



FEATURE ARTICLE

Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals

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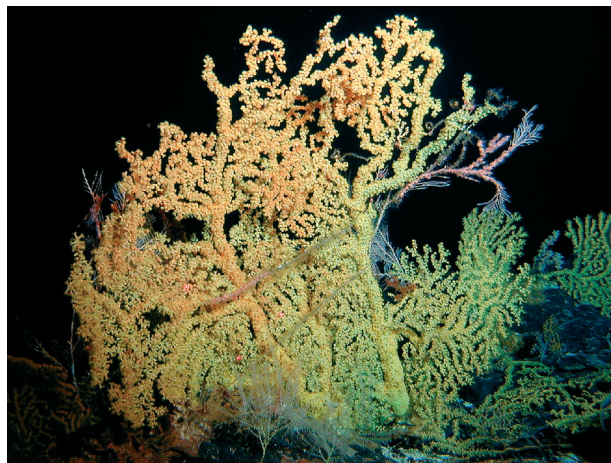
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ABSTRACT: The radial growth rates and ages of 3 different groups of Hawaiian deep-sea 'corals' were determined using radiocarbon measurements. Specimens of *Corallium secundum*, *Gerardia* sp., and *Leiopathes glaberrima* were collected from 450 ± 40 m depth at the Makapuu deep-sea coral bed off the southeast coast of Oahu, Hawaii, USA, using a submersible vessel (PISCES V). Specimens of *Antipathes dichotoma* were collected at 50 m depth off Lahaina, Maui, Hawaii. The primary source of carbon to the calcitic *C. secundum* skeleton is *in situ* dissolved inorganic carbon (DIC). Using 'bomb ^{14}C ' time markers we calculated radial growth rates of $\sim 170 \mu\text{m yr}^{-1}$ and ages of 67 to 71 yr for specimens of *C. secundum* up to 28 cm tall. *Gerardia* sp., *A. dichotoma*, and *L. glaberrima* have proteinaceous skeletons, and labile particulate organic carbon (POC) is their primary source of architectural carbon. Using ^{14}C we calculated a radial growth rate of $15 \mu\text{m yr}^{-1}$ and an age of 807 ± 30 yr for a live collected *Gerardia* sp., showing that these organisms are extremely long lived. Radiocarbon measurements taken from the inner and outer portions of basal cross sections of 4 sub-fossil *Gerardia* sp. samples showed growth rates (range 14 to $45 \mu\text{m yr}^{-1}$) and ages (range 450 to 2742 yr) similar to that of the live collected sample. Similarly, with a growth rate of $< 10 \mu\text{m yr}^{-1}$ and an age of ~ 2377 yr, *L. glaberrima* at the Makapuu coral bed is also extremely long lived. In contrast, the shallow-collected *A. dichotoma* samples yielded growth rates ranging from 130 to $1140 \mu\text{m yr}^{-1}$ (12 to 32 yr). These results show that Hawaiian deep-sea corals grow more slowly and are older than previously thought.

KEY WORDS: Deep-sea coral · Age · Growth rate · Radiocarbon · *Corallium secundum* · *Gerardia* sp. · *Leiopathes glaberrima* · *Antipathes dichotoma*

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Radiocarbon dating shows that deep-sea corals grow more slowly and are far older than previously thought. Some species, such as gold coral *Gerardia* sp. (above, specimen from Cross Seamount probably damaged by fishery long lines), have life-spans of several millenia.

Photo: Maximilian Cremer
(Hawaii Undersea Research Laboratory)

INTRODUCTION

Compared to surface corals, little is known about the biology, growth rates, and longevity of most deep-sea corals (DSC), in part due to difficulties with sampling and observation. Increased interest in the ecology and biology of DSC and the habitat that they provide for other organisms has occurred in response to an increasing awareness of the threat of physical destruction caused by pelagic and benthic fisheries. Many DSC provide habitat important to adult or juvenile recruit-

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ment of commercially important fish (Witherell & Coon 2000, Witherell et al. 2000). Deep-sea trawling can cause extensive damage to DSC and to the deep-water reefs they form (Krieger 2000, Witherell & Coon 2000, Hall-Spencer et al. 2002). Additionally, several DSC coral species are commercially harvested as part of the world-wide trade in precious corals used in jewelry and art industries (Grigg 1976, 1993, 2001). Geochemical and isotopic data derived from DSC provide views of past climate and environmental change as observed from the ocean interior, an area for which almost no other high resolution paleoclimate records exist (e.g. Smith et al. 1997, Adkins et al. 1998, Smith et al. 2000, Weinbauer et al. 2000, Smith et al. 2002, Frank et al. 2004, Thresher et al. 2004). In order for the potential of this paleoceanographic archive to be fully realized, we must have a better understanding of growth rates and longevity so that the most accurate and precise chronological control can be developed. In addition, conservation and management of deep-sea ecosystems and DSC requires a knowledge of the growth rates and longevity of these sessile denizens of the deep.

Growth rates and ages of individual deep-sea corals have been estimated and measured by a variety of methods. Methods include tagging (Grigg 1976, Stone & Wing 2000), counting of skeletal rings that are assumed to form annually (Grigg 1974, 1976, Wilson et al. 2002), as well as applying radiometric techniques such as U/Th, ^{210}Pb and radiocarbon dating (Griffin & Druffel 1989, Druffel et al. 1990, Druffel et al. 1995, Cheng et al. 2000, Adkins et al. 2002, Andrews et al. 2002, Risk et al. 2002, Adkins et al. 2004). All methods estimate the age or longevity of individual specimens or sections by extrapolating the calculated linear or radial growth rates.

Here, we present the results of radial growth rates and age estimates from 4 different DSC species from Hawaiian waters, as determined by radiocarbon (^{14}C) measurements. We make use of both conventional radiocarbon ages as well as the time varying transient of 'bomb ^{14}C ' in the oceanic total dissolved CO_2 pool. We focus on *Corallium secundum* (pink coral), *Gerardia* sp. (gold coral) and 2 species of antipatharians (black corals: *Leiopathes glaberrima* and *Antipathes dichotoma*) because they are abundant in Hawaiian waters and have been studied as part of the precious coral fishery (Grigg 1976, 1993, 2001, 2002). Our results have significant implications for the conservation and management of the Hawaiian precious coral fisheries as well as for regional deep-sea corals potentially impacted by pelagic or benthic fisheries. In addition, our results establish a chronological framework for future paleoenvironmental reconstructions using these deep-sea corals.

The deep-sea corals used in this study are from different orders. *Corallium* spp. belong to the order

Gorgonacea. The black coral (order Antipatharia) is a hexacoral as is the gold coral, *Gerardia* sp. (order Zoantharia). *Gerardia* sp. is a colonial zoanthid anemone whose skeleton is made of a hard, dense, layered proteinaceous material. *Gerardia* sp. grows in a dendritic tree-like fashion to several meters in height with trunks typically 3 to 15 cm in diameter. Hawaiian black corals also have a proteinaceous skeleton that grows in tree-like shape to heights of almost 3 m, with basal diameters of 1 to 15 cm. *Corallium* sp. is a branching coral with a skeleton composed of calcite. The coral grows in a fan-like shape to about 75 cm high, with main trunks 10 to 50 mm in diameter.

Previous age and growth rate studies of Hawaiian deep-sea corals arose in part, because there is a local fishery harvesting *Corallium* spp., *Gerardia* sp., and black corals, for the jewelry industry. The industry has operated intermittently in Hawaiian waters since the mid 1960s (Grigg 1976, 1988, 1993, 2001, 2002). From 1966 to 1969, tangle net dredges were used to collect the coral until more selective harvesting operations using submersible vessels were mandated. The US 1983 Federal Fishery Management Plan included age and growth estimates using tagging and visual observations of black, pink and gold corals. This plan set the size and harvesting limits for the respective species. (e.g. for *Corallium* a Hawaii-wide catch limit of 2000 kg every 2 yr with a minimum 10 inch [= 25.4 cm] vertical height requirement). The establishment of the Coral Reef Ecosystem Reserve in the Northwestern Hawaiian Islands (NWHI) in 2000 further limited direct access to exploitable beds (Grigg 2002). Despite the current dormancy of the fishery, research continues on the ecology (Parrish et al. 2002) and management of the precious coral beds, in part to identify new beds and refine the maximum sustainable yields (MSY) should collection resume (Grigg 1976, 1993, Western Pacific Regional Fishery Management Council 2001, Grigg 2001, 2002, National Marine Fisheries Service (NMFS) 2002).

