Extreme longevity in proteinaceous deep-sea corals

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Deep-sea corals are found on hard substrates on seamounts and continental margins worldwide at depths of 300 to ≈3,000 m. Deep-sea coral communities are hotspots of deep ocean biomass and biodiversity, providing critical habitat for fish and invertebrates. Newly applied radiocarbon age dates from the deep water proteinaceous corals *Gerardia* sp. and *Leiopathes* sp. show that radial growth rates are as low as 4 to 35 μm year^{-1} and that individual colony longevities are on the order of thousands of years. The longest-lived *Gerardia* sp. and *Leiopathes* sp. specimens were 2,742 years and 4,265 years, respectively. The management and conservation of deep-sea coral communities is challenged by their commercial harvest for the jewelry trade and damage caused by deep-water fishing practices. In light of their unusual longevity, a better understanding of deep-sea coral ecology and their interrelationships with associated benthic communities is needed to inform coherent international conservation strategies for these important deep-sea habitat-forming species.

age and growth rate | *Gerardia* sp. | *Leiopathes* sp. | radiocarbon | stable isotopes

Most of the interior of the global ocean remains unobserved. This leaves questions of trophic connectivity, longevity, and population dynamics of many deep-sea communities unanswered. Deep-sea megafauna provide a complex, rich, and varied habitat that promotes high biodiversity and provides congregation points for juvenile and adult fish (1–3). Here we present results on Hawai'ian live pruned and subfossil specimens of the octocoral *Gerardia* sp. and live-collected specimens of the deep-water black coral *Leiopathes* sp. (Antipatharia). Age and growth rates were determined using radiocarbon, while trophic level and food source assessment was made using stable isotopes (δ^{13}C and δ^{15}N).

Gerardia sp. is a colonial zoanthid with a hard skeleton of hard proteinaceous matter that forms tree-like structures with heights of several meters and basal diameters up to 10s of a centimeter. *Leiopathes* sp. also has a hard proteinaceous skeleton and grows to heights in excess of 2 m. In Hawai'ian waters, these corals are found at depths of 300 to 500 m on hard substrates, such as seamounts and ledges. *Gerardia* are also found in the Atlantic. *Leiopathes* is also ubiquitous and has been found south of Australia and throughout the equatorial and northwest Pacific. Corals used in this study were collected at the Makapuu and Lanikai deep-sea coral (DSC) beds (Oahu, HI), Keahole Point DSC bed (Big Island, HI), and Cross Seamount (18°40′N, 158°10′W).

Previous radiocarbon studies have shown that individual *Gerardia* colonies from the Atlantic and Pacific Oceans have life spans of ≈1,800 ± 300 (4) and 2,740 ± 15 years (5), respectively. These results contrast with a life span of 250 ± 70 years calculated for the same Atlantic specimen using amino acid racemization (6) and a maximum life span of 70 years for Hawai'ian *Gerardia* specimens, based on counts of what were assumed to be annual growth rings (7). The discrepancies between the radiocarbon, amino acid, and growth-band age estimates were attributed to the incorporation of ^{14}C-free (i.e., old) carbon into the *Gerardia* skeleton, thereby producing anomalously old ^{14}C ages (6, 7). ^{210}Pb measurements on 2 Atlantic *Leiopathes* specimens suggested life spans of ≈200 to ≈500 years and radial growth rates of ≈15 μm year^{-1} (8). A Hawai'ian *Leiopathes* specimen from the Makapuu DSC bed had a ^{14}C-estimated life span of 2,320 ± 20 years (radial growth rate ≈5 μm year^{-1}) (5). Resolution of the food (carbon) source and its impact, if any, on radiocarbon age estimates remains a contentious issue.

