counts, growth of red tree coral ranged from 1.60 to 2.32 cm per year in height and was approximately 0.36 mm per year in diameter. These growth rates suggest that the fishery habitat created by red tree coral is extremely vulnerable to bottom fishing activities and may take over 100 years to recover.

Introduction

Many species of deep-sea corals provide high relief habitat for a number of ecologically important species of invertebrates and fishes (Heezen & Hollister, 1971; Marshall, 1979; Mortensen et al., 1995; Risk et al., 1998), some of which may be undescribed species (James Orr, Alaska Fisheries Science Center, NMFS, Seattle, WA 98115, Pers. Comm.). With some fish stocks on the decline and others increasing in utilization, it is essential that biogenic habitat impacted by fishing be studied in more detail. This perspective was mandated for fisheries management practices in the United States with the Sustainable Fisheries Act of 1996, where protecting Essential Fish Habitat (EFH) has become paramount. Information on the longevity and growth rates of habitat-forming coral species is necessary before their importance and sensitivity as fisheries habitat can be fully understood (Bloeser,

1999). As age determination studies have been completed, it has become increasingly common to find that deep-sea corals, as well as some of the associated fishes they support, may attain ages that are on the order of decades to hundreds or thousands of years (Grigg, 1974; O'Connell & Funk, 1986; Abbiati et al., 1991; Druffel, 1995; Risk et al., 1998).

Primnoa resedaeformis (Gunnerus, 1763), commonly known as the red tree coral, is a holaxonian gorgonian distributed throughout the North Atlantic and North Pacific Oceans. In the Gulf of Alaska and Bering Sea, it inhabits hard substrata along the shelf and upper slope from 10 to 800 m depth (Cimberg et al., 1981; Krieger, 1998), where the upper limit is questionable and may be closer to 100 m (Ken Krieger, Auke Bay Laboratory, NMFS, Juneau, AK 99801, personal communication). While much of the *Primnoa* collected from the Gulf of Alaska is highly variable in its growth form and has historically been assigned to

Figure 1. A yelloweye rockfish (*Sebastes ruberrimus*), with several other rockfishes, associated with a red tree coral. Photograph taken by Victoria O'Connell (Alaska Department of Fish and Game) from the Delta Submersible at 146 m off of Whale Bay, Baranof Island, southeast Alaska.

three different species (*P. pacifica*, *P. resedaeformis*, *P. willeyi*; Kinoshita, 1908; Hixson, 1915), recent work suggests that these species are synonymous and should be placed within the species *Primnoa resedaeformis* (Bruce Wing, Auke Bay Laboratory, NMFS, Juneau, AK 99801, personal communication). Red tree coral grows in small isolated groups and can form massive stands 2–3 m tall (Krieger & Wing, 2002). These corals have been documented as providing the substrate for habitats with high biodiversity (Heifetz, 2002; Krieger & Wing, 2002), which includes juveniles and adults of commercially important rockfishes (e.g. rougheye ((i) *Sebastes aleutianus*), shortraker (*S. borealis*), and yelloweye (*S. ruberrimus*)). At a site in the Gulf of Alaska known to have red tree coral, a manned submersible transect revealed that 85% of the large rockfish were associated with red tree coral (Krieger & Wing, 2002; Fig. 1). Studies of red tree coral off of Nova Scotia, Canada indicate the colonies are slow-growing and may exceed 100 years in age; the largest colonies may attain ages in the hundreds of years (Risk et al., 1998 and 2002).

The age and growth characteristics of most corals, gorgonians in particular, are largely unknown. For gorgonians, growth has been estimated by counting growth rings in skeletons (Grigg, 1974, 1976; Mitchell et al., 1993; Mistri & Ceccherelli, 1994) and by extrapolating linear extension rates (Yoshioka & Yoshioka, 1991; Brazeau & Lasker, 1992; Weinbauer & Velimirov, 1996; Kim & Lasker 1997); however, age validation is limited to a few radiometric analyses (Griffin & Druffel, 1989; Druffel et al., 1990; Risk et al. 2002).

The objective of this study was to describe the age and growth characteristics of red tree coral by (1) examining the basal structure of two colonies using CAT scans, (2) estimating age and growth by counting growth rings in cross sections, and (3) validating the estimated age and growth from ring counts using a radiometric method. These findings are discussed in the context of biogenic habitat and EFH management.

Materials and methods

Growth characteristics

Two complete colonies (colony 1 and colony 2) and several colony fragments, collected from Dixon Entrance in southeast Alaska, were used for age and growth estimation and validation. Growth characteristics were investigated using two approaches. To explore the interior structure of the knob-shaped basal region in the two complete colonies without cutting, a series of Computed Axial Tomography scans (CAT scans) was performed at the Community Hospital of the Monterey Peninsula.