Early estimates of growth rate (linear extension rates) of Hawaiian precious corals were made on individual colonies. Using 21 tagged colonies from water depths of ~50 m Grigg (1976) measured a linear extension rate of 6.42 cm yr^{-1} for *Antipathes dichotoma* and 6.12 cm yr^{-1} for *A. grandis* over a 3.5 yr study. This extension rate was then applied to the whole colony to provide an age estimate of ~25 yr for colonies ~1.5 m tall. The estimated age (based on extension rate) of these shallow dwelling colonies, coupled with the number of counted growth bands in X-radiographs of 47 basal or stem cross-sections, suggested that the bands are deposited annually (Grigg 1976). Based on the inference that growth bands in *A. dichotoma* are annual, Grigg (1976, 2002) assumed that similar bands observed in

Corallium secundum and *Gerardia* sp. were also annual and provided estimated linear growth rates of 0.9 cm yr^{-1} and 6.6 cm yr^{-1} , respectively (Grigg 1976, 2002). Using these growth rates, the greatest ages reported were 45 yr (~40 cm tall) for *C. secundum* (from 350 to 475 m water depth) and 70 yr (~2.6 m tall) for *Gerardia* sp. (380 to 410 m depth) (Grigg 1976, 2002).

Druffel et al. (1990) used excess ^{210}Pb measurements to calculate a radial growth rate of 0.11 mm yr^{-1} and an age of $180 \pm 40 \text{ yr}$ for a trunk of *Corallium niobe* from the Atlantic Ocean. Radiocarbon measurements (0.13 mm yr^{-1} , $135 \pm 90 \text{ yr}$) on the same sample, assuming a constant growth rate and the fact that bomb carbon had not been detected in the coral, agreed with the ^{210}Pb result (Griffin & Druffel 1989). Using similar assumptions, a ^{14}C -based radial growth rate of $\sim 5 \mu\text{m yr}^{-1}$ and a basal age of $1800 \pm 300 \text{ yr}$ were determined on an Atlantic *Gerardia* specimen (Druffel et al. 1995). Amino acid racemization dating on this specimen yielded a maximum age of $250 \pm 70 \text{ yr}$ (Goodfriend 1997). However, the amino acid date was based on racemization rates determined by high temperature heating experiments that may not extrapolate in a linear fashion to the low ambient temperatures in which the coral grew.

Despite the uncertainty between the various methods employed, including different species from different oceans, it is clear that there are significant differences in the estimated growth rates and ages, particularly in the case of *Gerardia* sp. In an effort to refine and validate the ages and growth rates of Hawaiian *Corallium* spp., black corals, and *Gerardia* sp., we used high-resolution ^{14}C measurements to determine radial growth rates and ages. Radial growth rates are important as radial sampling across the basal section is the most likely source of paleo-environmental proxy time-series, much like tree ring analyses. The derived colony ages can be correlated to specimen height for the purposes of management censuses.

MATERIALS AND METHODS

Field collection. The majority of the samples used in this study were collected alive in 1997 from $450 \pm 40 \text{ m}$ depth using the PISCES V submersible vessel on Makapuu Bank off the island of Oahu (Fig. 1, Table 1). External tissues were removed aboard ship and intact skeletons returned to the laboratory. Initial species identifications were at the time of collection by the divers (R. Dunbar, B. Linsley and R. Grigg) using visual characteristics. Where uncertainty existed, dive tapes and photographs have been reviewed and identifications confirmed by comparison with more recent surveys of the Makapuu coral beds. Samples of *Corallium*

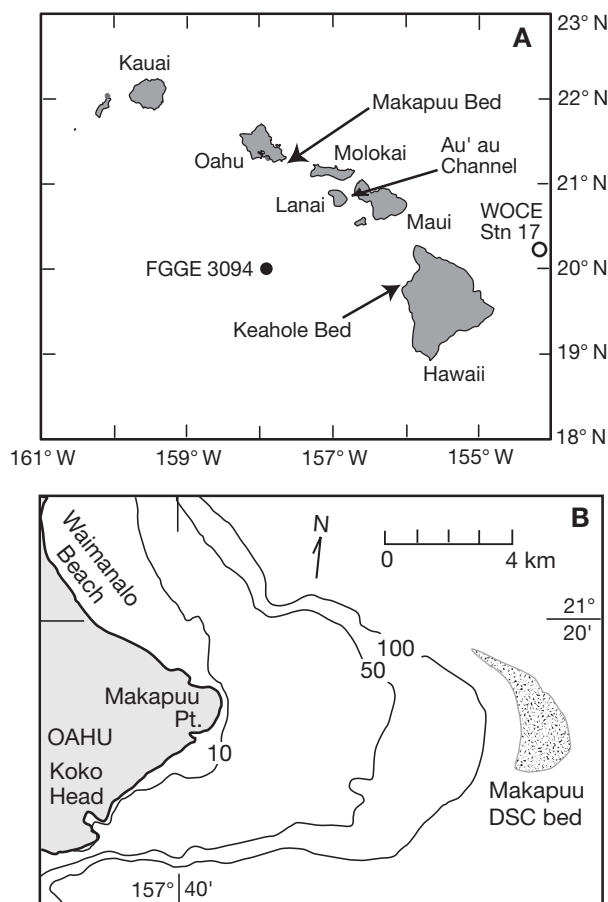


Fig. 1. (A) The Hawaiian Islands showing the location of the Makapuu and Keahole deep-sea corals beds, and the location of 2 hydrographic profiles, WOCE (World Ocean Circulation Experiment) Stn 17 and FGGE (First GARP [Global Atmospheric Research Program] Global Experiment 3094). (B) Detailed map of the Makapuu bed (shaded region) from Grigg (1998). Bathymetric contours in meters. DSC = deep-sea coral

secundum, *Leiopathes glaberrima*, and *Gerardia* sp. were all collected at the Makapuu bed (Fig. 1, Table 1). Basal sections of additional samples collected by R. Grigg during the course of his research (Table 1) were also provided. While the *Antipathes dichotoma* (family Antipathidae: colloquially black corals) were collected alive from 50 m in the Au'au channel off Lahaina, Maui, the collection date was uncertain. The *Gerardia* sp. samples were collected dead at ~400 m from DSC beds off the island of Hawaii (Table 1). Samples collected alive have one known time marker: the date of collection. As a consequence, these samples were used preferentially in the high-resolution sampling age models.

Sample preparation. Disks 3 to 10 mm thick were cut from the basal portion of all samples. The disks were mounted on glass slides and were incrementally milled using a Merchantek computer controlled micromill or manual micromill along a radial transect from

Table 1. *Corallium secundum*, *Gerardia* sp. and *Leipathes glaberrima*. Summary of sample information, radiocarbon measurements, ages and growth rates

Sample ID	Taxon	Location	Depth (m)	$\Delta^{14}\text{C}$ (‰)		^{14}C years		Calendar years		Age (yr)	Growth rate ($\mu\text{m yr}^{-1}$)
				Inner	Outer	Inner	Outer	Inner	Outer		
COR-RD97-01 ^a	<i>Corallium secundum</i>	Makapuu, Oahu	450 ± 40	-104 ± 5	3.5 ± 2.2	835 ± 40	>Modern	1997 ^a		71 ± 9	170
COR-RD97-02 ^a	<i>Corallium secundum</i>	Makapuu, Oahu	450 ± 40	-96 ± 5	5 ± 4	760 ± 35	>Modern	1997 ^a		67 ± 9	170
GER-RD97-01 ^a	<i>Gerardia</i> sp.	Makapuu, Oahu	450 ± 40	-144.3 ± 2.4	71 ± 4	1200 ± 25	>Modern	760 ± 30 ^b	1997 ^a	807 ± 30	15
GER-#1 ^c	<i>Gerardia</i> sp.	Makapuu, Oahu	400 ± 20	-139 ± 4	-74.5 ± 2.7	1150 ± 35	570 ± 25	710 ± 25 ^b	260 ± 15 ^b	450 ± 30 ^e	45
GER-#2 ^c	<i>Gerardia</i> sp.	Makapuu, Oahu	400 ± 20	-317.8 ± 2.2	56.1 ± 2.8	3020 ± 30	>Modern	2730 ± 15 ^b	1962 ^d	2742 ± 15	14
GER-#4 ^c	<i>Gerardia</i> sp.	Makapuu, Oahu	400 ± 20	-236.8 ± 2.5	-120.0 ± 2.6	2120 ± 30	980 ± 25	1740 ± 35 ^b	585 ± 25 ^b	1155 ± 45 ^e	31
GER-HI-RG-01 ^c	<i>Gerardia</i> sp.	Hawai'i	410 ± 10	-332.4 ± 2.6	-261.8 ± 2.5	3200 ± 35	2390 ± 30	3040 ± 45 ^b	2055 ± 40 ^b	985 ± 60 ^e	24
Black coral (BC)#5 ^a	<i>Leipathes glaberrima</i>	Makapuu, Oahu	450 ± 40	-280.7 ± 2.9	-69 ± 4	2600 ± 35	530 ± 40	2320 ± 15 ^b	1997 ^a	2377 ± 15	≤10