Results

Sources of Carbon. Carbon and nitrogen isotopic composition of living polyp tissue taken from specimens collected at the Lanikai DSC bed and Cross Seamount is compared with the isotopic ratios of water particulate organic matter (POM) (Fig. 1). The δ^{13}C of Hawai'ian particulate carbon at 150 m at Station ALOHA varies from –18 to –22 ‰ (average –21 ± 1 ‰; http://hahana.soest.hawaii.edu/hot/hot-dogs/) (9, 10), while the δ^{15}N of sinking particulate nitrogen range from +2 to +4 ‰ (11). δ^{13}C values of live polyp tissues from both *Gerardia* (10 specimens) and *Leiopathes* (2 specimens) from 2 different locations are similar. The average values (1 SD) for all *Gerardia* measurements are δ^{13}C: –19.3‰ (±0.8 ‰), δ^{15}N: +8.3 ± 0.3 ‰, carbon-to-nitrogen ratios (C:N) 3.3 ± 0.3. The average values for all *Leiopathes* are δ^{13}C: –19.7 ± 0.3 ‰, δ^{15}N: +9.3 ± 0.6 ‰, C:N 5.1 ± 0.1. The slight difference in δ^{15}N that we observe is not statistically significant because of the small *Leiopathes* sample size. Typical skeletal δ^{15}N (+8.7 ± 0.2 ‰) values of one *Gerardia* specimen are within the error of the tissue measurements, while the skeletal δ^{13}C (–16.3 ± 0.3 ‰) measurements are ≈3 ‰ more positive because lipids from the tissues are most likely not being incorporated into the skeleton. Assuming classic trophic level enrichments (12, 13), these results indicate *Gerardia* and *Leiopathes* are low-order consumers, primarily feeding upon freshly exported POM.

To confirm the trophic-level interpretation and acquire additional growth-rate estimates, we determined the ^{14}C content at 100-μm resolution on the outer few millimeters of a live-collected *Gerardia* branch from Cross Seamount, and the basal stalk of 1 live-collected *Leiopathes* from Lanikai, Hawai'i. Radiocarbon measurements were also done on living polyp tissue samples from both specimens. Polyp tissue Δ^{14}C values are similar to surface water dissolved inorganic carbon Δ^{14}C values, and proteinaceous skeleton Δ^{14}C values over the outermost 3 mm of the *Gerardia* branch are indistinguishable from a reconstruction of the Hawai'ian surface-water ^{14}C history (1950–1990) derived from a shallow-water scleractinian coral (Fig. 2*A*). Most significantly, the *Gerardia* skeleton captures the surface-ocean uptake and redistribution of "bomb"-^{14}C with little to no

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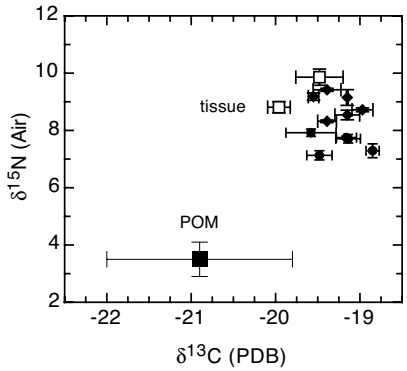

Fig. 1. Carbon and nitrogen isotopic composition of outermost living polyp tissue (*solid symbols*) of *Gerardia* (10 specimens) from the Lanikai DSC bed (*closed circles*), Cross Seamount (*closed diamonds*), and *Leiopathes* (2 specimens) from the Lanikai and Makapuu DSC beds (*open squares*). Error bars reflect the SD of 3 repeat analyses. The average $\delta^{13}C$ (http://hahana.soest.hawaii.edu/hot/hot-dogs/) (9, 10) and $\delta^{15}N$ (11) of Hawai'ian POM (*closed square*) at 150 m at Station ALOHA is also shown. $\delta^{13}C$ error bars reflect the SD of monthly cruise measurements from March 2000 to December 2007, and the $\delta^{15}N$ error bars reflect the SD of annual particulate export flux from 1991 to 2000 (11).

