FEATURE ARTICLE

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

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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’ 14C time markers we calculated radial growth rates of ~170 μm 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 14C we calculated a radial growth rate of 15 μm 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 μm yr⁻¹) and ages (range 450 to 2742 yr) similar to that of the live collected sample. Similarly, with a growth rate of <10 μm 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 μm yr⁻¹ (12 to 32 yr). These results show that Hawaiian deep-sea corals grow more slowly and are far older than previously thought.

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

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-
Deep-sea corals 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, 210Pb 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 (14C) measurements. We make use of both conventional radiocarbon ages as well as the time varying transient of ‘bomb 14C’ in the oceanic total dissolved CO2 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, 1986, 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 tail) for C. secundum (from 350 to 475 m water depth) and 70 yr (2.6 m tail) 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 ± 40 yr for a trunk of Corallium niobe from the Atlantic Ocean. Radiocarbon measurements (0.13 mm yr\(^{-1}\), 135 ± 90 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 5 pm yr\(^{-1}\) and a basal age of 1800 ± 300 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 ± 70 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 ± 40 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 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...
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 CO₂ 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 CO₂ (cf., Guilderson et al. 1998). The CO₂ 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 ¹⁴C results are reported as Δ¹⁴C (%) as defined by Stuiver & Polach (1977) and include δ¹³C correction for isotope fractionation, and a blank subtraction based on ¹⁴C-free calcite or coal depending on sample matrix. Stable isotopic transects near the ¹⁴C transects were made on both *C. secundum* samples. The average δ¹³C value of -5.7% for COR-RD97-01 and -5.8% for COR-RD97-02 were used for the isotope fractionation correction. δ¹³C values of -16% and -17% were used for the isotope fractionation correction of the *Gerardia* sp. and black corals sample, respectively. Where appropriate, the ¹⁴C results are also reported in ¹⁴C and calendar yr BP (before present) (Stuiver & Polach 1977). To convert the ¹⁴C age to a calendar age, a reservoir age correction must be applied. The reservoir age is a result of the depletion...
The outermost $\Delta^{14}C$ 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 $1\sigma$ error of the measurements to the central core (Fig. 3, Table A1).

For the *Gerardia* sp. samples, the outermost $\Delta^{14}C$ value along the radial transect of the GER-RD97-01 sample was $71 \pm 4\%$, dropping to $-60 \pm 4\% (445 \pm 5$ WWCE 1993 value).

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**RESULTS**

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Fig. 4. *Gerardia* sp. 

**A** radial transect across a gold coral sample (GER-RD97-01). The center of the sample had a 

\[ ^{14}C \] age of 1200 ± 25 yr and a calendar age of 807 ± 30 yr resulting in a calculated radial growth rate of ~15 μm yr\(^{-1}\).

1σ errors are no larger than symbols.

35 \[ ^{14}C \] yr) at the next sampling interval. Over the remaining 11 mm, \[ ^{14}C \] 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%. \[ ^{14}C \] 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 slower over the innermost 5 mm (Fig. 5). The outer (inner) \[ ^{14}C \] 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>
<thead>
<tr>
<th>Sample ID</th>
<th>Depth (m)</th>
<th>Inner [ ^{14}C ] (%)</th>
<th>Outer [ ^{14}C ] (%)</th>
<th>Calendar age [^{a}]</th>
<th>Life-span</th>
<th>Radius (mm)</th>
<th>Growth Rate (μm yr(^{-1}))</th>
<th>Height (cm)</th>
<th>Age, growth rate [^{c}]</th>
<th>Age, growth band [^{d}]</th>
</tr>
</thead>
<tbody>
<tr>
<td>BC#1</td>
<td>50 ± 5</td>
<td>143.0 69.4</td>
<td>87.0 107 ± 4</td>
<td>1966/1972-1983</td>
<td>19-32</td>
<td>5.9</td>
<td>180 390</td>
<td>81.3 12</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>BC#2</td>
<td>50 ± 5</td>
<td>140 87.0 107 ± 4</td>
<td>87.0 107 ± 4</td>
<td>1966/1972-1983</td>
<td>12 29</td>
<td>13.7</td>
<td>470 1140</td>
<td>129.5 20</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>BC#3</td>
<td>50 ± 5</td>
<td>57.4 107 ± 4</td>
<td>107 ± 4</td>
<td>pre 1957</td>
<td>20 109</td>
<td>13.6</td>
<td>130 560</td>
<td>130 560</td>
<td>20 25</td>
<td>20 25</td>
</tr>
</tbody>
</table>

\[^{a}\]Post-bomb data are reflected by positive \[ ^{14}C \] values.