^aCollected alive by R. Dunbar in 1997
^b ^{14}C results calibrated using INTCAL v5.0 and ΔR of -28 ± 4 ^{14}C years; results in calendar yr BP (before present) and 1 sigma error reported
^cCollected by R. Grigg
^dPost-bomb data are reflected by positive $\Delta^{14}\text{C}$ values. AD (Anno Domini) years were determined by comparison with a Hawaiian surface water $\Delta^{14}\text{C}$ time-series (T. P. Guilderson & D. P. Schrag unpubl.). See Fig. 8
^eError calculated by the least squares method using the uncertainty of the inner and outer calendar yr

the outer edge to the center of the sample. The advantage of the computer controlled system is that the x-y-z stage directional control allows for sampling along straight or curved growth contours with a precision better than 5 μm . *Corallium secundum* (Fig. 2) and *Gerardia* sp. samples were milled using the Merchantek micromill at ~0.5 mm and ~0.5 to 0.6 mm increments respectively (Table A1 Appendix 1 available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m327p001_app.xls). The only exception is that the outermost sample of COR-RD97-01 (Table 1) was milled over a 1 mm increment. Black coral samples were milled at 0.5 to 0.7 mm increments using the manual micromill. Only the outermost and central sections, as best identified by any visible banding structure, of the remaining samples were milled using either the manual micromill or a Dremel power tool, resulting in age determinations on the inner (core) and outermost material. No more than 1 mm along the radial distance was sampled. Approximately 1.0 to 4.0 mg per sample of carbonate material was obtained from the *C. secundum* samples, and ~1.0 to 3.0 mg of proteinaceous material was obtained from the *Gerardia* sp. and black coral samples.

Laboratory methods. Proteinaceous samples from the *Gerardia* sp. and black corals were decarbonated with weak HCl, rinsed with deionized water and dried on a heating block. Samples were combusted and converted to CO_2 in individually sealed quartz tubes with CuO and silver. Carbonate samples from *Corallium secundum* were placed in individual reaction cells, evacuated, heated and acidified with orthophosphoric acid at 90°C to produce CO_2 (cf., Guilderson et al. 1998). The CO_2 from carbonate and gorgonian samples was purified, trapped, and converted to graphite using an iron catalyst, following a method similar to that described by Vogel et al. (1987). The graphite targets were analyzed at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. The ^{14}C results are reported as $\Delta^{14}\text{C}$ (‰) as defined by Stuiver & Polach (1977) and include $\delta^{13}\text{C}$ correction for isotope fractionation, and a blank subtraction based on ^{14}C -free calcite or coal depending on sample matrix. Stable isotopic transects near the ^{14}C transects were made on both *C. secundum* samples. The average $\delta^{13}\text{C}$ value of -5.7‰ for COR-RD97-01 and -5.8‰ for COR-RD97-02 were used for the isotope fractionation correction. $\delta^{13}\text{C}$ values of -16‰ and -17‰ were used for the isotope fractionation correction of the *Gerardia* sp. and black corals sample, respectively. Where appropriate, the ^{14}C results are also reported in ^{14}C and calendar yr BP (before present) (Stuiver & Polach 1977). To convert the ^{14}C age to a calendar age, a reservoir age correction must be applied. The reservoir age is a result of the depletion

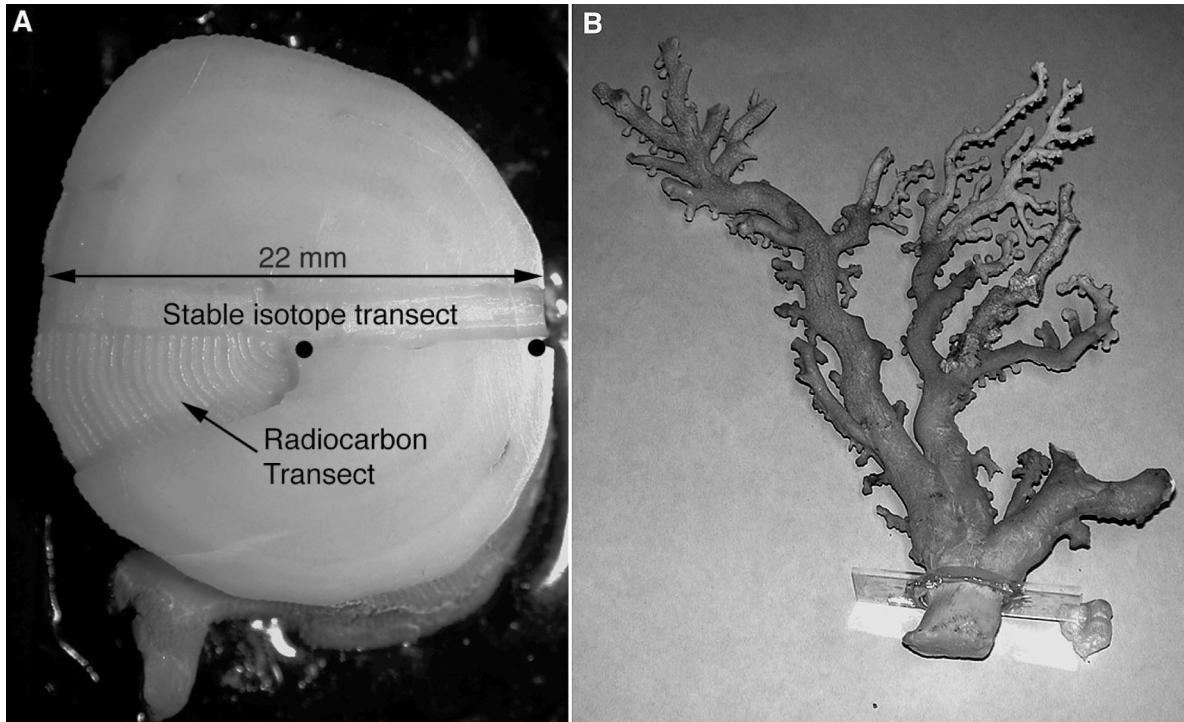


Fig. 2. *Corallium secundum*. (A) Disk cut from the basal portion of a sample mounted on a glass slide, and (B) complete specimen with a height of 28 cm and basal diameter of 22 mm. The radiocarbon and stable isotope sampling tracks are shown in (A). Note each ridge in the radiocarbon sampling track is one sample. Dots are an example of where inner and outer samples were taken

in the radiocarbon content of surface waters brought about by the mixing of surface waters equilibrated with the atmosphere with older water from subsurface depths. This makes surface waters appear older than the atmosphere. Typically, the reservoir age is calculated by assuming a global average value of 404 ^{14}C yr and adding a regional reservoir correction (or ΔR value). All calibrations were done using a ΔR of -28 ± 4 ^{14}C yr (Druffel et al. 2001), the CALIB 5.0 (Stuiver & Reimer 1993) computer calibration program and the marine04 calibration dataset (Hughen et al. 2004) (Table A2 in Appendix 1 available at: www.int-res.com/articles/suppl/m327p001_app.xls). When determining growth rates on live collected specimens we added 47 yr to account for the time between collection and the radiocarbon 1950 reference year.

RESULTS

The outermost $\Delta^{14}\text{C}$ values for 2 individuals of Makapuu *Corallium secundum* (COR-RD97-01 and -02) were $3.5 \pm 2.2\%$ and $5 \pm 4\%$, respectively (Fig. 3, Table 1). Approximately 4 mm inwards from the surface, both corals had similar values of ca. -100% and with a few exceptions remained within the 1σ error of the measurements to the central core (Fig. 3, Table A1).

