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Hawaiian deep-sea coral age and growth rates

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1.1 ABSTRACT

The radial growth rates and ages of three 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 at the Makapuu deep-sea coral bed using a submersible (PISCES V). Specimens of *Antipathes dichotoma* were collected at 50 m off Lahaina, Maui. 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 calculate radial growth rates of ~170 µm y^{-1} and ages of 68-75 years on specimens as tall as 28 cm of *C. secundum*. *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 calculate a radial growth rate of 15 µm y^{-1} and an age of 807 ± 30 years for a live collected *Gerardia* sp., showing that these organisms are extremely long lived. Inner and outer ^{14}C measurements on four sub-fossil *Gerardia* spp. samples produce similar growth rate estimates (range 14-45 µm y^{-1}) and ages (range 450-2742 years) as observed for the live collected sample. Similarly, with a growth rate of < 10 µm y^{-1} and an age of ~2377 years, *L. glaberrima* at the Makapuu coral bed, is also extremely long lived. In contrast, the shallow-collected *A. dichotoma* samples yield growth rates ranging from 130 to 1,140 µm y^{-1}. These results show that Hawaiian deep-sea corals grow more slowly and are older than previously thought.

2 INTRODUCTION

Unlike 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 which they provide for other organisms has occurred in response to an increasing awareness of the threat of physical destruction caused by pelagic/benthic fisheries. Many DSC provide important adult or juvenile recruitment habitats for commercially important fish (Witherell et al. 2000, Witherell & Coon 2000) though 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

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from the ocean interior, an area for which almost no other high resolution climate records exist (e.g., Smith et al. 1997, e.g., 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 firm 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 from 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). All methods then 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 growth rate and age estimates from four 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 two 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/benthic fisheries. In addition, our results establish a chronological framework for future paleoenvironmental reconstructions using these deep-sea corals.

3 BACKGROUND

Hawaiian deep-sea corals are all Coelenterates. *Corallium* spp. is an octocoral of the order Gorgonacea. The black coral (order Antipathidae) is a hexacoral as is the gold coral, *Gerardia* sp. (order Zoanthidae). *Gerardia* sp. is a colonial zoanthid anemone whose skeleton is made of a hard, dense, layered proteinaceous material called gorgonin. *Gerardia* sp. grow in a

dendritic tree-like fashion to several meters in height with trunks 3-9 cm in diameter typical, and some trunks as large as 15 cm in diameter. Hawaiian black corals also have a gorgonin skeleton that grows in fan-like shape to heights of almost 2 m with basal diameters of 1-2 cm. *Corallium* spp. is a branching coral with a skeleton composed of calcite. The coral grows in a fan-like shape to tens of centimeters high, with main trunks 15-30 mm in diameter.

Previous age and growth rate studies of Hawaiian deep-sea corals arose in part because, a local fishery exists harvesting *Corallium* spp*., Gerardia* sp*.,* black corals, and bamboo (Isididae) 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 submersibles were mandated. The 1983 Federal Fishery Management Plan included age and growth estimates using tagging and visual observations of black 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 2,000 kg every 2 years with a minimum 10 inch vertical height requirement). The establishment of the Coral Reef Ecosystem Reserve in the North-western 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 branches. Using tagged colonies from water depths less than 100 m Grigg (1976) determined a linear extension rate of 6.42 cm y^{-1} for *Antipathes. dichotoma* and 6.12 cm y^{-1} for *A. grandis* over a 3.5 year study. This extension rate was then applied to the whole colony to provide an age estimate of ~40 years for colonies larger than 1.5 m tall. The estimated age of these shallow dwelling colonies, coupled with the number of growth bands observed in an x-radiograph of a basal cross-section, suggest that the bands may be annual (Grigg 1976). Based on the inference that growth bands in *A. diochotoma* are annual, Grigg (1976, 2002) assumed that similar bands observed in *C. secundum* and *Gerardia* sp*.* were also annual and provided estimated linear growth rates of 0.9 cm y^{-1} and 6.6 cm y^{-1} respectively (Grigg 1976, 2002). By this method, the maximum estimated ages of deep water Hawaiian *C. secundum* (from 350-475

m water depth) and *Gerardia* sp. (380-410 m) were 45 (~40 cm tall) and 40 (~2.6 m tall) years, respectively (Grigg 1976, 2002).

Druffel et al. (1990) used excess ^{210}Pb measurements to calculate a radial growth rate of 0.11 mm y^{-1} and an age of 180 ± 40 years for a trunk of *Corallium niobe* from the Atlantic. Radiocarbon measurements on the same sample agreed with this result (Griffin & Druffel 1989) assuming a constant growth rate and the fact that bomb carbon had not been detected in the coral. A radial growth rate of ~5 μm y^{-1} on an Atlantic *Gerardia* specimen was determined by radiocarbon measurements, using similar assumptions. The basal age of this sample was determined to be 1800 ± 300 years (Druffel et al. 1995), whereas amino acid racemization dating yielded a maximum age of 250 ± 70 years (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 orders of magnitude 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 and determining acceptable size limits for harvesting.

4 MATERIAL and METHODS

4.1 Field Collection

The majority of the samples used in this study were collected alive in 1997 using the PISCES V submersible from 450 ± 40 m depth on Makapuu Bank off the island of Oahu (Fig. 1 and Table 1). External tissues were removed aboard ship and intact skeletons returned to the laboratory. Initial species identifications were made aboard the ship by the divers (R. Dunbar, B. Linsley and R. Grigg) using visual characteristics and where uncertainty existed, dive tapes and photographs were recently reviewed and identifications confirmed by comparison to more recent (2004) PISCES V surveys of the Makapuu coral beds. Samples of *Corallium secundum*,

Leiopathes glaberrima, and *Gerardia* sp. were all collected at the Makapuu bed (Fig. 1 and Table 1). Basal sections of additional samples collected by R. Grigg during the course of his research (Table 1), were also provided. These samples may not have been alive at the time of collection. These include several *Antipathes dichotoma* (family Antipathidae: colloquially black corals), collected from 50 m. at "Stonewall" off Lahaina, Maui, and some of the *Gerardia* sp. samples collected 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 preferentially used in the high-resolution sampling age models.

4.2 Sample Preparation

Disks 3-10 mm thick were cut from the basal portion of all samples. The disks were mounted on glass slides and incrementally milled using a Merchantek computer controlled micromill, or using a 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 control allows for sampling along straight or curved growth contours with a precision better than 5µm. *Corallium secundum* and *Gerardia* sp. samples were milled using the Merchantek micromill at ~0.5 mm and ~0.5-0.6 mm increments respectively (Fig. 2). The only exception is that the outer most sample of COR-01 was milled over a 1 mm increment. Black coral samples were milled at 0.5-0.7 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 tool resulting in age determinations on the inner (core) and outer-most material. No more than 1 mm along the radial distance was sampled. Approximately 1.0-4.0 mg per sample of carbonate material was obtained from the *C. secundum*, samples and ~1.0-3.0 mg of gorgonin material was obtained from the *Gerardia* sp. and black coral samples.

4.3 Laboratory Methods

Gorgonin samples from the *Gerardia* sp. and black corals were decarbonated with 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 (c.f., 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 $\Delta^{14}C$ (‰) as defined by Stuiver and Polach (1977) and include $\delta^{13}C$ 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 $\delta^{13}C$ value of -5.7 ‰ for COR-RD97-01 and -5.8 ‰ for COR-RD97-02 were used for the isotope fractionation correction. $\delta^{13}C$ values of –16 ‰ and –17 ‰ were used for the isotope fractionation correction of the *Gerardia* sp. and black corals sample, respectively. Where appropriate, conventional ages are reported including a local surface water reservoir correction of 374 ^{14}C years (ΔR –28 ± 4)(Druffel et al. 2001).

5 RESULTS

The outermost $\Delta^{14}C$ values for two individuals of Makapuu *Corallium secundum* (COR-RD97-01 and -02) are 3.5 ± 2.2 ‰ and 5.3 ± 3.7 ‰ respectively (Fig. 3, Table 2). Approximately 4 mm in from the surface both corals have similar values of ~-100 ‰ and remain reasonably invariant to the central core (Fig. 3, Table 3). For the *Gerardia* sp. samples, the outermost $\Delta^{14}C$ value along the radial transect of the GER-RD97-01 was 71.3 ± 3.7‰, dropping to –59.6 ± 3.9‰ (445 ± 35 ^{14}C years) at the next sampling interval. Over the remaining 11mm $\Delta^{14}C$ systematically decrease to –144 ± 2.4‰ at the center of the trunk (Fig. 4; Table 2 and 3). This is equivalent to a conventional ^{14}C age of 1200 ± 25 years. Outer values of the four (4) additional living and dead *Gerardia* sp. samples range from modern (post-bomb) to 2390 ± 30 ^{14}C years old. Inner values of the same specimens range from 1150 ± 35 to 3200 ± 35 ^{14}C years (Table 2).