To estimate age visually, thin cross sections were taken from the limbs of two colonies in unbranched regions along the axis of the skeletal structure using either a band saw or a water lubricated diamond-blade rock saw. Section thickness was 3–5 mm. These sections were polished using a Buehler® Ecomet III lapping wheel with 120–600 grit silicon-carbide wet/dry sandpaper. Polished sections were mounted to glass plates (0.5 cm thick window glass cut into 10 by 10 cm squares) and viewed with a dissecting microscope, where estimates of age were made by counting growth rings illuminated with reflected and transmitted light. Reflected light was used on the opaque wood-like region, composed of mostly gorgonin (horn-like protein), and transmitted light was used for the translucent marble-like region, composed of calcite. The growth rings counted in the marble-like regions were enhanced by grinding the section to a thickness of approximately 1 mm. The radial direction that produced the most growth rings was determined by each reader and counted three times. Average percent error (APE) and index of precision (D) were used to describe intra- and inter-reader variability (Beamish & Fournier, 1981; Chang, 1982). Age estimates for each section were combined to create an average of the final age estimates from the three independent readers. Growth was described by plotting estimated age from growth ring counts versus colony height and trunk diameter. A linear regression was used to determine estimates of growth rate in height and diameter. To assess the variability of growth among colonies, a limb from each of the two colonies and two colony fragments was aged.

Age estimate validation

Radiometric analysis was performed on two full colony limbs, where sections 3–6 cm in length along the axis, contiguous to the thin cross sections were cored. Core material was extracted by hand using a Dremel® tool with a circular diamond bit and needle-nose pliers. The toothpick-sized portion typically cracked out of the fragile skeletal structure and was handled with gloves so that radioactive contamination was minimized. Because the activity levels of ^{210}Pb and ^{226}Ra are typically very low, trace-metal precautions were exercised during sample cleaning and processing (Andrews, 1999b). All acids used were double distilled (GFS Chemicals®) and dilutions were made using Millipore® filtered Milli-Q water ($18~M\Omega~cm^{-1}$).

Once samples were rigorously cleaned and dried to constant weight, samples were first analyzed for ^{210}Pb. Due to the low activity of ^{210}Pb, detection was accomplished through the autodeposition and α-spectrometric determination of its daughter, ^{210}Po (Flynn, 1968). To ensure that all of the ^{210}Po activity was due to the ingrowth from ^{210}Pb and that ^{210}Po:^{210}Pb was in secular equilibrium, all samples were at least 2 yr old (from date of collection). Samples prepared for ^{210}Po analysis were spiked with a yield tracer, ^{208}Po.

To isolate the polonium isotopes for the purpose of α-spectrometry, the isotopes were autodeposited onto a purified silver planchet (99.999% Ag; A.F. Murphy Die and Machine Co.). Spiked samples in 100 mL teflon beakers were dissolved in approximately 50 mL of 0.5 N HCl on a hot plate elevated to 90 °C. The ^{210}Po and ^{208}Po-tracer were autodeposited onto the silver planchet held in a rotating teflon holder over a 4 h period (Flynn, 1968). Planchets were analyzed using ion implant detectors in eight Tennelec TC256 alpha-spectrometers interfaced with a multi-channel analyzer and an eight channel digital multi-plexer. Counts were collected with Nucleus® software on an IBM-PC. The sample solution remaining after polonium autodeposition was dried and used for ^{226}Ra analysis, the details of which are discussed elsewhere (Andrews et al. 1999b).