For the *Gerardia* sp. samples, the outermost $\Delta^{14}\text{C}$ value along the radial transect of the GER-RD97-01 sample was $71 \pm 4\%$, dropping to $-60 \pm 4\%$ ($445 \pm$

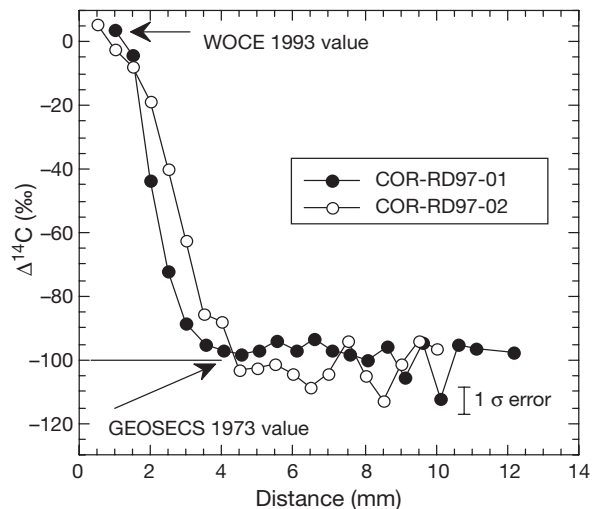


Fig. 3. *Corallium secundum*. $\Delta^{14}\text{C}$ radial transect across 2 pink coral samples (COR-RD97-01 and COR-RD97-02). Based on the GEOSECS (Geochemical Ocean Sections Study) hydrographic profile, a $\Delta^{14}\text{C}$ value of -100% is assigned a time marker of 1973 and growth rates were calculated by linear interpolation between that point and the outer edge with a known collection date of 1997. Both samples had a radial growth rate of $170 \mu\text{m yr}^{-1}$ and ages of ~ 70 yr

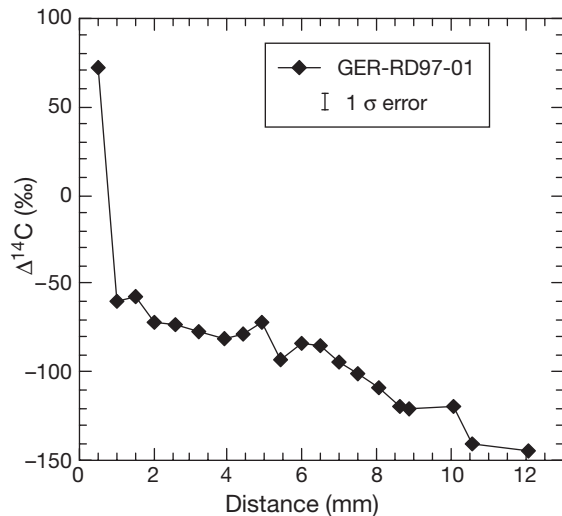


Fig. 4. *Gerardia* sp. $\Delta^{14}\text{C}$ radial transect across a gold coral sample (GER-RD97-01). The center of the sample had a ^{14}C age of 1200 ± 25 ^{14}C yr and a calendar age of 807 ± 30 yr resulting in a calculated radial growth rate of ~ 15 $\mu\text{m yr}^{-1}$. 1σ errors are no larger than symbols

35 ^{14}C yr) at the next sampling interval. Over the remaining 11 mm, $\Delta^{14}\text{C}$ systematically decreased to -144 ± 2.4 ‰ at the center of the trunk (Fig. 4, Tables 1 & A1). This is equivalent to a ^{14}C age of 1200 ± 25 yr. Outer values of the 4 additional living and dead *Gerardia* sp. samples ranged from modern (post-bomb) to 2390 ± 30 ^{14}C yr. Inner values of the same specimens range from 1150 ± 35 to 3200 ± 35 ^{14}C yr (Table 1).

The outer value of the radial transect across the *Antipathes dichotoma* sample (BC#3) collected at 50 m depth was 107 ± 4 ‰. $\Delta^{14}\text{C}$ decreased to a value of -57 ± 4 ‰ over the first 5 mm, and remained unchanged over the inner ~ 13 mm (Fig. 5, Tables 2 & A1). In contrast, the 'deep-water black coral', *Leiopathes glaberrima* (BC#5), collected at 450 ± 40 m showed a linear decrease from an outer value of -70 ± 4 ‰ to a value of -280.7 ± 2.9 ‰ (2600 ± 35 ^{14}C yr) at the center (Fig. 5, Table A1). The rate of decrease was

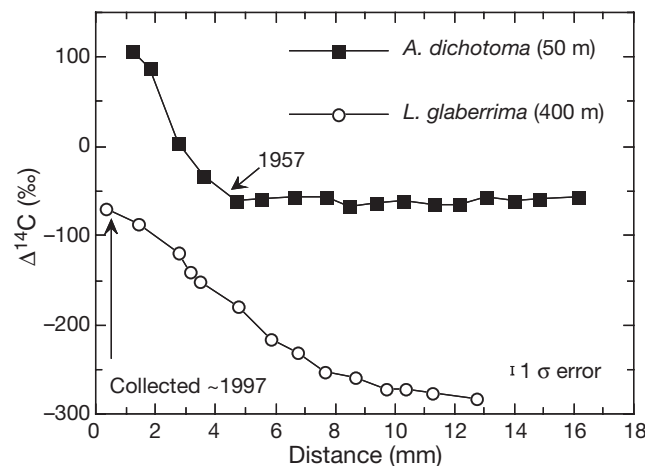


Fig. 5. *Antipathes dichotoma* and *Leiopathes glaberrima*. $\Delta^{14}\text{C}$ radial transect across an *A. dichotoma* specimen (sample BC#3, ■) collected at 50 m and an *L. glaberrima* specimen (sample BC#5, ○) collected at 450 m. $\Delta^{14}\text{C}$ values > -50 ‰ are indicative of bomb ^{14}C and can be used to set an initial time marker of 1957 for sample BC#3. 1σ errors are no larger than symbols

slower over the innermost 5 mm (Fig. 5). The outer (inner) $\Delta^{14}\text{C}$ values of specimens BC#1 and BC#2 of the shallow-collected *A. dichotoma* were 69‰ (143‰) and 87‰ (140‰), respectively (Table 2).

DISCUSSION

Sources of carbon

In order to calculate growth rates and ages using ^{14}C , it is necessary to determine the sources of carbon (and corresponding radiocarbon content) for the skeletal matrix or material being analyzed. Potential sources of carbon utilized by DSC include particulate organic carbon (POC), dissolved inorganic carbon (DIC), sedimentary organic carbon (SOC), and dissolved organic carbon (DOC). After exchange across the air-sea

Table 2. *Antipathes dichotoma*. Summary of sample information, radiocarbon measurements, ages and growth rates of the black corals collected by R. Grigg

Sample ID	Depth (m)	$\Delta^{14}\text{C}$ (‰) ^a		Calendar age ^b		Life-span Min	Life-span Max	Radius (mm)	Growth rate ($\mu\text{m yr}^{-1}$)		Height (cm)	Age, linear growth rate ^c	Age, growth band ^c
		Inner	Outer	Inner Min/Max	Outer Min/Max				Min	Max			
BC #1	50±5	143.0	69.4	1966/1972-1983	Post 1992/~1998	15	32	5.9	180	390	81.3	12	15
BC #2	50±5	140 ^d	87 ^d	1966/1972-1983	Post 1992/~1995	12	29	13.7	470	1140	129.5	20	25
BC #3	50±5	-57±4	107±4	pre 1957	1962/1992	25	109	13.6	130	560			

^aPost-bomb data are reflected by positive $\Delta^{14}\text{C}$ values

^bAD (Anno Domini) years were determined by comparison with a Hawaiian surface water $\Delta^{14}\text{C}$ time-series (see Fig. 8)

^cAge calculated from linear growth rates and on the relationship between annual growth rings and height (Grigg 1976)

^dBC#2 results are the average of 2 inner and outer ^{14}C measurements as the sample appeared to have 2 growth centers fused together

boundary, CO_2 is hydrated and mixed in the upper layer of the ocean as DIC. DIC is then fixed by photosynthesis in the euphotic zone to POC with some recently fixed carbon leaking into the DOC pool. The operational definition of the difference between POC and DOC is size dependent, where POC is defined as particulate matter larger than $1 \mu\text{m}$ in size that is suspended and sinking out of the ocean surface mixed layer, while DOC is organic matter less than $1 \mu\text{m}$ in size suspended in the seawater (Druffel & Williams 1990, Druffel et al. 1992). SOC is particulate organic matter contained in sediments on the ocean floor that can be resuspended by bottom water currents or biological activity.