The outer value of the radial transect across the *Antipathes dichotoma* (BC3) collected at 50 m depth was 106.5 ±4.3‰. $\Delta^{14}C$ decreased to a value of –57.1 ±3.6‰ over the first 5 mm and remained unchanged over the inner ~13 mm (Fig. 5, Table 3). In contrast the "deep-water black coral", *Leiopathes glaberrima* (BC5), collected at 450 ± 40 m showed a linear decrease from an outer value of –69.2 ± 4.1‰ to a value of –280.7 ± 2.9‰ at the center (Fig. 5, Table 3). The rate

of decrease was slower over the innermost 5 mm (Fig. 5). The outer (inner) Δ^{14}C values of specimens BC1 and BC2 of the shallow collected *A. dichotoma* were 69.4 ‰ (143 ‰) and 87 ‰ (140 ‰), respectively (Table 2).

6 DISCUSSION

6.1 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) to 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 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 that 1 µm in size that is 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 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 reveal significant Δ^{14}C differences with depth and between the various sources of carbon (Druffel & Williams 1990, Druffel et al. 1992). The Δ^{14}C values of DIC reveal the presence of bomb ^{14}C in the main thermocline (< 400 m, and average Δ^{14}C ~117 ‰), decreasing between ~300 and ~1000 m (to an average Δ^{14}C value of ~-240 ‰), after which Δ^{14}C was relatively constant down to 6000 m. POC Δ^{14}C values at the surface were nearly equivalent to surface DIC Δ^{14}C values and decreased only slightly with depth. DOC Δ^{14}C apparent ages were older, with an average Δ^{14}C value of ~-150 ‰ at the surface and significantly offset from the corresponding DIC Δ^{14}C values, although the structure of the two curves is similar. SOC Δ^{14}C values (~-500 ‰) at the sediment water interface are equivalent to DOC values at depth, after which they decrease by more than 250 ‰ within the upper 10 cm of sediment (Druffel et al. 1992). Based on measurements made in 1992, typical Δ^{14}C values of DIC, POC, and DOC in the upper 50 m of the water column are 132 ‰,

139 ± 9 ‰, and –163 ± 18 ‰ Δ^{14}C respectively (Druffel et al. 1992). Between 300 and 450 m, typical Δ^{14}C values of DIC, POC, and DOC are 77 ± 3 ‰ (300 m), 129 ± 11 ‰ (450 m), and – 363 ± 14 ‰ (300 m) Δ^{14}C respectively (Druffel et al. 1992). These numbers are not fixed in time, but in most cases they are significantly and measurably different from each other. 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 Δ^{14}C measurement in conjunction with the hydrograhic profiles of Δ^{14}C values in the water column described above as an indicator of the most recent source of carbon deposited in the skeleton. The outer Δ^{14}C value of two live collected *Corallium secundum* (5.3 ± 3.7 ‰, 3.5 ± 2.2 ‰), one *Gerardia* sp. (71.3 ± 3.7 ‰), and one black coral, *Leiopathes glaberrima* (-69.2 ± 4.1 ‰), are plotted in concert with water Δ^{14}C from hydrocasts spanning the last 30 years near Hawaii: GEOSECS, FGGE, and WOCE (Fig. 6). The outer values of 3 *Antipathes dichotoma* collected at 50 m are also plotted. The similarity of the outer Δ^{14}C values of the two *C. secundum* measured to the Δ^{14}C 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 Δ^{14}C value which will tag and be nearly equal to the Δ^{14}C signature of recently exported and labile POC, the expected source of skeletal C for deep water proteinaceous corals.

By analogy, we expect that the radiocarbon signature of the other proteinaceous corals, *Leiopathes glaberrima* and *Antipathes dichotoma,* to also reflect a POC source. However, because of their 50 m collection depth (where POC and DIC Δ^{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 is growing very slowly (5 µm y^{-1}; see section 6.4). With such a slow growth rate over the sampling interval of 500 µm, the outer sample of the *L. glaberrima* sample would be integrating ^{14}C from the last 100 years. To get an idea of what the integrated ^{14}C of DIC in surface water might be over the last 100 years, we averaged a Δ^{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 the last 100 years 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 -69.2 ‰ suggesting that POC is primary source of carbon to the *L. glaberrima*. In addition it has been shown that other DSC with a gorgonin skeleton such as bamboo corals and primnoids are deriving their carbon nearly exclusively from POC 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 either the *L. glaberrima* or the *A. dichotoma* should be any different.

6.2 *Corallium secundum*

Radial transects of $\Delta^{14}C$ measurements using discretely milled samples (0.5 mm intervals) from the outermost edge to the center of each specimen of *Corallium secundum* were derived from two live collect 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 years 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 carries the ^{14}C signature of the surrounding seawater DIC pool. These results are in agreement with those of Griffin and 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) and solitary corals such as *Lothelolia* spp. have shown similar results (Goldstein et al. 2001, Adkins et al. 2002, Frank et al. 2004). 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 $\Delta^{14}C$ is 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. Linear

interpolation between the (inferred) 1973 Δ^{14}C value at 3.5 mm and the outer edge with the known collection date in 1997 yields a ~170 µm y^{-1} radial growth rate for sample COR-01 (Fig. 3). Applying this growth rate to the entire radial diameter of ~12 mm suggests that sample COR-01 is 68 ± 13 years old. A similar calculation on COR-02 results in a growth rate of ~170 µm y^{-1} and an age of 77 ± 12 years. Given the rapid rise in Δ^{14}C during the bomb curve, a conservative uncertainty of ±0.5 mm in distance from the outer edge at which the 1973 Δ^{14}C value is assigned, results in an uncertainty of ± 20 µm y^{-1} in these estimated growth rates. Uncertainty in the age (1973) assignment for the –100 ‰ Δ^{14}C horizon of ±1 year results in an additional uncertainty of less than 10 µm y^{-1} in the growth rate. The maximum growth rates estimated in this fashion are consistent between the two specimens and the uncertainty estimates are conservative estimates.

The Hawaiian *Corallium secundum* growth rates are similar to the growth rate of 110 µm y^{-1} (± 20 µm y^{-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 (Druffel et al. 1990). Grigg (1976, Grigg 2002) developed an equation correlating colony height (length) and age based on the counting of growth rings that were assumed to be annual. Applying the Grigg equation to sample COR-01, which was 28 cm high, results in an age of 29 years (vs. 68 years by our Δ^{14}C method). Furthermore, examination of cross-section thin sections from COR-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 years the known age samples (20 years old)(Marschal et al. 2004). The organic growth rings only under estimated the known age by 3-4 years (Marschal et al. 2004). The counting of growth rings from the staining of the organic matrix resulted in growth rates ranging from 140 to 750 µm y^{-1} with a mean of 340 ± 150 µm y^{-1} for a suite of *C. rubrum* samples (Marschal et al. 2004), which is much closer the Δ^{14}C growth rates we calculated. In addition, both radiometric techniques, Δ^{14}C and ^{210}Pb^{ex}, support much lower growth rates than those inferred from growth ring estimates for Hawaiian *C. secundum* (Grigg 1976, 2002). Growth ring (size) relations appear to underestimate the age of individuals by at least a factor of two and possibly a factor of 10. While greater precision in Δ^{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 Δ^{14}C to be used as tracer of ocean circulation and further refine the age and growth rate estimates.

6.3 *Gerardia* sp.

The outermost Δ^{14}C value from the radial transect sampled at 0.5-0.6 mm intervals of the live collected *Gerardia* sp. specimen (GER-RD97-01) is 71.3 ± 3.7 ‰. This post-bomb Δ^{14}C value is very close to the expected Δ^{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 Δ^{14}C values suggest continuous and steady growth, with the center of the sample having a ^{14}C age of 1200 ± 25 ^{14}C years (-144.3 ± 2.4 ‰ Δ^{14}C; Fig. 4, Table 3). 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 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 years and adding a regional reservoir correction (or ΔR value). Using a ΔR of –28 ± 4 ^{14}C years (Druffel et al. 2001), a calibrated age of 760 ± 30 cal years BP was calculated for the central portion of GER-RD97-01 using the CALIB 5.0 (Stuiver & Reimer 1993) program and the marine04 calibration dataset (Hughen et al. 2004)(Table 4). Since the present is defined as 1950 in the calibrated age it is also necessary to add 47 years (1997-1950=47), yielding a life span of ~807 ± 30 years for the GER-RD97-01 *Gerardia* sp. sample. Interpolating between the inner (old) age and the known age of collection (1997), yields a radial growth rate of 15 μm y^{-1}. The trend in ^{14}C and calibrated ages over the life span of this *Gerardia* sp. implies a near constant radial growth rates (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. (Table 2, Fig. 7).