Because exogenous ^{210}Pb was present in high quantities, a technique was employed that is analogous to the determination of accumulation rates in sediments (Appleby & Oldfield, 1992). Measured ^{210}Pb activities in the series of cores, ranging from the tip (youngest) to near the base (oldest), were used to determine the growth rate of the colony based on the exponential decay of ^{210}Pb in accordance with the radioactive decay law. Sample specific ^{226}Ra activities were subtracted from the measured ^{210}Pb activity as-
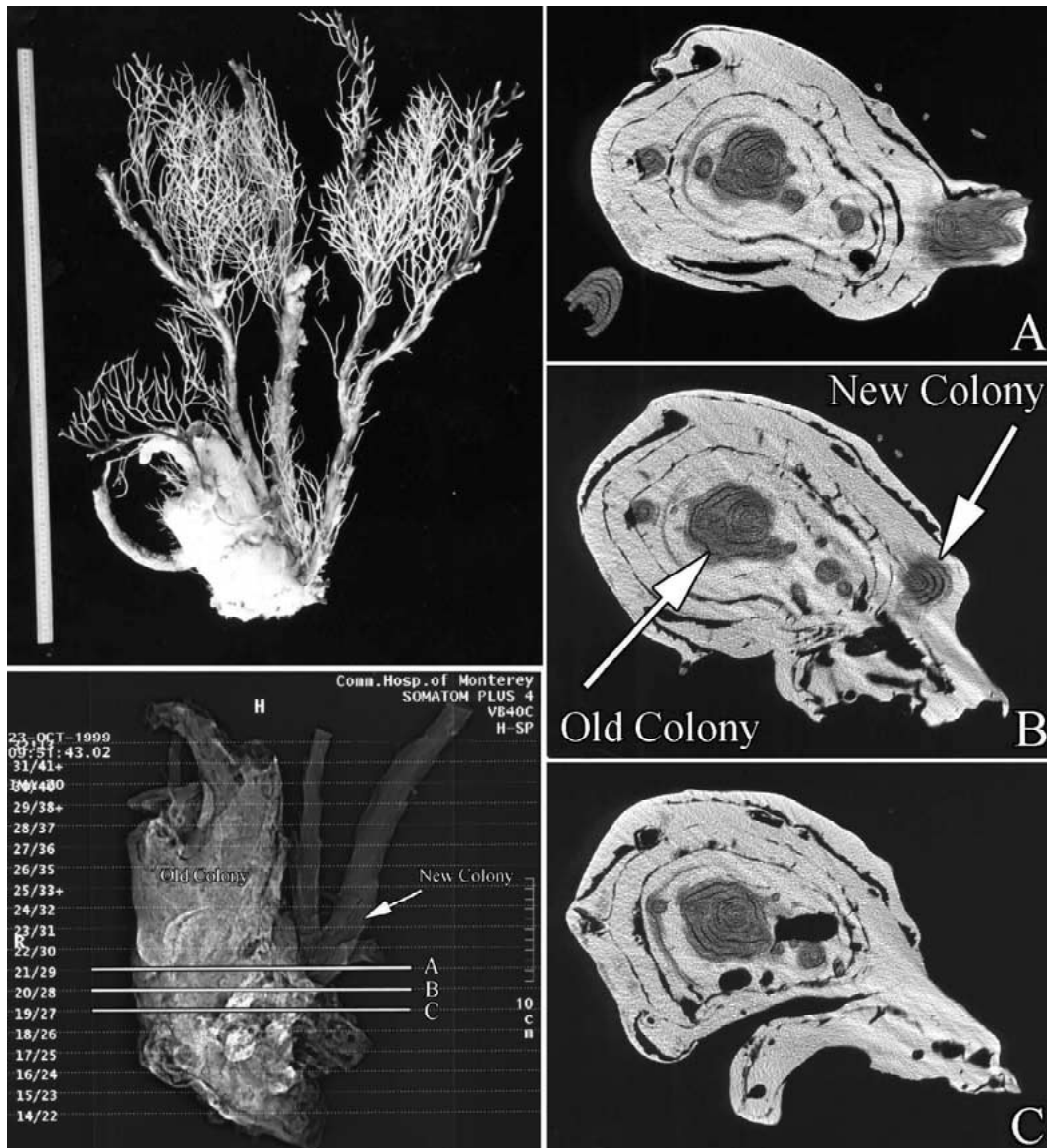
Figure 2. Photograph of a complete red tree coral skeleton (colony 2) with a large knob-shaped base (upper left with meter stick). To determine if the skeletal growth (limbs extending from the base on the right) was part of the old colony (broken off and decaying) or a new settlement, a series of CAT scans was taken (lower left). Three of the sections revealed that the limbs were the result of a more recent settlement event and were not an outgrowth of the old colony (A, B, C). Note that the new colony doesn't exist in section C, appears in section B, and begins to diverge and split into two limbs in section A.

suming ^{210}Pb was in secular equilibrium with ^{226}Ra, as in previous studies (Druffel et al., 1990), resulting in the unsupported or exogenous ^{210}Pb (^{210}Pb$_{ex}$).

Assuming that there is no post-formational movement of the ^{210}Pb within the skeletal structure and that the flux of ^{210}Pb from the environment was relatively constant, the law of radioactive decay can be used to describe the decay of ^{210}Pb over time:

$$A = A_0 e^{-\lambda t},$$

where A is the ^{210}Pb$_{ex}$ activity at a given time, A_0 is the initial ^{210}Pb$_{ex}$ activity, λ is the decay constant for ^{210}Pb, and t is the age of the sample. To derive a growth rate from this relationship that is independent of age estimation, a regression was performed on the natural log transform of the ^{210}Pb$_{ex}$ activities plotted against the distance from the tip of the colony. By redefining t in the previous equation as length divided by growth rate and solving for the growth rate,
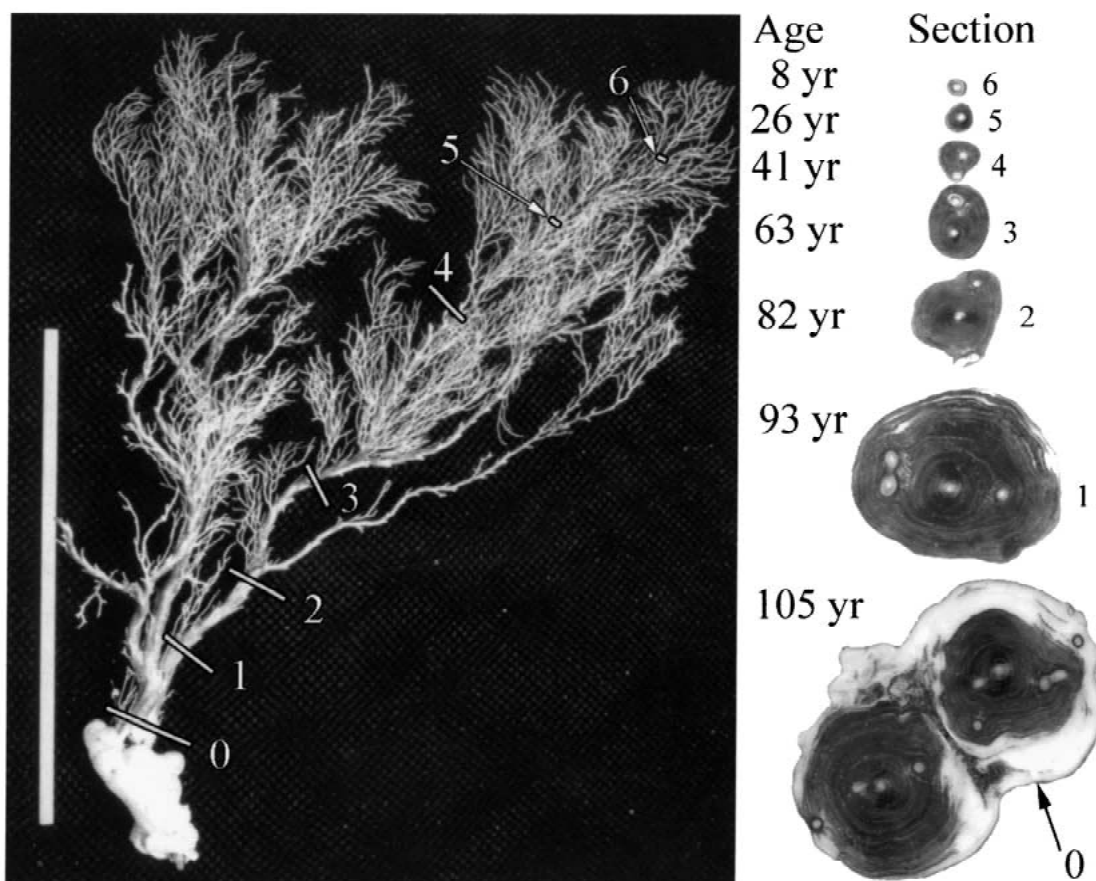
Figure 3. A complete red tree coral colony (colony 1) with markers indicating where thin cross sections (right) were taken. Age estimates were an average from three independent readers. Core sections used in the radiometric analysis were taken adjacent to the sections shown. In addition, another section was aged on the opposite side of the core section to allow for an average age determination of the core material.