Radiocarbon measurements of seawater samples collected from depth profiles in the North Central Pacific (NCP; $31^\circ 00' \text{N}$, $159^\circ 00' \text{W}$) from the late 1980s revealed significant $\Delta^{14}\text{C}$ differences with depth and between the various sources of carbon (Druffel & Williams 1990, Druffel et al. 1992). The $\Delta^{14}\text{C}$ values of DIC revealed the presence of bomb ^{14}C above the main thermocline ($<400 \text{ m}$, and average $\Delta^{14}\text{C} \sim 117\%$), decreasing between ~ 300 and $\sim 1000 \text{ m}$ (to an average $\Delta^{14}\text{C}$ value of ca. -240%), after which $\Delta^{14}\text{C}$ was relatively constant down to 5700 m . Suspended POC $\Delta^{14}\text{C}$ values at the surface and sinking POC (4200 m) were nearly equivalent to surface DIC $\Delta^{14}\text{C}$ values, and suspended POC values decreased only slightly with depth. DOC $\Delta^{14}\text{C}$ apparent ages were older, with an average $\Delta^{14}\text{C}$ value of ca. -150% at the surface and significantly offset from the corresponding DIC $\Delta^{14}\text{C}$ values, although the structure of the 2 curves was similar. SOC $\Delta^{14}\text{C}$ values (ca. -500%) at the sediment water interface were equivalent to DOC values at depth, after which they decreased by more than 250% within the upper 10 cm of sediment (Druffel et al. 1992). Based on measurements made in the NCP during 1992, typical $\Delta^{14}\text{C}$ values of DIC, POC, and DOC in the upper 50 m of the water column were 132% , $139 \pm 9\%$, and $-163 \pm 18\%$ $\Delta^{14}\text{C}$, respectively (Druffel et al. 1992). Between 300 and 450 m , typical $\Delta^{14}\text{C}$ values of DIC, POC, and DOC were $77 \pm 3\%$ (300 m), $129 \pm 11\%$ (450 m), and $-363 \pm 14\%$ (300 m) $\Delta^{14}\text{C}$, respectively (Druffel et al. 1992). The $\Delta^{14}\text{C}$ values of the different sources of carbon will change with time, but in most cases they were significantly and measurably different from each other at any one time. As a consequence, one can use the radiocarbon values to distinguish between DIC, POC, and the significantly more negative DOC and SOC as the predominant source of carbon to the deep-sea corals collected at 400 m .

For the live-collected DSC samples, it is possible to use the outer $\Delta^{14}\text{C}$ measurement in conjunction with the hydrographic profiles of $\Delta^{14}\text{C}$ values in the water column described above as an indicator of the most

recent source of carbon deposited in the skeleton. The outer $\Delta^{14}\text{C}$ value of 2 live collected specimens of *Coralium secundum* ($5 \pm 3\%$, $3.5 \pm 2.2\%$), 1 *Gerardia* sp. ($71 \pm 4\%$), and 1 black coral, *Leiopathes glaberrima* ($-69 \pm 4\%$), are plotted in concert with water $\Delta^{14}\text{C}$ from hydrocasts spanning the last 30 yr near Hawaii: GEOSECS (Geochemical Ocean Sections Study), FGGE (First GARP [Global Atmospheric Research Program] Global Experiment), and WOCE (World Ocean Circulation Experiment (Fig. 6; see Fig. 1 for locations of 2 FGGE and WOCE Stns). The outer values of 3 *Antipathes dichotoma* collected at 50 m are also plotted. The similarity of the outer $\Delta^{14}\text{C}$ values of the 2 *C. secundum* measured and the $\Delta^{14}\text{C}$ value of DIC at $\sim 450 \text{ m}$ suggest DIC is the primary source of carbon used for skeletogenesis. In contrast, the outer value of the $\sim 450 \text{ m}$ *Gerardia* sp. sample is similar to the surface water DIC $\Delta^{14}\text{C}$ value which will tag and be nearly equal to the $\Delta^{14}\text{C}$ signature of recently exported and labile POC, the expected source of skeletal C for deep water proteinaceous corals.

By analogy, we expected that the radiocarbon signature of the other proteinaceous corals, *Leiopathes glaberrima* and *Antipathes dichotoma*, would also

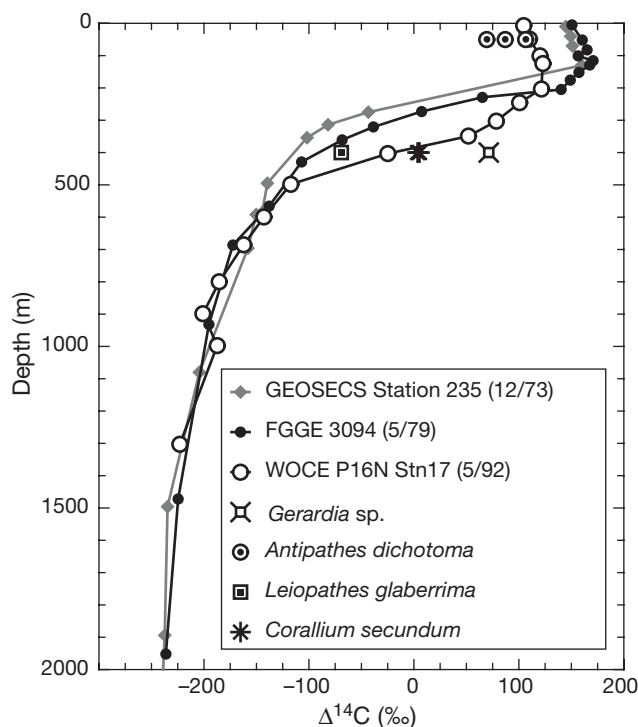


Fig. 6. Water $\Delta^{14}\text{C}$ from hydrocasts spanning the last 30 yr near Hawaii: GEOSECS (Geochemical Ocean Sections Study), FGGE (First GARP [Global Atmospheric Research Program] Global Experiment), and WOCE (World Ocean Circulation Experiment), plotted with the outer $\Delta^{14}\text{C}$ values of 2 *Corallium secundum* samples, 1 *Gerardia* sp. sample, 1 *Leiopathes glaberrima* sample (collected alive at 400 to 450 m) and 3 *Antipathes dichotoma* specimens (collected at 50 m)

reflect a POC source. However, because of their 50 m collection depth (where POC and DIC $\Delta^{14}\text{C}$ are similar), it is not possible to distinguish the primary C source for the *A. dichotoma* samples analyzed here. The value of the outermost sample from the *L. glaberrima* specimen is also not simply diagnostic of the source of carbon, because the specimen grew very slowly ($5 \mu\text{m yr}^{-1}$; see 'Discussion; Black corals, *Antipathes dichotoma* and *Leiopathes glaberrima*'). With such a slow growth rate over the sampling interval of 500 μm , the outer sample of the *L. glaberrima* specimen would be integrating ^{14}C from the last 100 yr. To estimate the integrated ^{14}C of DIC in surface water over the last ~100 yr, we averaged a $\Delta^{14}\text{C}$ record from a surface coral from Keauhou Bay, Kona spanning the time period from 1893 to 1966 (Druffel et al. 2001). The integrated ^{14}C values of surface water DIC over this time period should be nearly equal to the ^{14}C values of POC, as POC is tagged with the DIC ^{14}C values, and quickly exported from surface waters. The average $\Delta^{14}\text{C}$ from the Keauhou Bay record was -43% (Druffel et al. 2001), which is reasonably close to the measured value of -69% , suggesting that POC is primary source of carbon for *L. glaberrima*. In addition it has been shown that other DSC with a proteinaceous skeleton such as bamboo corals and primnoids derive their carbon almost exclusively from POC, either directly or indirectly through active feeding on pelagic zooplankton over their entire life time (*Gerardia* sp., this study, Druffel et al. 1995; bamboo corals, Roark et al. 2005; *Primnoa resedaeformis* Sherwood et al. 2005). Nothing in this study suggests that either *L. glaberrima* or *A. dichotoma* would be any different.