amplitude attenuation (see Fig. 2*A*). Two wafer-thin (≈10 μm) flakes from the outermost skeleton of *Leiopathes* also contain bomb-^{14}C. When the sampling interval is increased to 100 μm, we recover an averaged value that is less than modern and does not exhibit ^{14}C enrichment. ^{14}C ages from 100-μm increments over the outermost 0.9 mm of the *Leiopathes* skeleton increase to ≈700 cal years (1,050 ± 45 ^{14}C years) (Fig. 3). This equates to ≈80 years of averaging in each 100-μm increment. The *Leiopathes* and *Gerardia* isotope results suggest that these organisms are acquiring their tissue and skeletal carbon from surface-water organic matter after relatively rapid transport to depth. The radiocarbon results also imply little to no carbon turnover of the proteinaceous skeleton and also demonstrate that ^{14}C-derived age estimates of *Gerardia* sp. and *Leiopathes* are unaffected by the animals feeding upon old resuspended sedimentary carbon.

Ages and Growth Rate. Coral ages and growth rates are acquired by 2 different methods: identification of the bomb-spike as a local radiocarbon inflection point that is assigned to the year 1957, and conventional ^{14}C age based on radioactive decay. Radiocarbon analyses and conversion of ^{14}C-years to calendar years (14) of outer and inner samples from a suite of cross sections cut from subfossil *Gerardia* specimens allow us to calculate radial growth rates and longevity of a larger sample pool. The long-term radial growth rate of the live-collected *Gerardia* branch shown in Fig. 2*A* is 35 μm year^{-1}, similar to the rate derived from the 1957-bomb ^{14}C inflection point at 2.1 mm (45 μm year^{-1}). This branch spans ≈315 years (585 ± 30 ^{14}C years). The average radial growth rate from the larger sample pool is 36 ± 20 μm year^{-1} (1 SD, n = 17) with a range of 11 to 85 μm year^{-1} [Fig. 2*B* and supporting information (SI) Table S1]. The average life span of the analyzed specimens is 970 years and ranges from ≈300 years for a small branch (radius, 11 mm) to ≈2,700 years (radius, 38 mm) (Fig. 4). These ages indicate a longevity that far exceeds previous estimates based on amino acid racemization and growth-band counting (6, 7). We note that many of the subfossil *Gerardia* samples that we have analyzed are branches, not the oldest portions of the colony, and thus the ages may not document the maximum potential age of this species.

Three live-collected specimens of *Leiopathes* were also radiocarbon dated along radial transects of inner to outer samples.

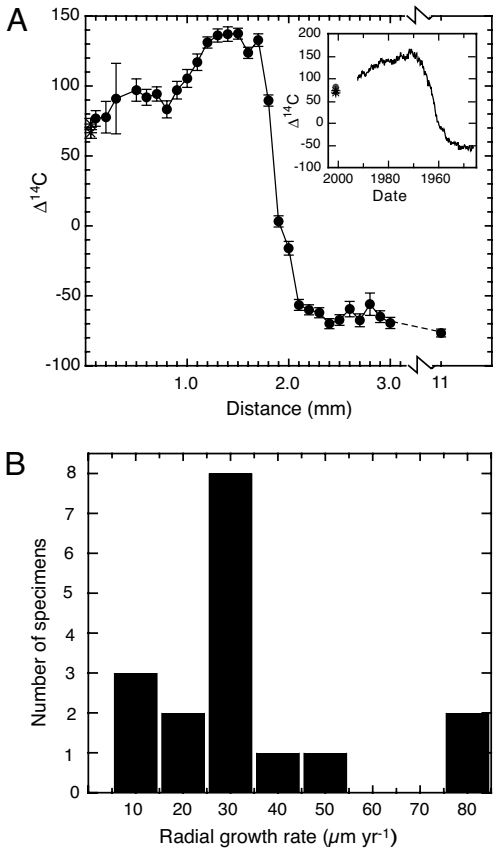

Fig. 2. *Gerardia* sp. ^{14}C results. (*A*) Radiocarbon values of samples collected by microtome over the outermost 3 mm from a radial cross-section transect (*solid symbols*) and tissue (*stars*) from a pruned branch of a living *Gerardia* sp. The Gerardia^{14}C profile is indistinguishable from surface-water $\Delta^{14}C$ history derived from a *Porites* coral (drilled in 1990) from the west side of the Big Island, HI (*inset*), and a discrete water sample collected at NEHLA, Keahole Point (Kona HI) in 2005. Center age is 315 calendar years (585 ± 30 ^{14}C years). Error bars are 1 SD. (*B*) Radial growth rate (μm year^{-1}) determined on 17 individuals. The average radial growth rate is 36 ± 20 μm year^{-1} (1 SD, n = 17).

