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Authors

Druffel, Ellen RM
Griffin, Sheila
Witter, Amy
et al.

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LETTER

Gerardia: Bristlecone pine of the deep-sea?

Ellen R. M. Druffel,[1] Sheila Griffin,[1] Amy Witter,[2] Erle Nelson,[3] John Southon,[4]
Michaele Kashgarian,[4] and John Vogel[4]

[1]University of California, Department of Earth System Science, Irvine, CA 92717, USA
[2]University of California, Facility for Advanced Instrumentation, Davis, CA 95616, USA
[3]Simon Fraser University, Department of Archeology, Burnaby, British Columbia V5A 1S6, Canada
[4]Center for AMS Research, Lawrence Livermore National Lab, Livermore, CA 94550, USA

Abstract—We measured carbon isotope abundances in the layered, proteinaceous skeleton of a zoanthid *Gerardia* collected from 620 m depth off the Little Bahama Bank (27°N, 79°W). The $\Delta^{14}C$ values decreased from $-76‰$ in the outer growth edge to an average of $-267‰$ in the center of three portions of the skeleton. These $\Delta^{14}C$ data suggest an age for this living organism of 1800 ± 300 years. The possibility that the large decrease in $\Delta^{14}C$ reflects the gradual input of bomb ^{14}C over the entire growth of the organism is inconsistent with the post-bomb $\Delta^{14}C$ values obtained for the most recent growth tips. If the age estimate of two millennia is correct, it may be the longest-lived animal yet observed in the ocean. *Gerardia* may serve as a long-lived recorder of ocean chemistry, similar to the Bristlecone pine tree that has served as a millennial-timescale recorder for atmospheric $^{14}CO_2$ (Suess, 1980) and climate. In particular, there is potential for *Gerardia* to serve as a millennial-scale integrator of upper ocean particle flux, and possibly reveal past changes in the productivity of the surface ocean.

1. INTRODUCTION AND BACKGROUND

Little is known about the growth of many organisms that live in the deep-sea, largely owing to their remoteness from observation. Growth rate measurements available for deep-sea corals and gorgonians are orders of magnitude lower than those for surface-dwelling species. Radiocarbon, excess ^{210}Pb, and $^{239,240}Pu$ measured in a specimen of the deep-sea precious coral *Corallium niobe* demonstrated that the trunk growth rate was $0.11 \pm .02$ mm/y and that it grew during a 200 year period (Druffel et al., 1990). In contrast, surface-dwelling corals grow at a linear extension rate of 2–25 mm/y. A tagging study of the slow-growing, black corals *Antipathes dichotoma* and *A. grandis* from Hawaii revealed a significant correlation between the height of the colony and its age (Grigg, 1977). In a study of a deep-sea solitary coral *Bathypsammia tintinnabulum* from the Blake Plateau, carbon and oxygen isotopic ratios in growth rings approached equilibrium values with seawater with decreasing growth rate (Emiliani et al., 1978).

The organism studied here, *Gerardia*, is a colonial zoanthid sea anemone, not a coral. *Gerardia* was earlier classified with *Antipatharia*, but the different structure of its polyps led researchers to reclassify it with another group of Coelenterata called the Zoanthidea. The colony initially encrusts a stem of a Gorgonia, and then forms a hard organic skeleton that grows to great size. A specimen collected from the Mediterranean Sea was reported to have been 2 m high, with a main trunk diameter of 14 cm (Bell, 1891).

The skeleton of *Gerardia* is a hard, dense, layered proteinaceous material that more closely resembles a modern plastic than a natural tissue. This skeletal form is unique among skeletal accreting animals. Also, *Gerardia savaglia* (a Mediterranean species) has been found to contain large amounts of an ecdysterone, ajugasterone-C, which was previously thought to be exclusively a terrestrial plant product (Vallentyne, 1964). *Gerardia* is the first animal and the only marine organism observed thus far to produce this steroid.

Our previous study of *Gerardia* (Griffin and Druffel, 1989) demonstrated that $\Delta^{14}C$ measurements of whole stem samples with diameters greater than 1.2 mm revealed $\Delta^{14}C$ values that were equal to or lower than those of pre-bomb ($<$ AD 1950) temperate, surface ocean carbon ($-50 \pm 20‰$; Broecker et al., 1960; Druffel and Linick, 1978). The $\Delta^{14}C$ value for the thinnest stems or tips ($+58 \pm 13‰$; diameter $\leq$ 1.2 mm) was clearly reflective of bomb-produced carbon and illustrated that the outer 0.6 mm of stem growth had formed during the past 30 years. As bomb radiocarbon had penetrated neither the dissolved inorganic carbon (DIC) nor the dissolved organic carbon (DOC) pools at 620 m depth in the northwestern Atlantic by 1982 (Ostlund and Grall 1987; Druffel et al., 1992), the presence of bomb radiocarbon in *Gerardia* proves that surface-derived, particulate organic carbon (POC) is a major source of carbon to the skeleton. It is believed that organic-rich particles are the food source for deep-sea zoantharia and corals (T. Bayer, pers. commun., 1984).