Corallium secundum

Radial transects of $\Delta^{14}\text{C}$ measurements on discretely milled samples (0.5 mm intervals) from the outermost edge to the center of each specimen of *Corallium secundum* were derived from 2 live collected individuals (COR-RD97-01 and COR-RD97-02) (Fig. 3). The results are compared to water $\Delta^{14}\text{C}$ from hydrocasts spanning the last 30 yr near Hawaii: GEOSECS, FGGE, and WOCE (Fig. 6). The hydrographic profiles exhibit the characteristic penetration of bomb ^{14}C into subthermocline waters. The *Corallium secundum* profiles show a similar rise in $\Delta^{14}\text{C}$ values from ~3.5 mm to the outer edge, with the outermost samples indistinguishable from the expected *in situ* water DIC $\Delta^{14}\text{C}$ value. This implies that the *C. secundum* skeleton carried the ^{14}C signature of the surrounding seawater DIC pool. These results are in agreement with those of Griffin & Druffel (1989), who found that the outer $\Delta^{14}\text{C}$ measurements of *C. niobe* from the Atlantic were

indistinguishable from values measured at nearby GEOSECS stations. Other DSC with carbonate skeletons, such as bamboo corals (Roark et al. 2005), *Desmophyllum cristagalli* (Goldstein et al. 2001, Adkins et al. 2002), and *Lophelia pertusa* (Frank et al. 2004), have shown similar results. The *C. secundum* results suggest a potential ability to explore past ocean dynamics as reflected in ^{14}C DIC. For example, the $\Delta^{14}\text{C}$ transect may be recording deep mixing/entrainment events as indicated by the low $\Delta^{14}\text{C}$ values at 9 and 10 mm in sample COR-01. A similar decrease in $\Delta^{14}\text{C}$ was seen in sample COR-02, suggesting that these events are not an artifact of sampling. To truly explore these 'events' will require a precise $\Delta^{14}\text{C}$ -independent chronology.

In order to develop our ^{14}C -based age model, we set an initial time-marker using GEOSECS data and assigned a $\Delta^{14}\text{C}$ value of -100% to be no later than 1973, the year in which bomb ^{14}C penetrated downward to 400 m (Fig. 6). Linear interpolation between the (inferred) 1973 $\Delta^{14}\text{C}$ value at 3.5 mm and the outer edge with the known collection date in 1997 yields a $\sim 170 \mu\text{m yr}^{-1}$ radial growth rate for sample COR-RD97-01 (Fig. 3). Applying this growth rate to the entire radial diameter of ~12 mm suggests that this sample is 71 ± 9 yr old. As documented by Stuiver & Quay (1981) among others, production rate variations and carbon cycle exchanges have interacted to make ^{14}C dating insensitive between ~1650 AD and the advent of the post-bomb era. This 'plateau' has a similar expression in the upper ocean (e.g. Druffel et al. 2001) and by extension, to the shallow sub-surface waters where *Corallium* grew. The estimated life span using the GEOSECS time marker is completely consistent with the ^{14}C history that we expect for (shallow) subthermocline waters, and does not require significant growth rate changes within the resolution of the dating during the life history of the *Corallium* specimen. A similar calculation on COR-RD97-02 results in a growth rate of $\sim 170 \mu\text{m yr}^{-1}$ and an age of 67 ± 9 yr. Given the rapid rise in $\Delta^{14}\text{C}$ during the bomb curve, a conservative uncertainty of ± 0.5 mm in distance from the outer edge at which the 1973 $\Delta^{14}\text{C}$ value is assigned results in an uncertainty of $\pm 20 \mu\text{m yr}^{-1}$ in these estimated growth rates. Uncertainty in the age (1973) assignment for the -100% $\Delta^{14}\text{C}$ horizon of ± 1 yr results in an additional uncertainty of less than $10 \mu\text{m yr}^{-1}$ in the growth rate. The maximum growth rates estimated in this fashion are consistent between the 2 specimens and the uncertainty estimates are conservative estimates.

The Hawaiian *Corallium secundum* growth rates are similar to the growth rate of $110 \mu\text{m yr}^{-1}$ ($\pm 20 \mu\text{m yr}^{-1}$) calculated from the best fit to an exponential curve through $^{210}\text{Pb}^{\text{ex}}$ values measured on samples from *Corallium niobe* from 600 m water depth in the

Atlantic Ocean (Druffel et al. 1990). Grigg (1976, 2002) developed an equation correlating colony height (length) and age based on growth ring counts (using X-radiograph thin sections under a microscope) that were assumed to be annual. Applying the Grigg equation to sample COR-RD97-01, which was 28 cm high, results in an age of 29 yr (vs. 71 yr by our $\Delta^{14}\text{C}$ method). Examination of thin cross-section (petrographic method) from COR-RD97-01 yielded a maximum of 7 density growth rings. We therefore conclude that the rings observed in thin sections of our specimen are not annual in nature. Support for this conclusion is found in a study comparing the petrographic method of growth ring counting to the counting of organic growth rings in *Corallium rubrum* from the Mediterranean, which showed that the petrographic method significantly underestimated by as many as 10 yr the known age samples (20 yr old) (Marschal et al. 2004). In contrast, The counting of growth rings from the staining of the organic matrix underestimated the known age by 3 to 4 yr, and resulted in growth rates ranging from 140 to 750 $\mu\text{m yr}^{-1}$ (mean of $340 \pm 150 \mu\text{m yr}^{-1}$) (Marschal et al. 2004), which is much closer to the $\Delta^{14}\text{C}$ growth rates we calculated. In addition, both radiometric techniques, $\Delta^{14}\text{C}$ and $^{210}\text{Pb}^{\text{ex}}$, support much lower growth rates than those inferred from growth ring-size relationships for Hawaiian *C. secundum* (Grigg 1976, 2002), which appear to underestimate the age of larger individuals by at least a factor of 2. Our results suggest that research into reproduction and recruitment that does not make use of the growth ring-size relationship to estimate age would improve our understanding of the biology of these organisms. While greater precision in $\Delta^{14}\text{C}$ based ages is certainly desirable, we note the robust nature of the growth rates calculated for the outer portion of the *C. secundum* skeleton. There is no other reasonable explanation for the presence and interpretation of the bomb- ^{14}C history recorded in the carbonate skeleton. Counting organic growth rings in *C. secundum* may provide an independent estimate of age and growth rate that would allow the $\Delta^{14}\text{C}$ to be used as a tracer of ocean circulation and further refine the age and growth rate estimates.

Gerardia sp.

The outermost $\Delta^{14}\text{C}$ value from the radial transect sampled at 0.5 to 0.6 mm intervals of the live collected *Gerardia* sp. specimen (GER-RD97-01) is $71 \pm 4\%$. This post-bomb $\Delta^{14}\text{C}$ value is very close to the expected $\Delta^{14}\text{C}$ of surface waters at the time of collection, showing that young, surface derived POC is the primary source of carbon to the skeleton (Fig. 6). The subsequent pre-bomb decreasing linear trend in the $\Delta^{14}\text{C}$ values suggests continuous and steady growth, with the center of the sample having a ^{14}C age of $1200 \pm 25 \text{ }^{14}\text{C yr}$ ($-144.3 \pm 2.4\%$ $\Delta^{14}\text{C}$; Fig. 4, Table A1). A calibrated age of $760 \pm 30 \text{ cal yr BP}$ was calculated for the central portion of GER-RD97-01 (Table A2), yielding a life span of $807 \pm 30 \text{ yr}$ (1997 to 1950 = 47). Interpolating between the inner (old) age and the known age of collection (1997) yields a radial growth rate of $15 \mu\text{m yr}^{-1}$. The trend in ^{14}C and calibrated ages over the life span of this *Gerardia* sp. implies a near constant radial growth rate (Fig. 4). Inner and outer ^{14}C measurements on 5 other sub-fossil *Gerardia* sp. specimens confirm the longevity and slow growth rates of *Gerardia* sp. (Tables 1 & A2, Fig. 7).

The radiocarbon based estimates of radial growth rate and longevity of an Atlantic *Gerardia* sp. (~ 5 to $20 \mu\text{m yr}^{-1}$, ~ 1800 years old; Druffel et al. (1995)) and those from this study are consistent. In contrast, Goodfriend (1997) calculated amino acid racemization ages of $250 \pm 70 \text{ yr}$ on the same Atlantic specimen studied by Druffel et al. (op. cit.). The amino acid racemization method relies upon a temperature-dependent calibration of known age samples. In the case of the Atlantic *Gerardia* sp. sample, known-age calibrations were not possible, rendering the estimated growth rates suspect. Additional work on low temperature racemization rates of *Gerardia* sp. may improve the veracity of amino acid results. Until then, ^{14}C derived ages and growth rates are the best available.