\[^{b}\]AD (Anno Domini) years were determined by comparison with a Hawaiian surface water \[ ^{14}C \] time-series (see Fig. 8).

\[^{c}\]Age calculated from linear growth rates and on the relationship between annual growth rings and height (Grigg 1976).

\[^{d}\]BC#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, CO₂ is hydrated and mixed in the upper layer of the ocean as DIC. DIC is then fixed by photosynthesis in the euphotic zone to DOC 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 μm in size that is suspended and sinking out of the ocean surface mixed layer, while DOC is organic matter less than 1 μm 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°00′N, 159°00′W) from the late 1980s revealed significant Δ¹⁴C differences with depth and between the various sources of carbon (Druffel & Williams 1990, Druffel et al. 1992). The Δ¹⁴C values of DIC revealed the presence of bomb ¹⁴C above the main thermocline (<400 m, and average Δ¹⁴C ~117‰), decreasing between ~300 and ~1000 m (to an average Δ¹⁴C value of ca. ~240‰), after which Δ¹⁴C was relatively constant down to 5700 m. Suspended POC Δ¹⁴C values at the surface and sinking POC (4200 m) were nearly equivalent to surface DIC Δ¹⁴C values, and suspended POC values decreased only slightly with depth. DOC Δ¹⁴C apparent ages were older, with an average Δ¹⁴C value of ca. −150‰ at the surface and significantly offset from the corresponding DIC Δ¹⁴C values, although the structure of the 2 curves was similar. SOC Δ¹⁴C 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 Δ¹⁴C values of DIC, POC, and DOC in the upper 50 m of the water column were 132‰, 139 ± 9‰, and −163 ± 18‰ Δ¹⁴C, respectively (Druffel et al. 1992). Between 300 and 450 m, typical Δ¹⁴C values of DIC, POC, and DOC were 77 ± 3‰ (300 m), 129 ± 11‰ (450 m), and −363 ± 14‰ (300 m) Δ¹⁴C, respectively (Druffel et al. 1992). The Δ¹⁴C 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 Δ¹⁴C measurement in conjunction with the hydrographic profiles of Δ¹⁴C values in the water column described above as an indicator of the most recent source of carbon deposited in the skeleton. The outer Δ¹⁴C value of 2 live collected specimens of Coralium secundum (5 ± 3‰, 3.5 ± 2.2‰), 1 Gerardia sp. (71 ± 4‰), and 1 black coral, Leiopathes glaberrima (~69 ± 4‰), are plotted in concert with water Δ¹⁴C 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 Δ¹⁴C values of the 2 C. secundum measured and the Δ¹⁴C value of DIC at ~450 m suggest DIC is the primary source of carbon used for skeletogenesis. In contrast, the outer value of the ~450 m Gerardia sp. sample is similar to the surface water DIC Δ¹⁴C value which will tag and be nearly equal to the Δ¹⁴C 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 Δ¹⁴C 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 Δ¹⁴C values of 2 Coralium 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 $\Delta^{14}C$ 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 $\mu$m yr$^{-1}$; see 'Discussion; Black corals, Antipathes dichotoma and Leiopathes glaberrima'). With such a slow growth rate over the sampling interval of 500 $\mu$m, 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 $\Delta^{14}C$ 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 $\Delta^{14}C$ 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 $\Delta^{14}C$ 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 $\Delta^{14}C$ 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 $\Delta^{14}C$ values from $-3.5$ mm to the outer edge, with the outermost samples indistinguishable from the expected in situ water DIC $\Delta^{14}C$ 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 $\Delta^{14}C$ 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 $\Delta^{14}C$ transect may be recording deep mixing/entrainment events as indicted by the low $\Delta^{14}C$ values at 9 and 10 mm in sample COR-01. A similar decrease in $\Delta^{14}C$ 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 $\Delta^{14}C$-independent chronology.