The center age of the cross-sectional disk taken from the stalk of the specimen discussed above is 4,200 ± 70 calendar years B.P. (4,105 ± 40 ^{14}C years) (see Fig. 3). The center of the basal attachment structure, some ≈8 cm below the cross-sectional disk on the stalk, is 4,265 ± 44 calendar years (4,150 ± 35 ^{14}C years). The other 2 *Leiopathes* colonies had ages of 350 calendar years B.P. (630 ± 35 ^{14}C years) and 2,370 calendar years (2,600 ± 35 ^{14}C years) (see Fig. 4 and Table S1). The radial growth rates of the 3 samples are <5 μm yr^{-1}. The 2,370-year-old specimen had a faster initial radial growth rate of ≈13 μm yr^{-1} over the inner-most 5 mm of a 13-mm radial ^{14}C transect, supporting faster initial growth (Fig. 5). Higher initial growth rates could be advantageous for a colony to establish itself. These results suggest that height may not be proportional to age for *Leiopathes*.

Discussion

Interest in conservation and protection of DSCs, resulting from their potentially long life spans, the recognition of their ecological importance, as well as threats posed by fishing practices (1, 15, 16) has increased. The extremely long life spans of *Gerardia* and *Leiopathes* shown here reinforce the need for further protection of DSCs and DSC beds. These results show that *Leiopathes* is the oldest skeletal-accreting marine organism known and, to the best of our knowledge, the oldest colonial

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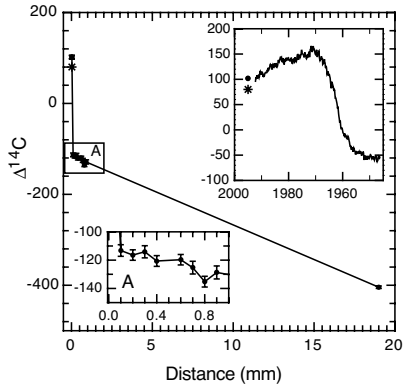

Fig. 3. *Leiopathes* ^{14}C results. Radiocarbon values of samples collected by microtome over the outermost 0.9 mm of a radial cross-section (*solid symbols*) and tissue (*stars*) from the stalk of a living *Leiopathes.* Two outer-most flakes (*solid symbols*) and tissue (*stars*) are indistinguishable from the expected surface-water Δ^{14}C based on the extrapolation of the *Porites* coral Δ^{14}C record (*inset*, citation). The center age is 4,200 ± 70 calendar years B.P. (4,105 ± 40 ^{14}C years). Error bars are 1 SD.

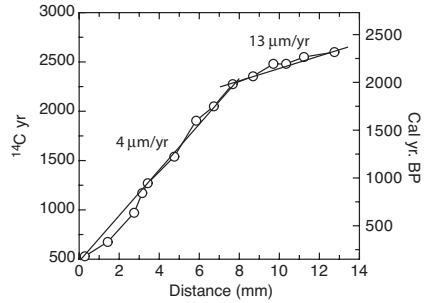

Fig. 5. Radiocarbon radial transect of specimen BC-RD97–05 (5) showing a faster radial growth rate of 13 μm year^{-1} over the initial 400 years (inner-most 5.1 mm) compared to the much slower growth rate of 4 μm year^{-1} over the last 1,960 years (outer most 7.7 mm). The age of the center of the basal attachment structure of specimen (Lan04-Leio1), some ≈15 cm below the cross-sectional disk on the stalk is 4,265 ± 44 years (4,150 ± 35 ^{14}C years), within the error of the age established for the center of the stalk discussed in the main text (4,200 ± 70 years).[Reproduced with permission from ref. 5 (Copyright 2006, Inter-Research Science).]

organism yet found. Based on ^{14}C, the living polyps are only a few years old, or at least their carbon is, but they have been continuously replaced for centuries to millennia while accreting their underlying proteinaceous skeleton.