In contrast to ^{14}C -derived radial growth rates and ages, Grigg (1976; 2002) estimated radial growth

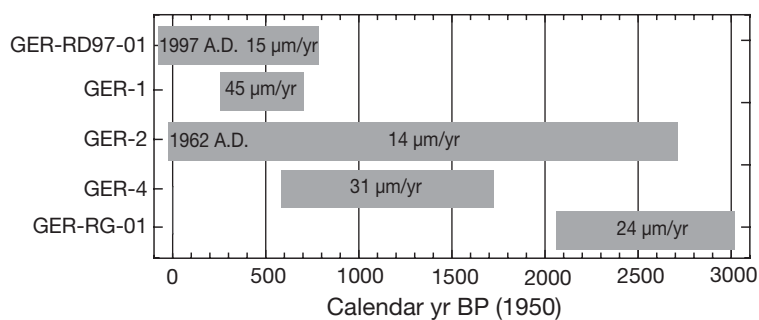


Fig. 7. *Gerardia* sp. Age ranges in calendar yr BP (1950) based on the outer and inner ^{14}C measurements of 5 gold coral samples. Radial growth rates are based on linear interpolations between the outer and inner ages. Sample GER-RD97-01 was collected live in 1997. The outer value of sample GER-2 had bomb ^{14}C ($> -50\%$) and the age was determined by comparison of this value with a $\Delta^{14}\text{C}$ time series in a surface coral from Hawaii (T. P. Guilderson & D. P. Schrag unpubl. data). See Fig. 8

rates for *Gerardia* sp. in excess of 1 mm yr⁻¹ from samples collected off Keahole Bay (380 to 410 m depth), with maximum ages on the order of 70 yr. Grigg's estimate is based on the assumption that growth banding observed in the gorgonian is annual in nature. This hypothesis or working assumption does not appear to be the case for many DSC. In addition to work on *Corallium rubrum*, in which calcitic growth bands identified by the petrographic method are shown not to be annual (Marschal et al. 2004), growth bands in bamboo corals from the Gulf of Alaska (Roark et al. 2005) and growth bands in *Enallopsammia rostrata* from the Atlantic Ocean have also been shown not to be annual (Adkins et al. 2004). The *Gerardia* sp. growth rates estimated by Grigg (1976; 2002) are 3 orders of magnitude higher than that measured by radiocarbon. Initially, Grigg (2002) attributed the different growth rate/longevity to different periodicity of growth bands in Atlantic *Gerardia* sp., and suggested that the ¹⁴C ages were skewed because the colonies from the Atlantic were feeding on old particulate carbon, making the sample appear older. The results presented here on Pacific samples support the earlier Atlantic results and indicate that *Gerardia* sp. is an extremely long-lived organism feeding on recently exported POC from surface waters.

With such great ages, the potential exists to use *Gerardia* sp. for paleoenvironmental reconstructions over centennial to millennial time scales. Since *Gerardia* sp. builds skeletal material using POC, it is likely that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in its skeleton record long-term changes in surface productivity or ecosystem structure (Druffel et al. 1995). Heikoop et al. (2002) measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the polyp (animal) tissues and contemporaneous proteinaceous fraction from a series of live collected *Primnoa resedaeformis* specimens from different ocean basins. Their results show no discernable difference between the proteinaceous skeleton and polyp tissue fractions. They also observed systematic regional differences in proteinaceous $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that mirrored regional differences in the isotopic composition of surface POC. This suggests that stable isotopic measurements from the proteinaceous skeletons of DSC may reflect variations in carbon cycle and nutrient utilization in surface waters. Longevity and slow growth are not unknown in deep-sea organisms. These (our) results beg additional research resulting in a more lucid understanding of the ecology (e.g. dispersal, recruitment, reproduction, mortality) not only of *Gerardia* sp. but also its relatives in the twilight benthic ecosystems of the ocean. With a fuller understanding we can craft appropriate conservation protocols to protect not only individual species but also whole ecosystems.

Black corals, *Antipathes dichotoma* and *Leiopathes glaberrima*

The age and growth rate of the black coral *Antipathes dichotoma* collected at 50 m were significantly different from the age and growth rate of a 'deep-water' black coral *Leiopathes glaberrima* collected at 450 ± 40 m. A radial transect at 0.5 to 0.6 mm intervals across one of the *A. dichotoma* specimens (BC#3) showed decreasing bomb carbon values over the outer 4.5 mm, after which the $\Delta^{14}\text{C}$ values did not change (Fig. 5, Table A1). The outer sample had a $\Delta^{14}\text{C}$ value (107 ± 4‰) that was indistinguishable from surface DIC (T. P. Guilderson & D. P. Schrag unpubl. data, Fig. 6). Using similar methods to those used for the *Corallium secundum* samples discussed above, the date (1957) that the increase in bomb carbon began can be determined by the surface coral $\Delta^{14}\text{C}$ time-series. The exact collection years of the *A. dichotoma* samples are unknown, thus the year of their 'death' must also be estimated from the surface coral $\Delta^{14}\text{C}$ time-series. In the case of sample BC#3, the outermost value (107 ± 4‰) is equivalent to the year of ~1965 or ~1992 in the surface coral $\Delta^{14}\text{C}$ time-series (Fig. 8). A linear interpolation between the increase in bomb ¹⁴C at 4.5 mm and the outermost edge (1957 to 1965 = 8 yr) gives a growth rate of 560 $\mu\text{m yr}^{-1}$ which, if assumed to be constant over the entire growth of the specimen, suggests that the sample was ~25 yr old (Table 2). Alternatively, a growth rate of 130 $\mu\text{m yr}^{-1}$ and an age of ~105 yr is calculated if the coral died in 1992. Inner and outer $\Delta^{14}\text{C}$ measurements on 2 other *A. dichotoma* samples (BC#1 and BC#2) were all above -50‰ and thus incorporated bomb ¹⁴C. Comparing these bomb ¹⁴C values to the surface coral $\Delta^{14}\text{C}$ time-series, the shortest and longest lifespan (growth rate) possible for BC#1 is ~15 to 32 yr (390 to 180 $\mu\text{m yr}^{-1}$) and the lifespan (growth rate) of BC#2 is ~12 to 29 yr (1140 to 470 $\mu\text{m yr}^{-1}$) (Table 2, Fig. 8). In view of these results an age of ~25 yr (560 $\mu\text{m yr}^{-1}$) for BC#3 is the most probable.

Using 21 tagged colonies of *Antipathes dichotoma*, a linear growth rate of 6.42 cm yr⁻¹ was measured over a 3.5 yr time span (Grigg 1976). In the same study, the height of *A. dichotoma* was also correlated to the assumed annual growth rings (Grigg 1976). Using the linear growth rate on samples whose height was known, we estimated the age of sample BC#1 to be ~12 yr and sample BC#2 to be 20 yr (Table 4). Using the linear relationship between height and growth rings yr⁻¹, BC#1 and BC#2 were estimated to be 15 and 25 yr old (Table 4), respectively. The minimum and maximum ages using the bomb ¹⁴C method bracket these ages (Table 4), supporting the linear growth rate and the annual growth band estimates (Grigg 1976).

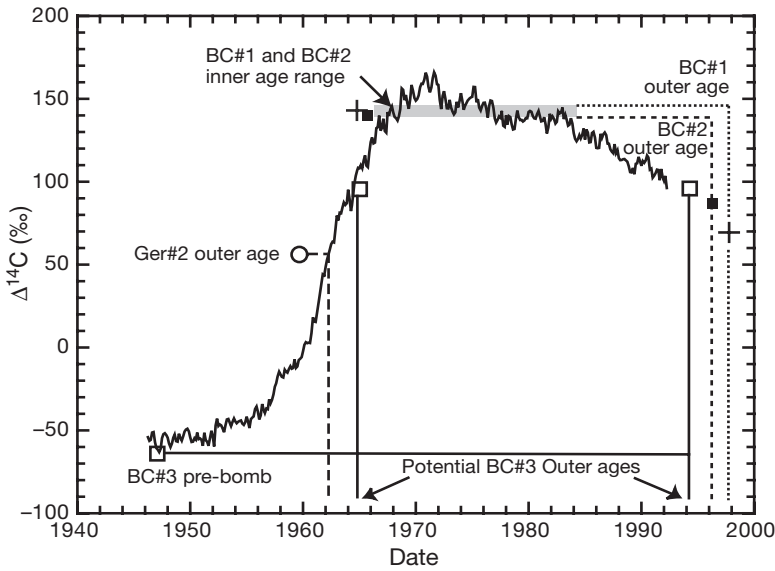


Fig. 8. $\Delta^{14}\text{C}$ time-series in a surface coral (solid line) from the island of Hawaii (T. P. Guilderson & D. P. Schrag unpubl. data). Inner and outer $\Delta^{14}\text{C}$ values of *Antipathes dichotoma* (BC#1, BC#2, and BC#3, Table 2) and the outer value of a *Gerardia* sp. sample (GER#2, Table 1) are plotted so that calendar dates may be estimated. Where the DSC $\Delta^{14}\text{C}$ value is equal to the surface coral $\Delta^{14}\text{C}$ value, an age can be estimated. Uncertainties in this method exist when the surface water ^{14}C is not changing quickly, resulting in large age estimate (e.g. inner BC#1 and BC#2 age range) and where one $\Delta^{14}\text{C}$ value can be associated with 2 time markers (e.g. outer BC#3 age). The pre-bomb $\Delta^{14}\text{C}$ values of BC#3 were assigned an age of 1957 (see Fig. 5). The outer age (1962) of GER#2 was used to determine the age and growth rate of the sample in Fig. 7

All 3 methods could be refined by the collection of live samples and reconstruction of the bomb curve using material from individual growth bands.