The radiocarbon based estimates of radial growth rate and longevity of an Atlantic *Gerardia* sp. (~20 μm y^{-1}, ~1800 years old; Druffle et al. (1995)) and those from this study are consistent with each other. In contrast, Goodfriend (1997) calculated amino acid racemization

ages of 250 ± 70 years on the same Atlantic specimen studied by Druffel. 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 the 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] estimates radial growth rates for *Gerardia* sp. in excess of 1 mm y^{-1} on samples collected off Keahole Bay (380-410 m), with maximum ages on the order of 40 years. Grigg's estimate is based on the assumption that growth banding observed in the gorgonin 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 have also been shown not to be annual (Adkins et al. 2004). The *Gerardia* sp. growth rates estimated by Grigg [1976; 2002] are three 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 ^{14}C 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 export POC from surface waters.

With such old ages, the potential exists to use *Gerardia* sp. for paleoenvironmental reconstructions over centennial to millennial time scales. Since *Gerardia* sp. is building skeletal material using POC from surface waters, it is likely that δ^{15}N and δ^{13}C values in *Gerardia* sp. gorgonin record long-term changes in surface productivity or ecosystem structure (Druffel et al. 1995). In another DSC with a proteinaceous skeletons, Heikoop et al., (2002) measured δ^{13}C and δ^{15}N in the polyp (animal) tissues and contemporaneous gorgonin fraction from a series of live collected *Primnoa resedaeformis* from different regions. Their results show that no discernable fractionation between the gorgonin skeleton and polyp tissue fractions. They also observed systematic regional differences in gorgonin δ^{13}C and δ^{15}N that mirrored regional differences in

the isotopic composition of surface POM. This suggests that stable isotopic measurements from the proteinaceous skeletons of DSC may reflect climate and productivity variations in surface waters.

6.4 Black Corals, *Antipathes dichotoma* and *Leiopathes glaberrima*

The ages and growth rates of the black corals, *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. Only the *L. glaberrima* is known to have been alive at the time of collection. A radial transect at 0.5-0.6 mm intervals across one of the *A. dichotoma* specimens (BC3) shows decreasing bomb carbon values over the outer 4.5 mm, after which the $\Delta^{14}C$ values did not change (Fig. 5, Table 3). The outer sample has a $\Delta^{14}C$ value (106.5 ± 4.3 ‰) that is indistinguishable from surface DIC (Guilderson and Schrag, unpublished 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 $\Delta^{14}C$ time-series. It is not clear that all the *A. dichotoma* samples were alive at the time of collection, thus the year of their "death" must also be estimated from the surface coral $\Delta^{14}C$ time-series. In the case of sample BC3, the outermost value (106.5 ± 4.3 ‰) is equivalent to an age of ~1965 or ~1992 in the surface coral $\Delta^{14}C$ time-series (Fig. 8). A linear interpolation between the increase in bomb ^{14}C at 4.5 mm and the outermost edge (1957 - 1992 = 35 years) gives a growth rate of 130 μm y^{-1} which, if assumed to be constant over the entire growth of the specimen, suggests that the sample is ~105 years old (Table 2). Alternatively, a growth rate of 560 μm y^{-1} and an age of 25 years is calculated if the coral died in 1965. Assuming a conservative uncertainty of ± 5 years in the assignment of the ages, the growth rate and ages would have an uncertainty of ± 20 μm y^{-1} and ± 20 years, respectively.

Inner and outer $\Delta^{14}C$ measurements on two other *Antipathes dichotoma* samples (BC1 and BC2) collected at 50 m were all above -50 ‰ and thus incorporated bomb ^{14}C. Comparing these bomb ^{14}C values to the surface coral $\Delta^{14}C$ time-series the shortest and longest lifespan (growth rate) possible for BC1 is ~ 15-32 years (390-180 μm y^{-1}) and the lifespan (growth rate) of BC2 is ~12-29 years (1,140-470 μm y^{-1}) (Table 5 and Fig. 8).

The $\Delta^{14}C$ values along the radial transect of the *Leiopathes glaberrima* collected at ~450 m (BC5) decreased gradually from a pre-bomb $\Delta^{14}C$ value of -69.2 ± 4.1 ‰ at the outer edge to a

value of -280.7 ± 2.9 ‰ (2600 ± 35 ^{14}C years) at the center (Fig. 5, Table 3). The ^{14}C values were calibrated in the same manner as the *Gerardia* sp. samples discussed above, yielding an age of 2320 ± 15 cal yr. BP at the center (Fig. 9, Table 4). With a life span of 2377 years and a growth rate of ~5 µm y^{-1}, this organism is similar to *Gerardia* sp. in terms of longevity and growth rates. However, the growth rate is not constant, with faster growth occurring when the sample was younger (Fig. 5).

Using tagged colonies of *Antipathes dichotoma*, a liner growth rate of 6.42 cm y^{-1} was measured over a 3.5 year 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 estimate the age of sample BC1 to be ~12 years old and sample BC2 to be 20 years old (Table 4). Using the linear relationship between height and growth rings y^{-1}, BC1 and BC2 were estimated to be 15 and 25 years old (Table 4), respectively. These results are in agreement with the younger and thus faster radial growth estimates using bomb ^{14}C (Table 4). Still, BC3 shows that slower growth rates and older ages are possible. Perhaps the large range in growth rates is due to different environmental conditions, such as exposure to different current conditions.

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 versus 450 m. *Antipathes dichotoma* is not found below 110 m in Hawaiian waters, near the top of the main thermocline (Grigg 1976, 2001). Food availability (POC, including living plankton) is different at 50 m than at 400 m, thus it is reasonable to assume that growth rates would be different as well. With differences as great as 15°C between 50 m and 420 m (http://www.soest.hawaii.edu/HOT_WOCE/), temperature may the biggest factor in determining growth rates. In short, it is not surprising that ecological differences may be important factors in the governance of growth rates. The effects of these and other factors on the biogeochemistry of skeletons is an important area of further study.

6.5 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, *A. dichotoma* has made up almost 90% of the commercial harvest of black corals (Western Pacific Regional Fishery Management Council 2001) and the existing maximum sustainable yields (MSY) were estimated using the linear growth rate for *Antipathes dichotoma*, (Grigg 1976, 2001) discussed above. The MSY calculated for the two known major beds, the Au'au Channel Bed and the Kauai Bed were 5,000 kg y^{-1} and 1,250 kg y^{-1} respectively, and included a minimum size limit (Western Pacific Regional Fishery Management Council 2001, National Marine Fisheries Service (NMFS) 2002). These MSY appear to be valid, if the fastest ^{14}C based growth rate are assumed to be correct. However, if the slower ^{14}C based growth rates are correct then the current MSY is based on a best case scenario. Given the uncertainty in the age and growth rates of the population of *A. dichotoma,* a conservative MSY based on the slower growth rates may be more appropriate for the sustainable management of the fishery. Like wise the growth rate and age estimates reported in this paper for *Corallium secundum* from Hawaii are significantly slower and older than those previously reported (Grigg 1976, 1993), thus the *Corallium* spp. MSY should also be revised.

The very slow growth rates and extremely old ages reported above for *Leiopathes glaberrima* and *Gerardia* sp. suggest any harvesting of these species in any locations is unlikely to be sustainable. Currently, *L. glaberrima* is not specifically included nor excluded from 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. While 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. For example at Ke-ahole Point the MSY is 20 kg/yr. The MSY is based entirely on the assumption that commercial sized individuals are 40 years of age. Our results show growth rates that are 10 to 70 times slower than those predicting 40 year ages and thus these individuals are actually more than 400 years old (up to several millennia!). The discrepancy in ages and growth rates are likely the reason why gold coral stocks at the Makapuu Bed have experienced little to no recruitment and

re-growth (Western Pacific Regional Fishery Management Council 2001). 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.

7 CONCLUSIONS

Here, we reported 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 ^{14}C content of the North Pacific, we determine radial growth rates of ~170 µm y^{-1} and colony ages of 68-77 years 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 y^{-1} and an age of 807 ± 30 was calculated from a high resolution ^{14}C radial transect on a live collected *Gerardia* sp. Inner and outer ^{14}C measurements on 4 sub-fossil *Gerardia spp.* samples support the low growth rates (range 14-45 µm y^{-1}) and great ages (range 450-2742 years) for this organism. One organism was determined to have lived 2742 years.