an independent growth rate was determined using the following function:

$$S = \frac{\lambda}{m},$$

where S is equal to the growth rate (cm/yr), λ is the decay constant for ^{210}Pb, and m is the slope of the regression fitted to the data. Agreement between the growth rates (ring-count growth rate and ^{210}Pb$_{ex}$ decay growth rate) was used to validate the interpretation that growth rings were formed annually.

Results

Growth characteristics

Views of the interior structure of the knob-shaped base using CAT scans indicated the colonies consisted of multiple settlement events. The old basal structure of a colony provided for the settlement of a new colony (Fig. 2). Thin cross sections taken from various locations along the axis of the skeleton had clear growth rings that were easily counted (Fig. 3). The average percent error (APE) for each of the three readers was 4.3%, 9.8%, and 14.5% with an index of precision (D) of 6.5%. A regression of the age estimates from the thin cross sections over the length of the colony limb for colony 1 indicated the average growth rate was 1.74 ± 0.19 cm per year in height (Fig. 4) and 0.36 ± 0.05 mm per year in trunk diameter (Fig. 5). Aged sections taken from an additional colony (colony 2) and fragments of two other colonies indicated the growth rate for the colonies studied ranged from 1.60 to 2.32 cm per year (Table 1).

Table 1. Summary of sample details and growth rate determination results

Sample	Depth (m)	Length of portion (cm)	Number of sections	Ring count growth rate (cm/yr)	Radiometric growth rate (cm/yr)
Colony 1	263	197.5	14	1.74±0.19[a]	1.77±0.75[a]
Colony 2	263	72.6	8	2.32±0.09[a]	Not calculated[b]
Fragment 1	369	40.0	2	1.60[c]	Not determined[d]
Fragment 2	369	30.6	2	1.99[c]	Not determined[d]

[a]95% confidence interval.
[b]^{210}Pb activities for cores produced ambiguous results.
[c]Confidence interval not calculated for samples with only 2 sections
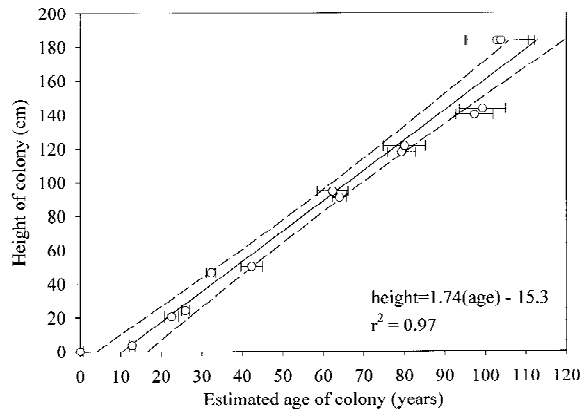[d]No cores were taken.

Figure 4. Relationship between total height of red tree coral colony and the estimated age of the colony (colony 1). Height was calculated as distance from the lowest section taken from the colony. Age was calculated as the number of rings in cross section subtracted from number of rings in the lowest section (expressed here as age 0 yr and height 0 cm). A linear regression fitted to these data indicated an average growth rate of 1.74±0.19 cm per year in height for this colony. Error bars represent one standard deviation.

Age estimate validation

Radiometric analyses were performed on colony 1 and 2, where a total of 10 core samples was analyzed (Table 2). For colony 1 core samples were processed for both ^{210}Pb and ^{226}Ra. Activities for ^{210}Pb ranged from $0.179 \pm 8.6\%$ to $0.403 \pm 7.3\%$, where the lowest activities were near the base and the highest were near the tip. Activities for ^{226}Ra were fairly constant and ranged from $0.119 \pm 10.7\%$ to $0.162 \pm 1.8\%$ with an average of $0.153 \pm 11\%$. All ^{210}Pb:^{226}Ra activity ratios calculated for colony 1 exceeded 1.0; the maximum allowable ratio is 1.0 for the secular equilibrium model.