The $\Delta^{14}\text{C}$ values along the radial transect of *Leio- pathes glaberrima* collected at ~450 m (BC#5) decreased gradually from a $\Delta^{14}\text{C}$ value of $-69 \pm 4\text{‰}$ at the outer edge to a value of $-280.7 \pm 2.9\text{‰}$ (2600 ± 35 ^{14}C yr) at the center (Fig. 5, Table 3). Calibration of the ^{14}C ages resulted in an age of $2320 \pm 10/-20$ calendar yr BP at the center (Fig. 9, Tables 1 & A2), yielding a life span of 2377 yr and a growth rate of $\sim 5 \mu\text{m yr}^{-1}$. However, the growth rate was not constant, with faster growth occurring when the sample was younger (Fig. 9).

There are no other age or growth rate estimates for *Leio- pathes glaberrima* that we are aware of. It is inter-

esting that species from the same family have such different growth rates, though it should not be surprising as there are significant differences between life at 50 m versus 450 m. Food availability (POC and plankton) and/or temperature (15°C difference between 50 m and 420 m (www.soest.hawaii.edu/HOT_WOCE/) may, in part, explain the differences in growth rates. In Hawaiian waters *Antipathes dichotoma* is not found below 110 m near the top of the main thermocline (Grigg 1976, 2001), thus it is possible that environmental differences may be important factors governing growth rates. Ecological differences between and within DSC beds and their relationship to different species is an important area of further study from both the geochemistry and management standpoints.

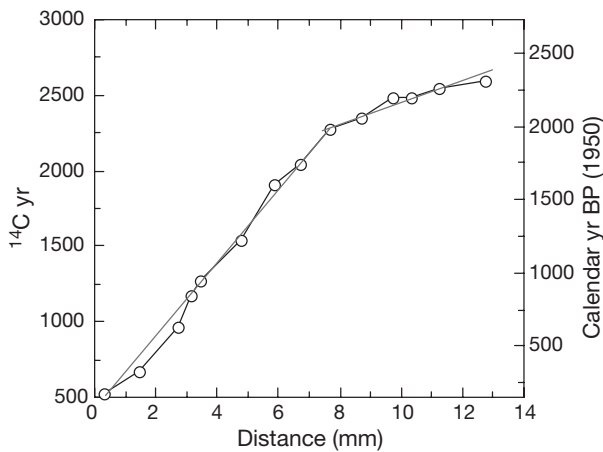


Fig. 9. *Leio- pathes glaberrima*. ^{14}C radial transect across a black coral sample (BC#5, ○) collected at 450 m. An age of ~ 2377 yr with a growth rate $\leq 10 \mu\text{m yr}^{-1}$ was calculated. Over the first 6 mm of growth, the growth rate was apparently faster than over the outer 8 mm

Management and conservation

The management of the precious coral fishery in Hawaiian waters is a complex issue, in part because of multiple jurisdictions (e.g. Federal and State), and because each DSC bed is treated as distinct management units. The largest complicating factor is that many aspects of the biology, including growth rates, and ecology of all DSC remain open areas of research and thus any new results may impact the precious coral fishery management plan. For example, the harvest quota of $2000 \text{ kg } 2 \text{ yr}^{-1}$ for *Corallium* spp. (pink coral) at the Makapuu DSC bed includes a minimum size limit of 10 inches (25.4 cm) that is based the existing maximum sustainable yields (MSY) that use a linear increase in colony height of 0.9 cm yr^{-1} (Grigg 1976, 2001; discussed above) to determine an age-frequency distribution (Western Pacific Regional Fish-

ery Management Council 2001, National Marine Fisheries Service (NMFS) 2002). The growth rate and age estimates reported in this paper for *Corallium secundum* from Hawaii are significantly slower and older than those used in the MSY calculations. Thus, a revised and more conservative MSY based on the slower growth rates may be more appropriate for the sustainable management of the fishery.

The very slow growth rates and extremely old ages reported above for *Leiopathes glaberrima* and *Gerardia* sp. suggest harvesting of these species in any locations is unlikely to be sustainable. Currently, *L. glaberrima* is not part of the black coral fishery, but given the much slower growth rates compared to *Antipathes dichotoma* it is clear that different species of black coral should be managed differently and *L. glaberrima* should not be commercially harvested. Currently the harvesting of *Gerardia* sp. has been suspended at the Makapuu bed until additional information is available on the impact of harvesting on subsequent recruitment (Western Pacific Regional Fishery Management Council 2001, National Marine Fisheries Service (NMFS) 2002). Harvesting is still allowed at other beds although a moratorium is being considered by the Western Pacific Regional Fishery Management Council until better research exists on age/height relationships and recruitment/reproductive biology to better calculate an MSY. The current MSY (e.g. Keahole Point DSC bed MSY is 20 kg yr⁻¹) is based entirely on the assumption that commercial sized individuals are 40 yr of age. Our results show growth rates that are 10 to 70 times slower than those predicting 40 yr ages and thus these individuals are actually more than 400 yr old (with life-spans up to ~2700 yr). There is also some discrepancy in the reported recruitment, with the gold coral stocks at the Makapuu Bed having reportedly experienced little to no recruitment and re-growth (Western Pacific Regional Fishery Management Council 2001), while Grigg (2002) reports a relative increase in the recruitment of young colonies at the same bed between 1997 and 2001. Irrespective of these discrepancies, and on the basis of the ages we report here, it is our firm belief that commercial harvesting of *Gerardia* sp. is not sustainable. The longevity of these amazing life forms and their role in maintenance of habitat and ecosystem health also requires consideration of closing areas to long lining and trawling and a frank and earnest discussion of any fisheries plans' incidental damage.

CONCLUSIONS

Here, we report radial growth rates and ages of the Hawaiian DSC, *Corallium secundum*, *Gerardia* sp.,

Leiopathes glaberrima, and *Antipathes dichotoma*, based on radiocarbon measurements, with the following results

- The primary source of carbon used for skeletogenesis by *Corallium secundum* is seawater DIC. Using time markers associated with the time-dependent bomb ¹⁴C content of the North Pacific, we determine radial growth rates of ~170 μm yr⁻¹ and colony ages of 67 to 71 yr for samples ~28 cm in height and ~12 mm in diameter
- The primary source of carbon used for skeletogenesis by *Gerardia* sp. is POC. A growth rate of 15 μm yr⁻¹ and an age of 807 ± 30 yr was calculated from a high resolution ¹⁴C radial transect on a live collected *Gerardia* sp. specimen. Inner and outer ¹⁴C measurements on 4 sub-fossil *Gerardia* sp. samples support the low growth rates (range 14 to 45 μm yr⁻¹) and great ages (range 450 to 2742 yr) for this organism. One organism was determined to have lived 2742 yr
- Similarly, with a growth rate of ~5 μm yr⁻¹ (basal radial diameter ~12 mm) and an estimated colony age of ~2377 yr, the deep dwelling black coral *Leiopathes glaberrima* is also extremely long lived
- In contrast, *Antipathes dichotoma* specimens from 50 m depth ranged in age from 12 to 32 yr, with growth rates on the order of 180 μm yr⁻¹ to 1140 μm yr⁻¹.

These results show that these DSC grow more slowly and are older than previously thought, especially the *Gerardia* sp. and *Leiopathes glaberrima* samples. As a result, fishing practices and the MSY calculations for the precious coral fishery in the Hawaii (and likely elsewhere) should be re-evaluated for preservation of the fishery and for the conservation of the DSC. The ¹⁴C chronologies presented here are accurate enough for studies of multi-decadal variability within the ocean interior. Thus, there is great potential to use long-lived DSC species in paleoclimate reconstructions.

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