- Similarly, with a growth rate of ~5 µm y^{-1} (basal radial diameter ~12 mm) and an estimated colony age of ~2377 years, 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 15 to 109 years, with growth rates on the order of 129 µm y^{-1} to 1,140 µm y^{-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. There is great potential to use long-lived DSC species in paleoclimate reconstructions. The ^{14}C chronologies presented here are accurate enough for studies of multi-decadal variability within the ocean interior.

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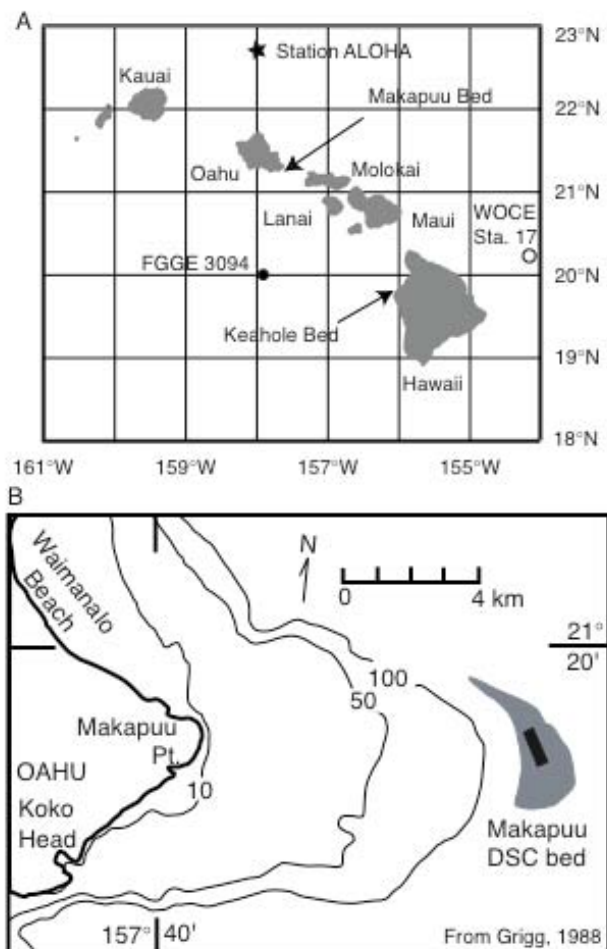
Figure 1: (A) Map of the Hawaiian Islands showing the location of the Makapuu and Keahole

deep-sea corals beds, and the location of two hydrographic profiles. (B) Detailed map of the