In order to develop our $^{14}C$-based age model, we set an initial time-marker using GEOSECS data and assigned a $\Delta^{14}C$ 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 $\Delta^{14}C$ value at 3.5 mm and the outer edge with the known collection date in 1997 yields a $\sim170$ $\mu$m yr$^{-1}$ radial growth rate for sample COR-RD97-01 (Fig. 3). Applying this growth rate to the entire radial diameter of $\sim12$ mm suggests that this sample is $71\pm9$ 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 $\sim1650$ 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 $\sim170$ $\mu$m yr$^{-1}$ and an age of $67\pm9$ yr. Given the rapid rise in $\Delta^{14}C$ during the bomb curve, a conservative uncertainty of $\pm0.5$ mm in distance from the outer edge at which the 1973 $\Delta^{14}C$ value is assigned results in an uncertainty of $\pm20$ $\mu$m yr$^{-1}$ in these estimated growth rates. Uncertainty in the age (1973) assignment for the $-100\%\Delta^{14}C$ horizon of $\pm1$ yr results in an additional uncertainty of less than $10$ $\mu$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 $110$ $\mu$m yr$^{-1}$ ($\pm20$ $\mu$m yr$^{-1}$) calculated from the best fit to an exponential curve through $^{210}Pb^{ex}$ 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 \( \Delta^{14}C \) 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 \( \mu \)m yr\(^{-1} \) (mean of 340 ± 150 \( \mu \)m yr\(^{-1} \)) (Marschal et al. 2004), which is much closer to the \( \Delta^{14}C \) growth rates we calculated. In addition, both radiometric techniques, \( \Delta^{14}C \) and \(^{210}Pb\)-\(^{210}Pb\), 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 \( \Delta^{14}C \) 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 \( \Delta^{14}C \) to be used as a tracer of ocean circulation and further refine the age and growth rate estimates.

**Gerardia sp.**

The outermost \( \Delta^{14}C \) 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 ± 4 \(^{14}C\)\(^{14}C\)\(^{14}C\). This post-bomb \( \Delta^{14}C \) value is very close to the expected \( \Delta^{14}C \) 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 \( \Delta^{14}C \) values suggests continuous and steady growth, with the center of the sample having a \( ^{14}C \) age of 1200 ± 25 \( ^{14}C \) yr (−144.3 ± 2.4 \(^{14}C\)\(^{14}C\)\(^{14}C\)) \( \Delta^{14}C \); Fig. 4, Table A1). A calibrated age of 760 ± 30 cal yr BP was calculated for the central portion of GER-RD97-01 (Table A2), yielding a life span of 807 ± 30 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 \( \mu \)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 \( \mu \)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 ± 70 yr on the same Atlantic specimens 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
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 Δ¹⁴C values did not change (Fig. 5, Table A1). The outer sample had a Δ¹⁴C 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 Δ¹⁴C 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 Δ¹⁴C 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 Δ¹⁴C time-series (Fig. 8). A linear interpolation between the increase in bomb ¹⁴C at 4.5 mm and the outermost edge (1957 to 1985 = 8 yr) gives a growth rate of 560 μm 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 μm yr⁻¹ and an age of ~105 yr is calculated if the coral died in 1992. Inner and outer Δ¹⁴C 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 Δ¹⁴C time-series, the shortest and longest lifespan (growth rate) possible for BC#1 is ~15 to 32 yr (390 to 180 μm yr⁻¹) and the lifespan (growth rate) of BC#2 is ~12 to 29 yr (1140 to 470 μm yr⁻¹) (Table 2, Fig. 8). In view of these results an age of ~25 yr (560 μm 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).
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 $\Delta^{14}$C values along the radial transect of *Leiopathes glaberrima* collected at ~450 m (BC#5) decreased gradually from a $\Delta^{14}$C value of $-69 \pm 4\%$ at the outer edge to a value of $-280.7 \pm 2.9\%$ (2600 $\pm$ 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 $\pm 5\,\mu$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 *Leiopathes glaberrima* that we are aware of. It is interesting 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.

**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 kg 2 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-
much slower growth rates compared to 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 location 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 Makapu'u 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 growth rate, with the gold coral stocks at the Makapu'u bed having reportedly lived 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 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 paleoclimatic reconstructions.

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