The decay of ^{210}Pb$_{ex}$ over the length of the colony limb provided an independent estimate of the growth rate for one colony. This estimate was in close agree-
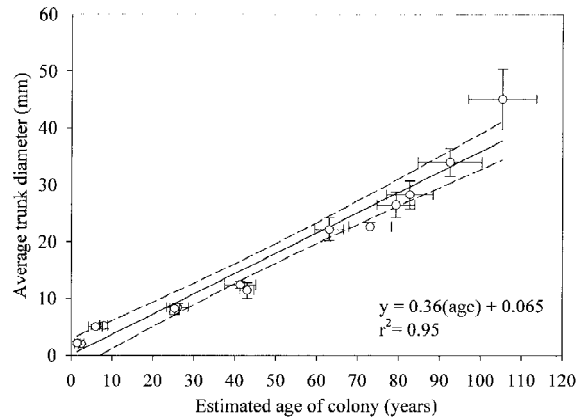

Figure 5. A regression fitted to the average diameter of the red tree coral sections versus estimated age indicated a growth rate of 0.36±0.05 mm per year in diameter. Error bars represent one standard deviation in the determination of average age and average trunk diameter. Based on this relationship, it may be possible to predict the age of red tree coral using trunk diameter in the field.
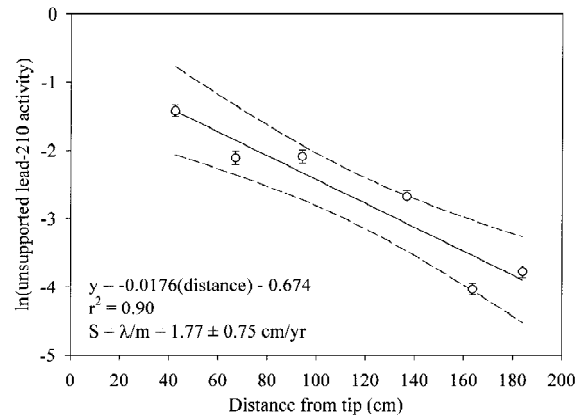

Figure 6. A regression fitted to the natural log transform of lead-210 activity in each cored section of red tree coral versus distance from the tip of the colony. Solving for the slope in this equation indicates an average growth rate of 1.77±0.75 cm per year in height. This determination validates the annual periodicity of the growth rings counted in sections.

ment with the estimated growth rate from growth rings (1.74 ± 0.19 cm/yr), where the calculated growth rate from $^{210}Pb_{ex}$ decay was 1.77 ± 0.75 cm per year in height (Fig. 6). An attempt was made to apply the technique to a second colony, but the results were ambiguous and no growth rate could be determined (Table 2). The annual periodicity of the growth rings found in these red tree coral samples was validated, as evidenced by the close agreement between the two independent growth rate estimates.

Discussion

Views created from the CAT scans and the cross sections taken near the base of the complete colonies suggest that red tree coral uses old calcified structures as settlement sites for new colonies (Fig. 2). For colony 2, initial settlement occurred on an older basal structure that surrounded what appeared to be a long dead colony. The settlement location for the dead colony appeared to be the carbonate skeleton of a solitary cup coral. It is possible that biogenic calcified substrates play an important ecological role in recruitment success.

Interpretation of growth rings by the readers was fairly consistent within and among readers. Most of the variation within and among readers could be explained by differences in the radial direction chosen for counting. It was often necessary to sweep along growth rings to find a suitable region for counting when definition of the rings degraded. This is commonly a factor in age estimation of fish otoliths (Chilton & Beamish, 1982). Overall, aging was not difficult and agreement was good, where APE ranged from 4.3 to 14.5% within readers and D was 6.5% among readers. Growth rings in the marble-like regions, however, were more difficult and poorly defined. Further investigation is needed on enhancing the visibility of these rings.

The examination of growth rings in cross sections from four different samples (partial and full limbs) provided a range of growth rates. Age estimates from sections taken from the limb of colony 1 (Fig. 3) indicated the limb grew at an average rate of 1.74 ± 0.19 cm per year in height (Fig. 4). This estimate falls near the middle of the range of growth rates determined from the limb of colony 2 and the two other colony fragments, where the growth rates ranged from 1.60 to 2.32 ± 0.09 cm per year in height (Table 1). These results were about 10 times greater than described for

Table 2. Summary of radiometric analysis results

Coral sample	Section number	^{210}Pb activity (dpm/g)	^{226}Ra activity (dpm/g)	^{210}Pb:^{226}Ra activity ratio
Colony 1	0	No core	N.A.	N.A.
	1	$0.185 \pm 3.8\%^{a}$	$0.162 \pm 1.8\%^{a}$	1.14
	2	$0.179 \pm 8.6\%^{a}$	$0.162 \pm 1.8\%^{a}$	1.10
	3	$0.225 \pm 9.0\%^{a}$	$0.157 \pm 4.3\%^{a}$	1.43
	4	$0.243 \pm 7.2\%^{a}$	$0.119 \pm 10.7\%^{a}$	2.04
	5	$0.282 \pm 6.4\%^{a}$	$0.161 \pm 3.9\%^{a}$	1.75
	6	$0.403 \pm 7.3\%^{a}$	$0.161 \pm 1.1\%^{a}$	2.50
Colony 2	1	$0.603 \pm 5.0\%^{a}$	Not measured	N.A.
	2	$0.236 \pm 6.5\%^{a}$	Not measured	N.A.
	3	$0.324 \pm 5.5\%^{a}$	Not measured	N.A.
	4	$0.328 \pm 5.1\%^{a}$	Not measured	N.A.