Makapuu bed (shaded region) from Grigg, 1998.
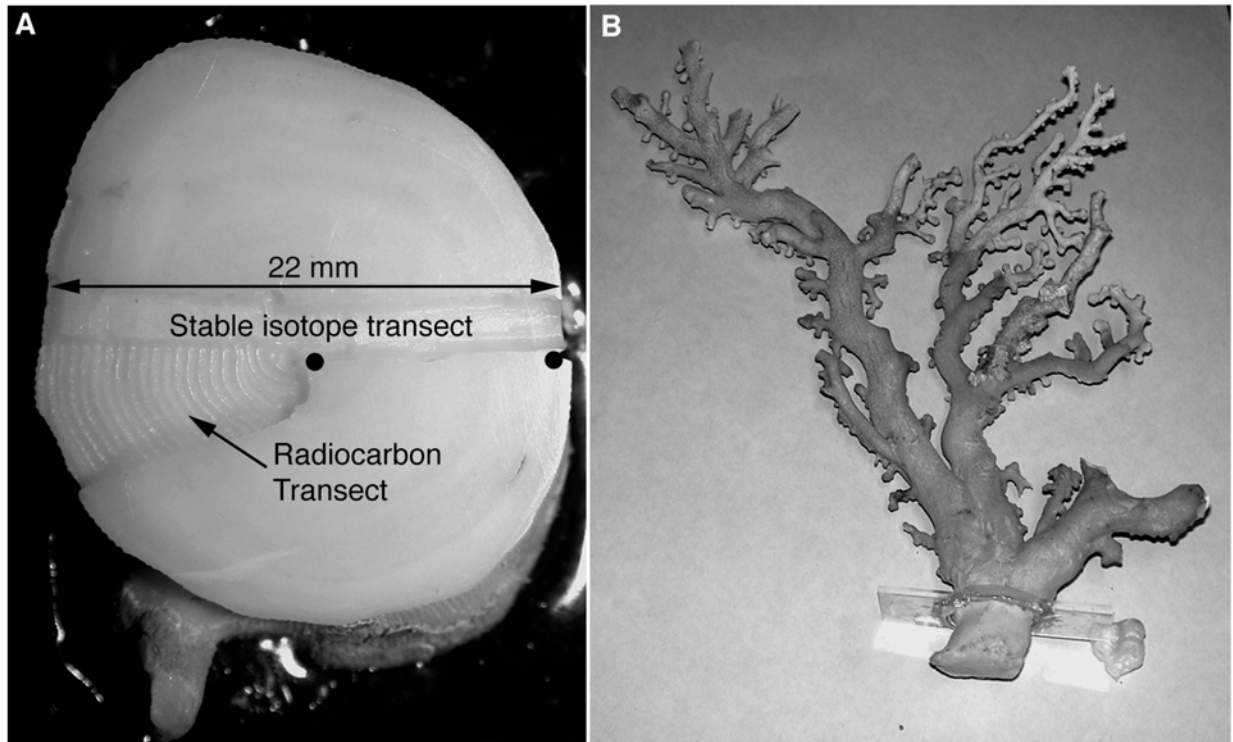
Figure 2 Picture of a *Coralliun secundum* disk cut from the basal portion of a sample mounted on a glass slide (Panel B). The radiocarbon and stable isotope sampling tracks are shown in panel A. Note each ridge in the radiocarbon sampling track is one sample. Dots are an example of where inner and outer samples are taken.
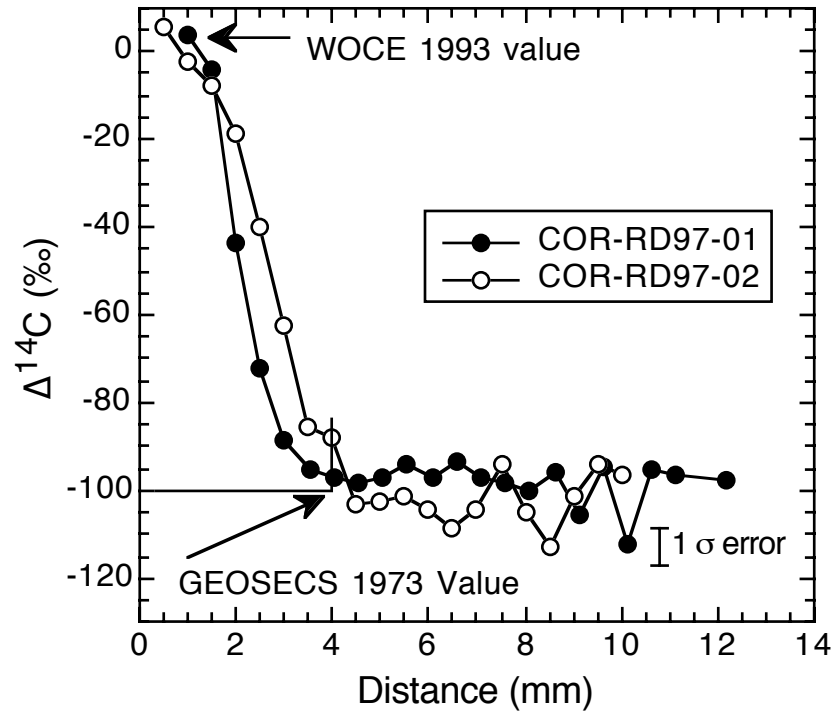
Figure 3: $\Delta^{14}C$ radial transect across two *Coralliun secundum* samples. Based on the GEOSECS hydrographic profile a $\Delta^{14}C$ value of –100 ‰ is assigned a time marker of 1973 and growth rates are calculate by linear interpolation between that point and the outer edge with a known collection date of 1997.
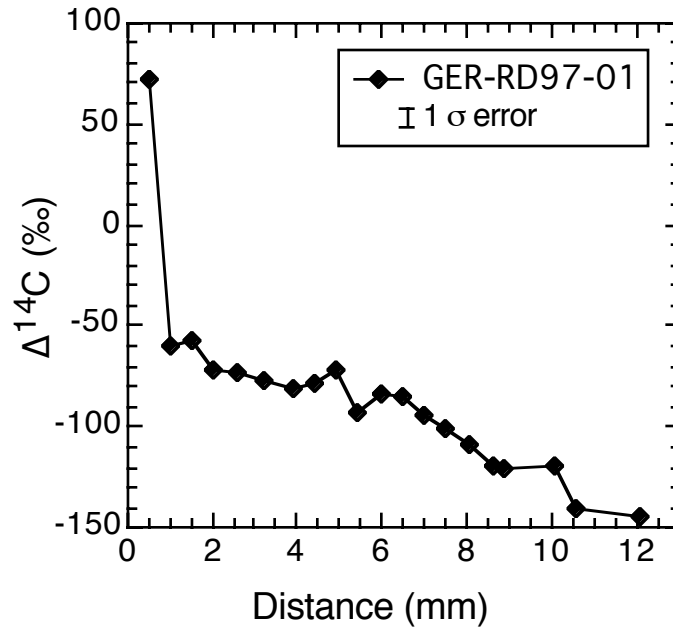
Figure 4: $\Delta^{14}C$ radial transect across a *Gerardia* sp. sample (GER-RD97-01). The center of the sample had a ^{14}C age of 1200 ± 35 ^{14}C years and a lifespan of 828 ± 30 years resulting in a calculated growth rate of ~14 μm y^{-1}.
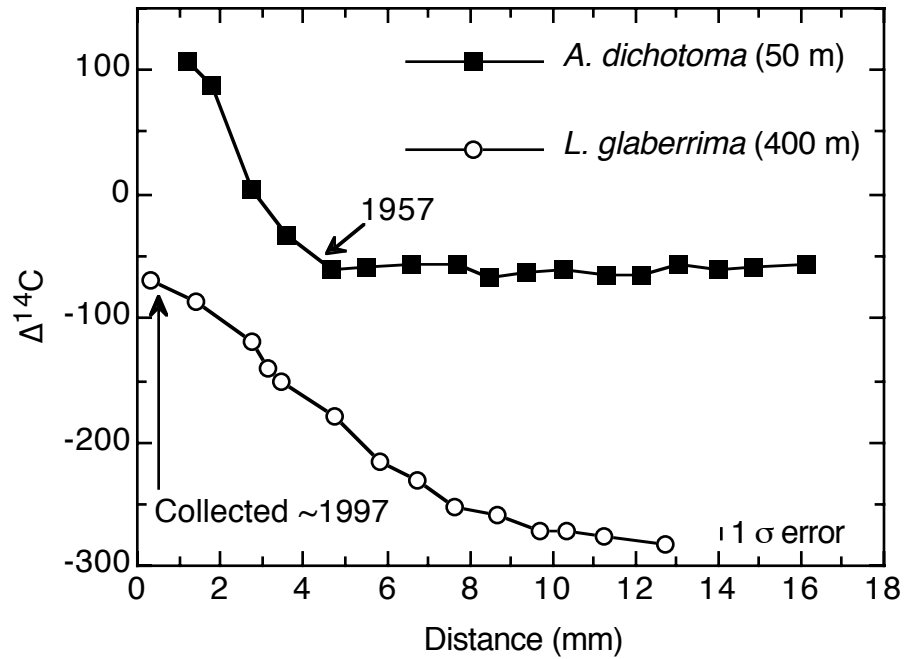
Figure 5: Δ^{14}C radial transect across a *Antipathes dichotoma* (sample BC#3, closed squares) collected at 50 m and a *Leiopathes glaberrima* (sample BC#5, open circles) collected at 400 m. Δ^{14}C values > -50 ‰ are indicative of bomb ^{14}C and can be used to set an initial time marker of 1957 for sample BC#3.
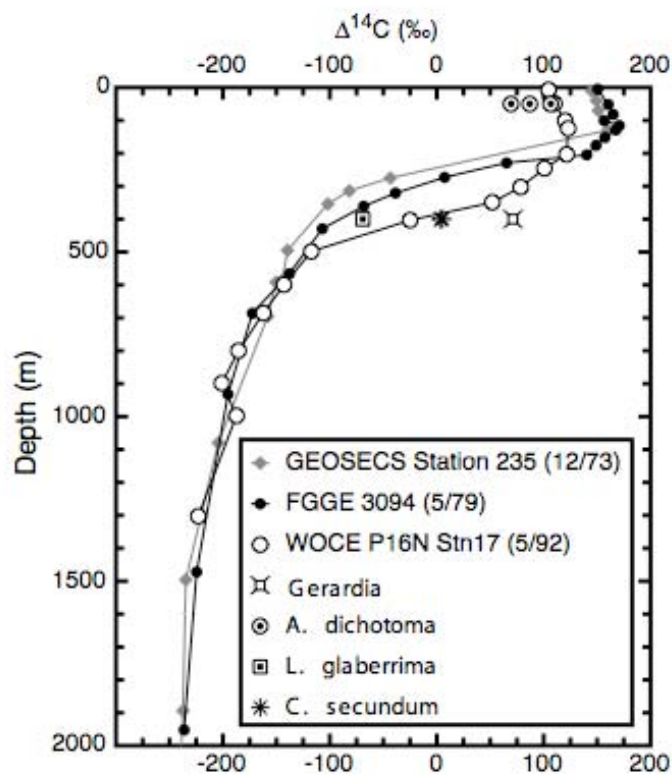
Figure 6: Water Δ^{14}C from hydrocasts spanning the last 30 years near Hawaii: GEOSECS (closed diamonds), FGGE (closed circles), and WOCE (open circles), plotted with the outer values of two *Coralliun secundum* samples, one *Gerardia* sp. sample and one *Leiopathes glaberrima* sample collected alive at 400 m. The outer Δ^{14}C values of three *Antipathes dichotoma* collected at 50 m are also plotted.
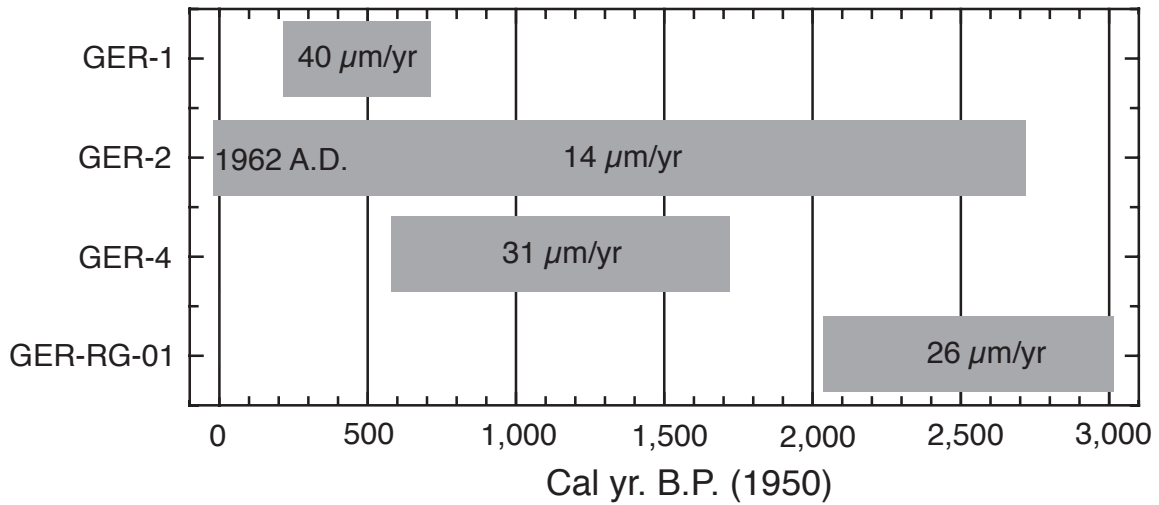
Figure 7: Age ranges in cal yr. B.P. (1950) based on the outer and inner ^{14}C measurements of four *Gerardia* sp. samples. Radial growth rates are based on linear interpolations between the outer and inner ages. The outer value of sample GER-2 had bomb ^{14}C (> -50 ‰) and the age was determined by comparison of this value with a Δ^{14}C time series in a surface coral from Hawaii (Guilderson and Schrag, unpublished data). See figure 8.
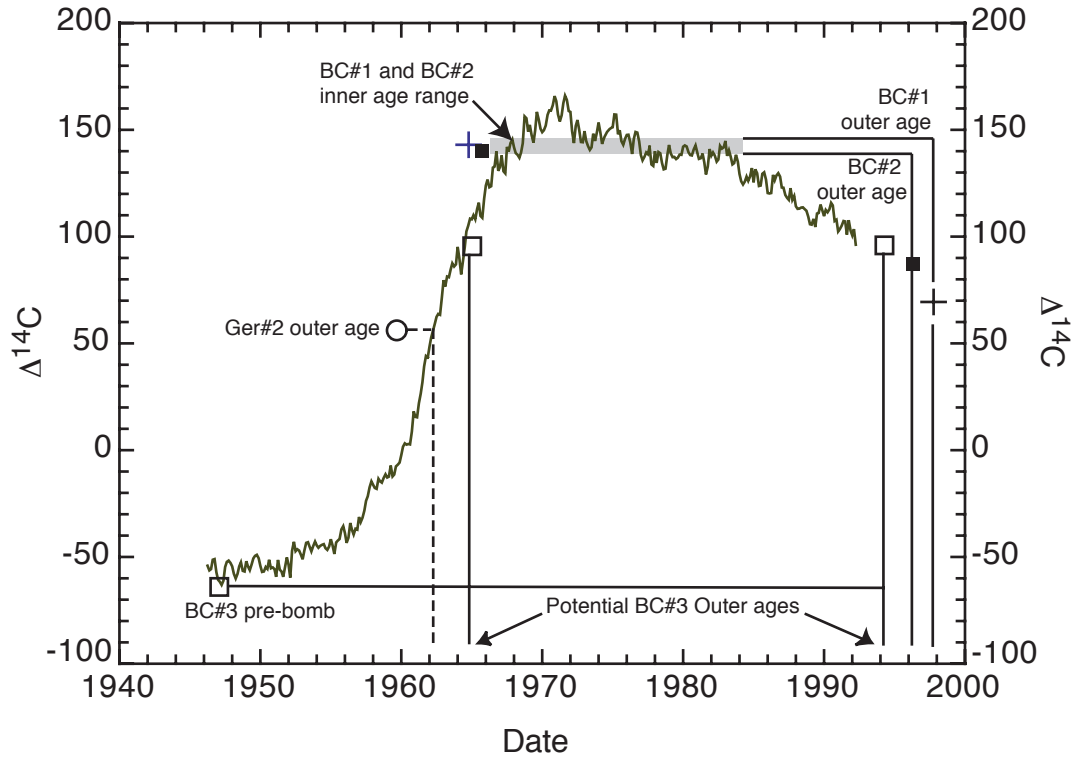
Figure 8: Δ^{14}C time-series in a surface coral (solid line) from the island of Hawaii (Guilderson and Schrag, unpublished data). Inner and outer Δ^{14}C values of *Antipathes dichotoma* (BC#1, BC#2, and BC#3) and the outer value of a *Gerardia* sp. sample (GER#2) are plotted so that calendar dates may be estimated. Where the DSC Δ^{14}C value is equal to the surface coral Δ^{14}C value an age can be estimate. 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 Δ^{14}C value can be associated with two time markers (e.g. outer BC#3 age). The pre-bomb Δ^{14}C values of BC#3 where assigned an age of 1957 (see figure 5). The outer age (1962) of GER#2 was used to determine the age and growth rate of the sample in figure 7.
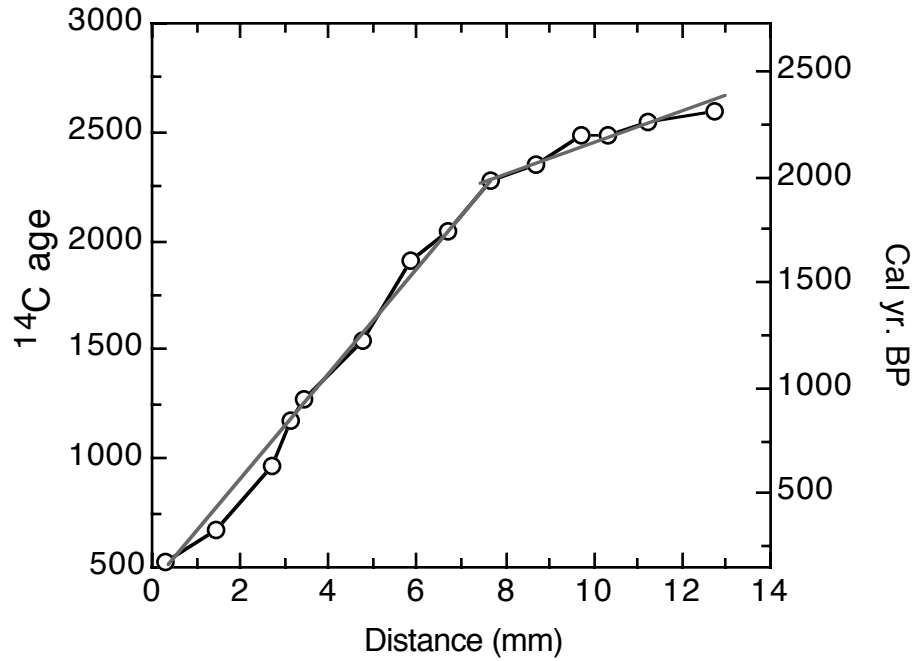
Figure 9: [14]C radial transect across a *Leiopathes glaberrima* (sample BC#5, open circles) collected at 400 m. The ^{14}C ages were calibrated using a reservoir correction of 410 ^{14}C years. An age of ~2330 years with a growth rate ≤ 10 µm y^{-1} was calculated. Over the first 6 mm of growth the growth rate is apparently faster than over the outer 8 mm.