Emergent structure-forming deep-sea megafauna increase the complexity of seafloor habitat and provide shelter and feeding areas for commercial and noncommercial fish species and their prey (2, 17, 18). *Gerardia* and *Leiopathes* are two of the largest megafauna invertebrates in Hawai'ian DSC beds. They have clear associations with a diverse assemblage of invertebrates and fish that, in turn, make these communities prime foraging targets for Hawai'ian monk seals (19). Activities that contact the seafloor, of which bottom trawling is the most significant, damage DSC beds (20–22). Hawai'ian DSCs face direct threats via harvesting for jewelry (7) and from commercial fishing, as by-catch from trawling and entanglement and damage associated with lines and gear. The extreme longevity of *Gerardia* and *Leiopathes* challenges the concept that these species are renewable in the context of fisheries management. In addition, damage to these coral species has far-reaching implications for biodiversity, ecosystem structure, and functional extinctions in the deep sea (23).

Quantitative information regarding symbiosis between free-swimming fish, other invertebrates, and *Gerardia* and *Leiopathes* is lacking. During our own submersible dives and viewing dive tapes of other dives from nearby locations, we observe an increase in fish and invertebrate biomass and diversity within and adjacent to colonies of *Gerardia* and *Leiopathes*. Structure-forming fauna, such as *Gerardia* and *Leiopathes*, in the deep-sea have a similar ecological functional purpose as their shallow-water reef-building counterparts. We posit that the newly discovered longevity of poorly studied yet widely distributed deep-sea organisms, such as proteinaceous corals, provides an increased impetus for the development of a coherent and effective international conservation strategy, particularly with regards to deep-sea trawling and activities that physically disturb the benthic environment.

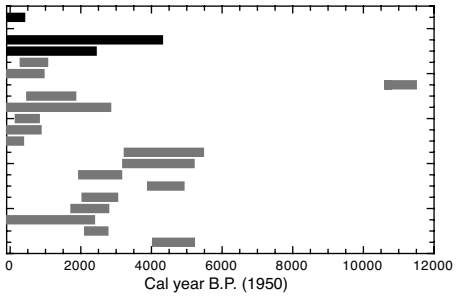

Fig. 4. Life spans of *Gerardia* sp. and *Leiopathes* during the Holocene. Longevity estimates (age-range) as a function of calendar age (Cal year B.P.) for *Gerardia* sp. (*gray*) and *Leiopathes* (*black*). The average life span of the *Gerardia* sp. specimens is 970 years and ranges from ≈300 years to ≈2,700 years. Overlapping specimens in the same manner as tree ring studies will allow continuous records going back ≈5,000 years.

In addition to direct and indirect threats of physical disturbance at depth, the tight coupling observed between DSCs and surface ocean primary production implies that these communities can be influenced by natural and anthropogenic changes in surface ocean conditions. Predicted surface-water impacts, such as ocean acidification, warming, and altered stratification, can all influence community structure and rates of primary production, both of which may influence the delivery of food to the deep sea. The potential effects of human activities not only transgress international and domestic boundaries but conventional management strategies. To be effective and successful, management and conservation policies require a transboundary ecosystem-based approach that considers impacts from the surface ocean to depth.

United States fisheries management law has established a legal trigger for fisheries management measures to protect seafloor habitats based on criteria of whether the effects of fishing are "more than minimal and not temporary" (24). Recruitment, growth rate, and longevity of these and other DSC ultimately determine the rate at which these habitats may recover from damage (25). Given that longevity is one of the most important factors in determining habitat recovery time, the loss of proteinaceous species such as those described here cannot be considered temporary on human time scales. Growth rates and longevity of DSC also indicate the extent to which they can be harvested. In the Hawai'ian precious coral fishery, growth rates for *Gerardia* suggest that current maximum sustainable yield limits are grossly overestimated (26). We suggest that any future harvesting be considered in the context of a nonrenewable resource framework.