[a] σ expressed as percentage.

Atlantic *P. resedaeformis* (0.15–0.25 cm per year; Risk et al., 2002). Average growth in trunk diameter for the limb of colony 1 was estimated to be 0.36 ± 0.05 mm per year (Fig. 5). This was about 4 times greater than described for Atlantic *P. resedaeformis* (0.090 mm per year; Risk et al., 2002). Variation in growth and the error observed for growth rate is not unusual given the variable nature of growth in gorgonian corals (Velimirov, 1975; Grigg, 1976; Mitchell et al., 1993; Mistri, 1995).

To determine the validity of these estimates an independent growth rate was calculated from the decay of $^{210}Pb_{ex}$. The estimate using this technique (1.77 ± 0.75 cm per year) was in close agreement with the growth rate determined from visually counting growth rings (1.74 ± 0.19 cm per year). This validated the interpretation that growth rings counted in cross sections were annual (Fig. 6). Based on the average growth rate, the limb studied from colony 1 took approximately 112 years to grow from its initial settlement to a total height of 197.5 cm. An analysis of a limb from colony 2 resulted in ambiguous results and no growth rate could be determined (Table 2). Based on the appearance of the limb selected from colony 2, the limb may have been dead at the time of collection because (1) a large portion of the top was broken off, (2) the limb was discolored (blackened), and (3) the wood-like portion at the base, normally enclosed by calcite, had been exposed to sea water and was in a state of decay. It is uncertain what affect this would have on ^{210}Pb content, but this condition was different from the limb selected in colony 1. Based on

Table 3. Tabulated growth rate in height and highest reported or estimated maximum age from this and other gorgonian studies

Genus	Growth rate (cm/yr)	Age (yr)	Source
Primnoa	1.60–2.32	112	This study
Primnoa[a]	0.15–0.25	∼500, >210	Risk et al. (1998, 2002)
Antipathes	4.48–4.75[b], 6.4[c]	50	Grigg (1976, pers. comm.)
Briareum	2.02	N.A.	Brazeau & Lasker (1992)
Corallium	0.89, 0.45–0.71[d]	50, 140–220	Grigg (1976), Druffel et al. (1990)
Leptogorgia	4.5	10	Mitchell et al. (1993)
Muricea	1.69	100	Grigg (1974)
Paramuricea	2.7	15	Mistri & Ceccherelli (1994)
Plexaura	2.0–20.0	N.A.	Kim & Lasker (1997)
multiple	0.80–4.48	N.A.	Yoshioka & Yoshioka (1991)
multiple	2.3–7.88	N.A.	Goh & Chou (1995)

[a] Atlantic Ocean.
[b] Growth ring counts.
[c] Empirical rate (R. Grigg, pers. comm., SOEST, University of Hawaii, Honolulu, HI 96822).
[d] Calculated based on the colony diameter (1 m), estimated age and ageing error.

this observation, future samples used in ^{210}Pb analyses should be complete and living at the time of collection. In other studies, what appear to be post-formational calcification of hollows at or near the core created the potential for mixing younger material with older material (Risk et al., 2002). This was not observed in the sections taken from any of the colonies and the skeleton appeared to be a tightly sealed system, with the exception of circular cracks that formed when the skeleton dried.

Growth rates and age estimates for red tree coral in this study fall within the range of reported values for other gorgonian coral studies (Table 3). Few growth rates have been reported from deep-sea species with distributions starting below the photic zone. In gorgonians associated with coral reefs, slower growth rates (<1.0 cm per year) are generally reported for deeper water species (i.e. *Antipathes*), while shallow water species tend to exhibit more rapid growth (>2–3 cm per year). The growth rates reported here (1.60–2.32 cm per year) are at the slower end of the range reported for gorgonians (0.15–7.1 cm per year) and age estimates follow a similar trend. Shallow reef gorgonians generally have life spans measured in decades, while deeper species can attain ages in excess of 100 yr (Table 3). The maximum age calculated in this study (112 yr) is not from the tallest colony recor-

ded, suggesting that *Primnoa* spp. may attain ages far exceeding this estimate.

In summary, investigations of red tree coral using CAT scans, section age estimation and radiometric age validation provided valuable insights on red tree coral settlement and growth. Colonies of red tree coral can be the result of multiple settlement events, where the age of individual limbs can exceed 100 years. Once the colonies approach this age, they begin to form thick basal skeletal structures. These large calcified accretions appear to provide settlement sites for a variety of deep-sea organisms as well as conspecifics (Mortensen et al., 1995; Yoshioka, 1996; Risk et al., 1998); therefore, large groups of red tree coral may consist of multiple settlement events, where the basal skeletal structure may be 100s of years old.