Table 1: Deep-sea coral sample list.

Sample ID	Genus	Depth (m)	Location	Height (cm)	Dia (mm)	Collector	Collection date	Sampling	Notes
COR-RD97-01	Corallium secundum	450 ±40	Makapuu, Oahu	28	20 x 29	Rob Dunbar	8/22/1997	Radial	Alive (PISCES V)
COR-RD97-02	Corallium secundum	450 ±40	Makapuu, Oahu		22	Rob Dunbar	8/22/1997	Radial	Alive (PISCES V)
GER-RD97-01	Gerardia sp.	450 ±40	Makapuu, Oahu			Rob Dunbar	8/22/1997	Radial	Alive (PISCES V)
GER-#1	Gerardia sp.	400±20	Makapuu, Oahu		33 x 43	Rick Grigg		I/O	
GER-#2	Gerardia sp.	400±20	Makapuu, Oahu		30 x 62	Rick Grigg		I/O	
GER-#4	Gerardia sp.	400±20	Makapuu, Oahu		38 x 50	Rick Grigg		I/O	
GER-HI-RG-01	Gerardia sp.	400-420	Hawaii			Rick Grigg	Dead	I/O	Dead
Black coral-BC1	Antipathes dichotoma	50±5	Hawaiian islands	81.3	14 x 22	Rick Grigg		I/O	
Black coral-BC2	Antipathes dichotoma	50±5	Hawaiian islands	129.5	21, 27	Rick Grigg		I/O	
Black coral-BC3	Antipathes dichotoma	50±5	Hawaiian islands		17 x 25	Rick Grigg		Radial	
Black coral-BC5	Leiopathes glaberrina	450 ±40	Makapuu, Oahu		26	Rob Dunbar	8/22/1997	Radial	Alive (PISCES V)

1) I/O = Inner and Outer

Table 2: Radiocarbon measurements, ages and growth rates of Hawaiian deep sea corals.