In the United States economic zone, and as a result of recognizing their importance to deep-sea ecosystems and habitat, DSC beds were accorded greater protection during the

2006/2007 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act (MSA). Although they are considered by many of the nation's Fisheries Management Councils to constitute "essential fish habitat," the use of this designation has varied widely among councils and in some cases has been challenged because of the difficulty of proving this attribute. The reauthorized MSA no longer requires a rigorous determination as an essential fish habitat as a trigger for protective measures. An increasing number of known DSC localities are now being designated as "Habitat Areas of Particular Concern" by the Fisheries Management Councils. Our work establishing the heretofore unknown great longevity of keystone members of DSC communities suggests an even more urgent need to accelerate the pace of governance and protection by the Fisheries Management Councils and local, state, and federal management authorities.

Stable isotope and radiocarbon analysis of living polyps (coral tissues) support the tenet that *Gerardia* and *Leiopathes* feed primarily on labile and therefore ^{14}C-young, particulate organic carbon. Analyses of living and subfossil *Gerardia* specimens indicate radial growth rates of 36 $\pm$ 20 μm year^{-1} and life spans of up to at least 2,700 years. These results greatly expand on and support previous life span and radial growth rate estimates (4, 5). *Leipathes* has even slower growth rates ($<$5 μm year^{-1}) and the longest known life span of any skeletal accreting marine organism. Longevity and slow growth are not unknown in deep-sea organisms. Our results suggest the need for new approaches and research directed toward a better understanding of deep-sea marine ecosystems that form in direct association with organisms of great longevity in the face of increased direct (physical habitat disturbance) and indirect (changes in ecosystem primary productivity, climate-related changes, or ocean acidification) threats.

Materials and Methods

Sample Collection. Hawai'ian *Gerardia* sp. and *Leiopathes* sp. samples from 400 to 500 m water depth were collected during the 2004 field season using the NOAA/HURL Pisces V submersible. *Gerardia* samples include pruned branches from living specimens, subfossil basal attachment stumps, and fallen branches. The 3 *Leiopathes* specimens were collected live. The identification of the specimens as *Leiopathes* were made on the basis of branch pattern, size, and lack of spines on the skeleton, as well as comparison with photos of specimens of *Leiopathes* identified in the HURL specimen identification guide. While the species identification in the identification guide are reviewed by other, more expert researchers, many DSC genuses, including *Leiopathes*, require significant revision. Until such revisions are complete, our identification should be treated as a tentative identification. Upon recovery and for the few samples from live individuals, the external polyps and tissue were removed and subsamples were air dried before transfer to microcentrifuge vials. Upon removing the tissue layer, the proteinaceous skeleton was washed with sea- and fresh water and allowed to air dry on deck.

Stumps and branches were cut into $\approx$0.7-cm thick cross-section disks. *Gerardia* disks taken closest to the basal attachment often include a center carbonate core from the *Isididae* (bamboo) coral that the *Gerardia* initially settled on and used as a preliminary attachment until it grew down and over it, thereby attaching itself directly to the substrate. Cursory sampling of the skeleton was done by microdrilling center (inner), middle, and outer samples from across radial transects. In addition, we extracted a small $\approx 2 \times 2$-mm rod from the basal cross-section from a live-collected *Gerardia* branch and from the stalk of a live-collected *Leiopathes* from the Lanikai DSC bed (Oahu, HI). The outer 1 to 3 mm of each rod was microtomed in 100-μm increments for ^{14}C analysis. To do this, the rod was frozen into a sample holder using deionized water, with the outer 3 mm of the rod extending beyond the end of the sample holder. Sampling was done with a cryogenic microtome to ensure the sample remained frozen. Sampled material was collected and allowed to dry before any further work was done.