The slow growth, high longevity and ecological importance of red tree coral make this species, and the habitat it creates, vulnerable to disturbances that damage or remove the colonies. During a submersible survey at a site in the Gulf of Alaska, it was reported that 50% of the red tree coral had been broken or removed by an experimental deployment of a fishing trawl, where a follow up on the site revealed little recovery after 7 years (Krieger, 2002). In the Atka mackerel (*Pleurogrammus monopterygius*) fishery of Seguam Pass in the Aleutian Islands, gorgonian corals were a major component of the bycatch (Krieger, 2002). Corals are now an infrequent part of the catch after 20 years of intensive fishing effort. Heifetz (1998) summarized the results of a submersible survey along the path of a bottom trawl at 365 m. Thirteen large red tree coral colonies were observed, of which 8 were damaged by the bottom trawl, and 5 had major damage in which 95–99% of the coral was removed.

Recovery from this kind of disturbance or removal may be prolonged because of confounding factors. Larval production in gorgonians has been shown to be positively related to both colony size and age (Abbiati et al., 1991; West et al., 1993; Weinbauer & Velimirov, 1996). Smaller colonies are less fecund and damaged colonies have been shown to reduce or cease reproduction while repairing the damage (Grigg, 1974, 1976; Abbiati et al., 1991; Mistri, 1995).

Further study and protection of red tree coral is warranted and in dire need of implementation, because red tree coral is ecologically important, sensitive to degradation, exposed to human activities, and slow to recover from damage. In 1996, the Sustainable Fisheries Act reauthorized the Magnuson Fishery and Conser-

vation Management Act of 1976 in the United States. This legislation recognized that healthy fish stocks and sustainable fisheries are dependent upon healthy fish habitat. As a result, the Essential Fish Habitat (EFH) program was started to promote the protection of this habitat. The North Pacific Fishery Management Council has identified living substrates in deep waters (coral, sponges, anemones, sea-whips, etc.) as types of habitat that are Habitat Areas of Particular Concern (HAPC). Hence, red tree coral is recognized as EFH (Witherell & Coon, 2002). Specific areas should be protected from fishing gear disturbance to allow for habitat recovery and scientific studies. Submersible surveys could be performed in these areas, where colony height and/or trunk diameter could be used to estimate the age distribution of colonies for the region of interest; however, further study is recommended at various locations (geographical and depth) to examine variability in growth in relation to environmental conditions.

ignated for research in the North Pacific Ocean and Bering Sea.

References

Abbiati, M., G. Buffoni, G. Di Cola & G. Santangelo, 1991. Red coral population dynamics: stability analysis and numerical simulation of time evolution of perturbed states. In: Terrestrial and Aquatic Ecosystems: Perturbation and Recovery. Ellis Horwood Series in Environmental Management, Science, and Technology. New York: 219–228.

Adkins, J. F., H. Cheng, E. A. Boyle, E. R. M. Druffel & R. L. Edwards, 1998. Deep-sea coral evidence for rapid ventilation of the deep north Atlantic 15 400 years ago. Science 280: 725–728.

Andrews, A. H., G. M. Cailliet & K. H. Coale, 1999a. Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. Can. J. Fish. Aquat. Sci. 56: 1339–1350.

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

Appleby, P. G. & F. Oldfield, 1992. Application of lead-210 to sedimentation studies. In: Ivanovich, M. & R. S. Harmon (eds), Uranium-series Disequilibrium: Applications to Earth, Marine, and Environmental Sciences. Clarendon Press, Oxford: 731–778.

Beamish, R. J. & D. A. Fournier, 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. aquat. Sci. 38: 982–983.

Bloeser, J. A., 1999. Diminishing returns: the status of west coast rockfish. Pacific Marine Conservation Council. P.O. Box 59, Astoria OR 97103: 94 pp.

Brazeau, D. A. and H. R. Lasker, 1992. Growth rates and growth strategy in a colonial marine invertebrate, the Caribbean octocoral *Briareum asbestinum*. Biol. Bull. 183: 269–277.

Cimberg, R. L., T. Gerrodette and K. Muzik, 1981. Habitat requirements and expected distribution of Alaska coral. Final Report, Research Unit 601, VTN Oregon, Inc. Report prepared for Office of Marine Pollution Assessment, Alaska Office.

Chang, W. Y. B., 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. aquat. Sci. 39: 1208–1210.

Chilton, D. E. & R. J. Beamish, 1982. Age determination methods for fishes studied by the groundfish program at the Pacific biological station. Can. Spec. Publ. Fish. Aquat. Sci. No. 60.

Dodge, R. E. & J. Thomson, 1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. Earth Planet. Sci. Lett. 23: 313–322.

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

Druffel, E. R. M., S. Griffin, A. Witter, E. Nelson, J. Southon, M. Kashgarian & J. Vogel, 1995. *Gerardia:* bristlecone pine of the deep-sea? Geochim. Cosmochim. Acta. 59: 5031–5036.

Edwards, R. L., J. W. Beck, G. S. Burr, D. J. Donahue, J. M. A. Chappell, A. L. Bloom, E. R. M. Druffel & F. W. Taylor, 1993. A large atmospheric ^{14}C/^{12}C and reduced melting in the Younger Dryas, documented with ^{230}Th ages of corals. Science 260: 962–968.