Sample ID	Genus	Depth (m)	Δ^{14}C (‰) Inner	Outer	^{14}C Years Inner	Outer	Calender Years Inner	Outer	Radius (mm)	Age (Years)	Growth Rate (μm/years)
COR-RD97-01	Corallium secundum	450 ±40	-104.4 ±4.5	3.5 ±2.2	835 ±40	>Modern	1997¥	1997¥	12.1	68	170
COR-RD97-02	Corallium secundum	450 ±40	-96.3 ±4.6	5.3 ±3.7	760 ±35	>Modern	1997¥	1997¥	11.5	77	170
GER-RD97-01	Gerardia sp.	450 ±40	-144.3 ±2.4	71.3 ±3.7	1200 ±25	>Modern	760 ±30§	1997¥	12.0	807±30	15
GER-#1	Gerardia sp.	400±20	-138.5 ±3.6	-74.5 ±2.7	1145 ±35	570 ±25	710 ±25§	260 ±15§	20	450	45
GER-#2	Gerardia sp.	400±20	-317.8 ±2.2	56.1 ±2.8	3020 ±30	>Modern	2730 ±15§	1962†	38.1	2742	14
GER-#4	Gerardia sp.	400±20	-236.8 ±2.5	-120.0 ±2.6	2120 ±30	980 ±25	1740 ±35§	585 ±25§	35.9	1155	31
GER-HI-RG-01	Gerardia sp.	400-420	-332.4 ±2.6	-261.8 ±2.5	3200 ±35	2390 ±30	3040 ±45§	2055 ±40§	23.2	985	24
Black coral (BC)#1	Antipathes dichotoma	50±5	143.0	69.4	>Modern	>Modern	1972†	1990s†	5.9	~23	240
Black coral (BC)#2	Antipathes dichotoma	50±5	140*	87*	>Modern	>Modern	1971†	1990s†	13.7	~23	450
Black coral (BC)#3	Antipathes dichotoma	50±5	-57.1 ±3.6	106.5 ±4.3	420 ±35	>Modern	pre-1955	1990s†	13.6	105	130
Black coral (BC)#5	Leipathes glaberrima	450 ±40	-280.7 ±2.9	-69.2 ±4.1	2600 ±35	530 ±40	2320 ±15§	1997¥	11.6	2377	≤10

* BC#2 results are the average of two inner and outer ^{14}C measurements as the sample appears to have two growth centers fused together.

§ ^{14}C results calibrated using INTELCAL v5.0 and ΔR of -28±4 ^{14}C years, results in cal yr BP

† Post-bomb data are reflected by positive Δ^{14}C values. AD years were determined by comparision with a Hawaiian surface water Δ^{14}C time-sereis (Guilderson and Schrag, unpublished data). See figure 8.

¥ Known age samples were collected alive.

Table 3: Radiocarbon data from radial transects.

Sample ID	CAMS #	Distance (μm)	δ¹³C (‰)	Fraction Modern	±	Δ¹⁴C (‰)	±	¹⁴C age	±
Corallium secundum									
COR-RD97-02-#1	107848	500	-5.8	1.0118	0.0037	5.3	3.7	>Modern	
COR-RD97-02-#2	107849	1,000	-5.8	1.0041	0.0035	-2.4	3.5	>Modern	
COR-RD97-02-#3	107850	1,500	-5.8	0.9987	0.0033	-7.8	3.3	Modern	
COR-RD97-02-#4	107851	2,000	-5.8	0.9877	0.0033	-18.7	3.3	100	30
COR-RD97-02-#5	107852	2,500	-5.8	0.9666	0.0034	-39.7	3.4	275	30
COR-RD97-02-#6	107853	3,000	-5.8	0.9436	0.0031	-62.5	3.1	465	30
COR-RD97-02-#7	107854	3,500	-5.8	0.9204	0.0030	-85.6	3.0	665	30
COR-RD97-02-#8	107855	4,000	-5.8	0.9180	0.0031	-88.0	3.1	685	30
COR-RD97-02-#9	107856	4,500	-5.8	0.9028	0.0031	-103.1	3.1	820	30
COR-RD97-02-#10	107857	5,000	-5.8	0.9035	0.0030	-102.4	3.0	815	30
COR-RD97-02-#11	107858	5,500	-5.8	0.9048	0.0039	-101.1	3.9	805	35
COR-RD97-02-#12	107859	6,000	-5.8	0.9016	0.0031	-104.2	3.1	830	30
COR-RD97-02-#13	107860	6,500	-5.8	0.8972	0.0025	-108.6	2.5	870	25
COR-RD97-02-#14	107861	7,000	-5.8	0.9016	0.0029	-104.2	2.9	830	30
COR-RD97-02-#15	107862	7,500	-5.8	0.9119	0.0036	-94.0	3.6	740	35
COR-RD97-02-#16	107863	8,000	-5.8	0.9011	0.0041	-104.8	4.1	835	40
COR-RD97-02-#17	107864	8,500	-5.8	0.8929	0.0040	-112.9	4.0	910	40
COR-RD97-02-#18	107865	9,000	-5.8	0.9049	0.0032	-101.0	3.2	805	30
COR-RD97-02-#19	107866	9,500	-5.8	0.9122	0.0038	-93.8	3.8	740	35
COR-RD97-02-#20	107867	10,000	-5.8	0.9096	0.0038	-96.3	3.8	760	35
COR-RD97-01-#1	85400	1,000	-5.7	1.0098	0.0022	3.5	2.2	Modern	
COR-RD97-01-#4	85401	1,507	-5.7	1.0021	0.0031	-4.1	3.1	Modern	
COR-RD97-01-#5	85402	2,014	-5.7	0.9623	0.0023	-43.7	2.3	310	20
COR-RD97-01-#6	85403	2,521	-5.7	0.9338	0.0026	-72.1	2.6	550	25
COR-RD97-01-#7	85404	3,028	-5.7	0.9175	0.0024	-88.3	2.4	690	25
COR-RD97-01-#8	85405	3,535	-5.7	0.9107	0.0025	-95.0	2.5	750	25
COR-RD97-01-#9	85406	4,042	-5.7	0.9086	0.0025	-97.1	2.5	770	25
COR-RD97-01-#10	85407	4,549	-5.7	0.9077	0.0025	-98.0	2.5	780	25
COR-RD97-01-#11	85408	5,056	-5.7	0.9089	0.0026	-96.8	2.6	765	25
COR-RD97-01-#12	85409	5,563	-5.7	0.9116	0.0026	-94.1	2.6	745	25
COR-RD97-01-#13	85410	6,070	-5.7	0.9089	0.0025	-96.8	2.5	765	25
COR-RD97-01-#14	85411	6,577	-5.7	0.9123	0.0026	-93.4	2.6	740	25
COR-RD97-01-#15	85412	7,084	-5.7	0.9085	0.0025	-97.2	2.5	770	25
COR-RD97-01-#16	85413	7,591	-5.7	0.9072	0.0020	-98.5	2.0	780	20
COR-RD97-01-#17	85414	8,098	-5.7	0.9057	0.0033	-100.0	3.3	795	30
COR-RD97-01-#18	85415	8,605	-5.7	0.9098	0.0025	-95.9	2.5	760	25
COR-RD97-01-#19	85416	9,112	-5.7	0.8998	0.0026	-105.8	2.6	850	25
COR-RD97-01-#20	85417	9,619	-5.7	0.9110	0.0027	-94.7	2.7	750	25
COR-RD97-01-#21	85418	10,121	-5.7	0.8933	0.0034	-112.3	3.4	905	35
COR-RD97-01-#22	85419	10,623	-5.7	0.9105	0.0032	-95.3	3.2	755	30
COR-RD97-01-#23	85420	11,125	-5.7	0.9093	0.0032	-96.4	3.2	765	30
COR-RD97-01-#24	85421	12,125	-5.7	0.9082	0.0045	-97.4	4.5	775	40
Gerardia sp.									
GER-RD97-01-#1	84986	512	-16	1.0781	0.0037	71.3	3.7	>MODERN	
GER-RD97-01-#3	84987	1,012	-16	0.9463	0.0039	-59.6	3.9	445	35
GER-RD97-01-#4	84988	1,512	-16	0.9483	0.0031	-57.6	3.1	425	30
GER-RD97-01-#5	84989	2,012	-16	0.9345	0.0035	-71.4	3.5	545	35
GER-RD97-01-#6	84990	2,612	-16	0.9329	0.0025	-72.9	2.5	560	25
GER-RD97-01-#9	84993	3,212	-16	0.9285	0.0026	-77.3	2.6	595	25