Analytical Methods. Stable carbon and nitrogen isotopic analyses were completed at the Stanford University Stable Isotope Lab on dried and ground polyp/tissue using a Finnigan MAT Delta plus connected to a Carlo Erba NA1500 Series II elemental analyzer. Results are reported in conventional parts per mil notation versus V-PDB for δ^{13}C and air for δ^{15}N. Analytical error is $\pm$ 0.10 ‰ and $\pm$ 0.14 ‰ respectively. For *Leiopathes*, 3 repeat analyses were done on tissue samples from 2 specimens (n = 6); for *Gerardia*, 3 repeat analyses were done on 10 specimens as well as 3 repeat analyses of tissues samples taken the tips and bases of 1 specimen (n = 33). Repeat analyses of tissue samples from the tip (δ^{15}N 7.13 $\pm$ 0.16 ‰; δ^{13}C –19.48 $\pm$ 0.15 ‰; C:N 3.55 $\pm$ 0.04; n = 3) and tissue samples from the base (δ^{15}N 7.75 $\pm$ 0.05 ‰; δ^{13}C –19.16 $\pm$ 0.12 ‰; C:N 3.35 $\pm$ 0.03; n = 3) are within the uncertainty of all specimens measured. The SD is reported for the average of all of the analyses; n = 6 for *Leiopathes* and n = 33 for *Gerardia*.

For all radiocarbon samples, proteinaceous and tissue samples were treated with weak HCl, copiously rinsed with miliQ water, and dried. Samples were converted to CO_2 via sealed tube combustion, and upon cyrogenic purification the CO_2 was reduced to graphite in the presence of iron catalyst and a stoichiometric excess of hydrogen. Graphite targets were analyzed at the Center for Accelerator Mass Spectrometry. Radiocarbon results are presented as Δ^{14}C (‰) and conventional ages (27) and include a δ^{13}C correction and a blank subtraction based on analysis of ^{14}C-free coal. Analytical uncertainty for all but the smallest microtome sample (because of loss during handling: $\leq$19 μg of carbon) was 3 to 4 ‰ or for Holocene samples or 30 to 40 ^{14}C years. Conventional ^{14}C ages are converted to calendar years using a reservoir age of 380 ^{14}C years (ΔR of –28 $\pm$ 4 ^{14}C years) (28) and Calib v5 (29, 30).

We compare our microtome ^{14}C "time-series" to a reconstruction of surface-water Δ^{14}C derived from a *Porites* coral (drilled in 1990) from the west side of the Big Island (28). The *Porites* age model utilizes the seasonal sea-surface temperature cycle recorded in δ^{18}O coral and [Sr/Ca] coral.

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1. Freiwald A, Fossa JH, Grehan A, Koslow T, Roberts JM (2004) *Cold-Water Coral Reefs* (UNEP-WCMC, Cambridge UK).
2. Husebo A, Nottestad L, Fossa J, Furevik D, Jorgensen S (2002) Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471, 91–99.
3. Smith CR, Levin LA, Koslow JA, Tyler PA, Glover AG (2008) in *Aquatic Ecosystems: trends and global prospects*, ed. Polunin N (Cambridge University Press, Cambridge)..
4. Druffel ERM, et al. (1995) *Gerardia*: Bristlecone pine of the deep-sea? *Geochim Cosmochim Acta* 59:5031–5036.
5. Roark EB, Guilderson TP, Dunbar RB, Ingram BL (2006) Radiocarbon based ages and growth rates: Hawaiian deep sea corals. *Mar Ecol Prog Ser* 327:1–14.
6. Goodfriend GA (1997) Aspartic acid racemization and amino acid composition of the organic endoskeleton of the deep-water colonial anemone *Gerardia*: Determination of longevity from kinetic experiments. *Geochim Cosmochim Acta* 61:1931–1939.
7. Grigg RW (2002) Precious corals in Hawaii: Discovery of a new bed and revised management measures for existing beds. *Marine Fisheries Review* 64(1):13–20.
8. Williams B, Risk MJ, Ross SW, Sulak KJ (2006) Deep-water antipatharians: Proxies of environmental change. *Geology* 34:773–776.
9. Druffel ERM, Bauer JE, Williams PM, Griffin S, Wolgast D (1996) Seasonal variability of particulate organic radiocarbon in the Northeast Pacific Ocean. *J Geophys Oceans* 101:20543–20552.
10. Hermes PJ, Benner R (2002) Transport and diagenesis of dissolved and particulate terrigenous organic matter in the North Pacific Ocean. *Deep-Sea Res I* 49:2119–2132.
11. Dore JE, Brum JR, Tupas LM, Karl DM (2002) Seasonal and interannual variability in sources of nitrogen supporting export in the oligotrophic subtropical North Pacific Ocean. *Limnol Oceanogr* 47:1595–1607.
12. DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351.
13. Rau GH (1982) in *Coastal Research Project Biennial Report for the Years 1981–1982*, ed. Bascom W. (Southern California Coastal Water Research Project, Long Beach, CA), pp. 143–148.
14. Stuiver M, Braziunas TF (1993) Modeling atmospheric ^{14}C influences and ^{14}C ages of marine samples to 10,000 BC. *Radiocarbon* 35:137–189.
15. Roberts S, Hirshfield M (2004) Deep sea corals: out of sight, but no longer out of mind. *Frontiers in Ecology and the Environment* 2:123–130.