Flynn, W. W., 1968. The determination of low levels of polonium-210 in environmental materials. Anal. Chim. Acta 43: 221–227.

Griffin, S. & E. R. M. Druffel, 1989. Sources of carbon to deep-sea coral skeletons. Radiocarbon. 31: 533–542.

Grigg, R. W., 1974. Growth rings: annual periodicity in two gorgonian corals. Ecology 55: 876–881.

Grigg, R. W., 1976. Fishery management of precious and stony corals in Hawaii. Sea Grant Technical Report. UNIHI-Seagrant-TR-77-03. HIMB Contribution No. 490: 48 pp.

Goh, N. K. C. & L. M. Chou. 1995. Growth of five species of gorgonians (sub-class Octocorallia) in the sedimented waters of Singapore. Mar. Ecol. 16(4): 337–346.

Heezen, B. C. & C. D. Hollister, 1971. Face of the deep. Oxford Press, New York: 659 pp.

Heifetz, J., 2002. Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia. 471: 19–27.

Hixson, S. J., 1915. Some *Alcyonaria* and a *Stylaster* from the West Coast of North America. Proc. Zool. Soc. Lond. 37: 541–557, 1 plate.

Kim, K. & H. R. Lasker, 1997. Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). J. exp. mar. Biol. Ecol. 215(1): 49–64.

Kinoshita, K., 1908. Primnoidae von Japan. Journ. Coll. Sci. Univ. Tokyo. 23(12): 1–74, 6 plates.

Krieger, K. J., 1993. Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fish. Bull. 91: 87–96.

Krieger, K., 1998. *Primnoa* spp. observed inside and outside a bottom-trawled path from a submersible. Abstract: 10th Western Groundfish Conference, Asilomar Conference Center, Pacific Grove, California, U.S.A. 1–5 February 1998.

Krieger, K. J., 2002. Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. In Willison, J. H. M., J. Hall, S. E. Gass, E. L. R. Kenchington, P. Doherty & M. Butler (eds), Proceedings of the First International Symposium on Deep Sea Corals. Ecology Action Center, Halifax, Canada: in press.

Krieger, K. J. & B. L. Wing, 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471: 83–90.

Marshall, N. B., 1979. Deep-sea Biology: Developments and Perspectives. Garland STPM Press, New York: 566 pp.

Mistri, M., 1995. Gross morphometric relationships and growth in the Mediterranean gorgonian *Paramuricea clavata*. Boll. Zool. 62: 5–8.

Mistri, M. & V. U. Ceccherelli, 1994. Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. Mar. Ecol. Prog. Ser. 103: 291–296.

Mitchell, N. D., M. R. Dardeau & W. W. Schroeder, 1993. Colony morphology, age structure, and relative growth of two gorgonian corals, *Leptogorgia hebes* (Verrill) and *Leptogorgia virgulata* (Lamarck), from the northern Gilf of Mexico. Coral Reefs. 12: 65–70.

Mortensen, P. B., M. Hovland, T. Brattegard & R. Farestveit, 1995. Deep water bioherms of the Scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian Shelf: structure and associated megafauna. Sarsia 80: 145–158.

Mortensen, P. B. & H. T. Rapp, 1998. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (Anthozoa, Scleractinia): implications for determination of linear extension rates. Sarsia 83(5): 433–446.

O'Connell, V. M. & F. C. Funk, 1986. Age and growth of yelloweye rockfish (*Sebastes ruberrimus*) landed in southeastern Alaska. In: Proc. Int. Rockfish Symp. Oct. 1986, Anchorage, Alaska. Alaska Sea Grant Report No. 87-2: 171–196.

Risk, M. J., D. E. McAllister & L. Behnken, 1998. Conservation of cold- and warm-water seafans: threatened ancient gorgonian groves. Sea Wind. 12(1): 2–21.

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

Shen, G. T., E. A. Boyle & D. W. Lea, 1987. Cadmium in corals as a tracer of historical upwelling and industrial fallout. Nature 328: 794–796.

Velimirov, B., 1975. Wachstum und altersbestimmung der gorgonie *Eunicella cavolinii*. Oecologia (Berl.) 19: 259–272.

Weinbauer, M. G. & B. Velimirov, 1996. Relative habitat suitablility and stability of the Mediterranean gorgonian coral *Eunicella cavolini* (Coelenterata: Octocorallia). Bull. mar. Sci. 58(3): 786–791.

Witherell, D. & C. Coon, 2002. Protecting gorgonian corals from fishing impacts. In Willison, J. H. M., J. Hall, S. E. Gass, E. L. R. Kenchington, P. Doherty & M. Butler (eds), Proceedings of the First International Symposium on Deep Sea Corals. Ecology Action Center, Halifax, Canada: in press.

West, J. M., C. D. Harvell & A. M. Walls, 1993. Morphological plasticity in a gorgonian coral (*Briareum asbestinum*) over a depth cline. Mar. Ecol. Prog. Ser. 94: 61–69.

Yoshioka, P. M. & B. B. Yoshioka, 1991 A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Mar. Ecol. Prog. Ser. 69: 253–260.

Yoshioka, P. M., 1996. Variable recruitment and its effects on the population and community structure of shallow-water gorgonians. Bull. mar. Sci. 59(2): 433–443.