GER-RD97-01-#10	84994	3,877	-16	0.9247	0.0026	-81.1	2.6	630	25
GER-RD97-01-#11	84995	4,377	-16	0.9268	0.0026	-79.0	2.6	610	25
GER-RD97-01-#12	84996	4,877	-16	0.9343	0.0033	-71.5	3.3	545	30
GER-RD97-01-#13	84997	5,377	-16	0.9134	0.0026	-92.3	2.6	725	25
GER-RD97-01-#16	85000	5,977	-16	0.9220	0.0026	-83.8	2.6	655	25
GER-RD97-01-#17	85001	6,477	-16	0.9203	0.0026	-85.5	2.6	665	25
GER-RD97-01-#18	85002	6,977	-16	0.9116	0.0037	-94.2	3.7	745	35
GER-RD97-01-#19	85003	7,477	-16	0.9049	0.0027	-100.8	2.7	805	25
GER-RD97-01-#20	85004	8,027	-16	0.8965	0.0025	-109.1	2.5	880	25
GER-RD97-01-#22	85006	8,627	-16	0.8865	0.0026	-119.1	2.6	970	25
GER-RD97-01-#23	85007	8,827	-16	0.8848	0.0025	-120.8	2.5	985	25
GER-RD97-01-#24	85008	10,027	-16	0.8867	0.0029	-118.9	2.9	965	30
GER-RD97-01-#26	85010	10,527	-16	0.8657	0.0026	-139.8	2.6	1160	25
GER-RD97-01-#27	85011	12,027	-16	0.8611	0.0024	-144.3	2.4	1200	25
Antipathes dichotoma									
BC3-#1	99827	1,219	-17	1.1136	0.0043	106.5	4.3	>MODERN	
BC3-#2	99828	1,803	-17	1.0944	0.0047	87.4	4.7	>MODERN	
BC3-#4	99829	2,743	-17	1.0102	0.0053	3.8	5.3	MODERN	
BC3-#5	99830	3,581	-17	0.9738	0.0041	-32.5	4.1	215	35
BC3-#6	99831	4,648	-17	0.9455	0.0042	-60.5	4.2	450	40
BC3-#7	99832	5,511	-17	0.9468	0.0047	-59.3	4.7	440	40
BC3-#8	99833	6,629	-17	0.9497	0.0036	-56.3	3.6	415	35
BC3-#9	99834	7,721	-17	0.9486	0.0040	-57.5	4.0	425	35
BC3-#10	99835	8,509	-17	0.9395	0.0037	-66.5	3.7	500	35
BC3-#11	99836	9,398	-17	0.9422	0.0036	-63.8	3.6	480	35
BC3-#12	99837	10,287	-17	0.9443	0.0046	-61.7	4.6	460	40
BC3-#13	99838	11,303	-17	0.9403	0.0041	-65.7	4.1	495	40
BC3-#14	99839	12,166	-17	0.9410	0.0036	-65.0	3.6	490	35
BC3-#15	99840	13,030	-17	0.9502	0.0038	-55.8	3.8	410	35
BC3-#16	99841	13,995	-17	0.9460	0.0036	-60.1	3.6	445	35
BC3-#17	99842	14,884	-17	0.9470	0.0036	-59.1	3.6	440	35
BC3-#18	99843	16,154	-17	0.9489	0.0036	-57.1	3.6	420	35
Leiopathes glaberrina									
BC5-#1	99727	279	-17	0.9362	0.0043	-69.8	4.3	530	40
BC5-#2	99728	1,422	-17	0.9193	0.0043	-86.6	4.3	675	40
BC5-#3	99729	2,743	-17	0.8862	0.0036	-119.4	3.6	970	35
BC5-#4	99730	3,149	-17	0.8643	0.0035	-141.2	3.5	1170	35
BC5-#5	99731	3,429	-17	0.8537	0.0034	-151.8	3.4	1270	35
BC5-#6	99732	4,749	-17	0.8254	0.0033	-179.9	3.3	1540	35
BC5-#7	99733	5,842	-17	0.7888	0.0032	-216.2	3.2	1910	35
BC5-#8	99734	6,731	-17	0.7746	0.0032	-230.3	3.2	2050	35
BC5-#9	99735	7,670	-17	0.7534	0.0039	-251.4	3.9	2280	45
BC5-#10	99736	8,686	-17	0.7460	0.0032	-258.7	3.2	2360	35
BC5-#11	99737	9,702	-17	0.7342	0.0030	-270.5	3.0	2480	35
BC5-#12	99738	10,337	-17	0.7344	0.0033	-270.3	3.3	2480	40
BC5-#13	99739	11,226	-17	0.7282	0.0030	-276.4	3.0	2550	35
BC5-#14	99740	12,750	-17	0.7235	0.0030	-281.1	3.0	2600	35

1) Distance is from outer edge into the center of the specimen.

2) $\delta^{13}C$ values are the assumed values based on measurements in other similar samples when given
   without decimal places. Values measured for the material itself are given with a single decimal place.

3) Radiocarbon concentration is given as fraction Modern, $\Delta^{14}C$, and conventional radiocarbon age.
   $\Delta^{14}C$ values are not age corrected (Stiuver and Polloch, 1977) nor are the conventional radiocarbon
   ages reservoir corrected.

Table 4: Radiocarbon calibration results.

Sample ID	CAMS#	^{14}C Age	^{14}C age ±	Minimum cal age range (1s) cal BP	Maximum cal age range (1s) cal BP	Relative area under distribution	Median Probability Age
GER-RD97-01-A3	84987	445	35	0	20	0.22	
				50	115	0.78	70
GER-RD97-01-A4	84988	425	30	0	65	1	45
GER-RD97-01-A5	84989	545	35	145	160	0.13	
				195	210	0.16	
				225	265	0.71	225
GER-RD97-01-A6	84990	560	25	235	275	1	250
GER-RD97-01-A9	84993	595	25	260	285	1	275
GER-RD97-01-A10	84994	630	25	275	305	1	295
GER-RD97-01-A11	84995	610	25	270	290	1	280
GER-RD97-01-A12	84996	545	30	150	160	0.13	
				195	210	0.16	
				225	265	0.71	225
GER-RD97-01-A13	84997	725	25	375	440	1	
GER-RD97-01-A16	85000	655	25	285	335	0.92	320
				345	350	0.08	
GER-RD97-01-A17	85001	665	25	295	360	1	335
GER-RD97-01-A18	85002	745	35	410	455	1	430
GER-RD97-01-A19	85003	805	25	460	490	1	475
GER-RD97-01-A20	85004	880	25	500	525	1	515
GER-RD97-01-A22	85006	970	25	555	610	1	585
GER-RD97-01-A23	85007	985	25	565	585	0.37	
				590	620	0.63	595
GER-RD97-01-A24	85008	965	30	550	605	1	580
GER-RD97-01-A26	85010	1160	25	695	745	1	720
GER-RD97-01-A27	85011	1200	25	730	785	1	760
GER1-Outer	89039	570	25	245	275	1	260
GER1-Inner	89040	1150	35	685	725	1	710
GER2-Inner	89046	2930	30	2720	2750	1	2730
GER4-Outer	89041	975	25	560	615	1	585
GER4-Inner	89042	2120	30	1710	1770	1	1740
GER-HI-RG-01_Outer	89047	2390	30	2020	2100	1	2060
GER-HI-RG-01_Inner	89050	3200	35	2990	3070	1	3040
BC#5-1	99727	530	40	150	165	0.21	
				190	250	0.79	200
BC#5-2	99728	675	40	305	370	1	345
BC#5-3	99729	970	35	555	610	1	585
BC#5-4	99730	1170	35	705	760	1	730
BC#5-5	99731	1270	35	820	885	1	850
BC#5-6	99732	1540	35	1100	1165	1	1130
BC#5-7	99733	1910	35	1450	1515	1	1480
BC#5-8	99734	2050	35	1620	1690	1	1650
BC#5-9	99735	2280	45	1880	1940	1	1910
BC#5-10	99736	2360	35	1970	2040	1	2010
BC#5-11	99737	2480	35	2130	2220	0.99	2180
				2230	2230	0.01	
BC#5-12	99738	2480	40	2130	2220	0.99	2180
				2230	2230	0.01	
BC#5-13	99739	2550	35	2210	2220	0.06	
				2230	2230	0.02	
				2250	2310	0.92	2270
BC#5-14	99740	2600	35	2300	2330	1	2320

Table 5: Radiocarbon measurements, ages and growth rates of the black coral, *Antipathes dichotoma*

Sample ID	Genus	Depth (m)	Δ¹⁴C (‰)†		Calender age ¥		Lifespan		Growth Rate (μm/years)		Age linear§ growth rate	Age, growth§ band
			Inner	Outer	Inner Min/Max	Outer Min/Max	Min	Max	Min	Max		
BC #1	*Antipathes dichotoma*	50±5	143.0	69.4	1966/1972-1983	Post 1992,~1998	15	32	180	390	12	15
BC #2	*Antipathes dichotoma*	50±5	140*	87*	1966/1972-1983	Post 1992,~1995	12	29	470	1140	20	25
BC #3	*Antipathes dichotoma*	50±5	-57.1 ±3.6	106.5 ±4.3	pre 1957	1962/1992	93	109	130	150		

* BC#2 results are the average of two inner and outer ¹⁴C measurements as the sample appears to have two growth centers fused together.

† Post-bomb data are reflected by positive Δ¹⁴C values.

¥ AD years were determined by comparision with a Hawaiian surface water Δ¹⁴C time-sereis (see Fig. 8)

§ Age calculated from linear growth rates and on the relationship between grow rings/years and hieght (Grigg, 1976).