16. Shester G, Warrenchuk J (2007) in *Conservation and Adaptive Management of Seamounts and Deep-Sea Coral Ecosystems*, eds. George RY, Cairns SD (Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida).
17. Krieger KJ, Wing BL (2002) Megafauna associations with deepwater corals (*Primnoa* spp.*)* in the Gulf of Alaska. *Hydrobiologia* 471:83–90.
18. Stone RP (2006) Coral habitat in the Aleution Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25:229–238.
19. Parrish FA, Abernathy K, Marshall GJ, Buhleier BM (2002) Hawaiian monk seals (*Monachus schauinslandi*) foraging in deep-water corals beds. *Marine Mammal Science* 18:244–258.
20. Auster PJ, Langton RW (1999) The effects of fishing on fish habitat. Fish habitat: essential fish habitat and rehabilitation. *Am Fish Soc Symp* 22:150–187.
21. National Research Council (2002) Effects of trawling and dredging on seafloor habitat. Ed. National Research Council, (National Academy of Sciences, Washington, DC) pp 1–126.
22. Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology* 12:1180–1197.
23. Thrush S, Dayton PK (2002) Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Ann Rev Ecol Syst* 33:449–473.
24. National Marine Fisheries Service (2002) EFH Final rule 600.10 in *Federal Register* (National Oceanic and Atmospheric Administration, Department of Commerce, Silver Spring, MD).
25. National Marine Fisheries Service (2005) *Alaska Regional Essential Fish Habitat Final Environmental Impact Statement.* Appendix B: Evaluation of fishing activities that may adversely affect essential fish habitat. Ed. Department of Commerce, (National Oceanic and Atmospheric Administration, Silver Spring, MD).
26. Western Pacific Regional Fishery Management Council (2001) *A Framework Adjustment to Measures in the Fishery Management Plan for the Precious Coral Fisheries of the Western Pacific Region: Regarding harvest quotas, definitions, size limits, gear restrictions, and bad classifications*. (Western Pacific Regional Fishery Management Council, Honolulu, HI), pp 1–71.
27. Stuiver M, Polach HA (1977) Discussion and reporting of ^{14}C data. *Radiocarbon* 19:355–363.
28. Druffel ERM, et al. (2001) Changes of subtropical North Pacific radiocarbon and correlation with climate variability. *Radiocarbon* 43:15–25.
29. Hughen KA, et al. (2004) Marine04 Marine radiocarbon age calibration, 26–0 ka BP. *Radiocarbon* 46:1059–1086.
30. Stuiver M, Reimer PJ (1993) Extended 14C database and revised CALIB V5.0 radiocarbon calibration program. *Radiocarbon* 35:215–230.