In this study, we reexamined three *Gerardia* specimens in order to determine the age of these organisms. We report ^{14}C age estimates based on beta-counting and AMS (accelerator mass spectrometry) radiocarbon measurements.

2. MATERIALS AND METHODS

We collected three specimens of *Gerardia* from 610–630 m depth atop lithoherms (30-m high deep-sea mounds) during three dives in

the Florida Straits (27°N, 79°W) using the Deep Submergence Vehicle *Alvin* in October 1982. All three samples were collected within a 4 km radius. The water temperature at the collection sites was between 11.9 and 12.8°C. Samples were frozen and returned to the lab. The yellow polyps on the skeletal surface of these branching zoanthids were removed using a 50% solution of bleach and a small brush. Specimens were air or oven dried and stored in plastic bags at room temperature. The trunk of specimen 1273-2 (27 mm diameter) was sectioned by peeling off nine layers, 1–2 mm in thickness, with a scalpel. From a large branch of this specimen (22 mm diameter) we analyzed four layers that ranged from 0.1 to 1.5 mm thickness; from its base (35 mm thick, located below the trunk and affixed to the carbonate lithoherm) we sectioned five layers (0.5 to 1.0 mm thick). From a medium-sized branch (13 mm diameter) of a separate *Gerardia* specimen (1274-2), two layers of 0.8 and 0.5 mm thickness were taken. Tips from a third specimen sampled previously (1278-3) (Griffin and Druffel, 1989) were reanalyzed for ^{14}C; the diameters of these tips ($\leq$1.0 mm) were slightly smaller than those of the sample previously analyzed (WH-202 dia. $\leq$ 1.2 mm, Table 1).

The radiocarbon analyses reported in Table 1 were conducted by two methods, beta counting and AMS techniques. Trunk layers 1 through 5 (1–2 g) were previously oxidized in an oxygen stream to CO_2 and converted to acetylene for radiocarbon analyses using gas proportional counting techniques (Griffin and Druffel, 1985). Subsamples of trunk layers 6 through 9 (5–10 mg) and the branch samples and tips were combusted at 850°C in evacuated, closed, quartz tubes with CuO and silver foil and the resultant CO_2 was converted to graphite for radiocarbon analyses by AMS techniques (Vogel et al., 1987) at the LLNL Center for AMS Research or McMaster University AMS Facility. Stable carbon isotope measurements were made on the reburned acetylene gas or the CO_2 obtained from closed-tube combustion on a VG 602E Micromass isotope ratio mass spectrometer (Griffin and Druffel, 1985).

Carbon/nitrogen ratios were determined using a Carlo-Erba CHN Analyzer, and amino acid analyses of the trunk layers were performed on a Maxima 820 Waters work station with a Waters 484 Absorbance Detector. The Pico-Tag method was used according to standard techniques (Cohen et al., 1989).

3. RESULTS

3.1. Radiocarbon Measurements

The Δ^{14}C values obtained for layers peeled off the trunk, branches, and base and for the tips are shown in Fig. 1 and listed in Table 1. Trunk Δ^{14}C values display a monotonic decrease from $-76 \pm 4\%o$ in outermost layer 1 to $-249 \pm 4\%o$ in layer 7 (an average of 9.5 mm from the edge). The three innermost layers (7–9) have Δ^{14}C values that are equal within 3σ uncertainty, suggesting that the radial growth rate was significantly higher during the earlier stages of the animal's life. A least-squares fit of the Δ^{14}C values for the outer seven layers reveals a decrease of $211 \pm 8\%o$ from the outer trunk edge to the inside of layer 7 (10.5 mm).

Δ^{14}C values for four layers from the large branch show a decreasing trend from $-58 \pm 6\%o$ in the outermost layer to $-294 \pm 5\%o$ in the center portion (9.5–11.0 mm radius). This reflects a decrease of $236 \pm 11\%o$ in Δ^{14}C. The value for the outermost layer of the large branch is higher than that for the trunk, owing to the fact that it is much thinner (0.1 mm thick), and better reflects the Δ^{14}C of the most recently accreted material (including some bomb ^{14}C).

Five layers of the base of the same specimen (1273-2) display a similar decrease in Δ^{14}C values. A monotonic decrease is observed from $-68 \pm 6\%o$ in the outer 0.8 mm to $-257 \pm 5\%o$ in the bottom layer (30.7–31.5 mm). This decline of $189 \pm 11\%o$ is within 2σ uncertainty of that found for the

trunk ($211 \pm 8\%o$). Δ^{14}C values for an outer and intermediate layer of a medium-sized branch from a separate specimen (1274-2) were $-66\%o$ and $-205\%o$, respectively. It is apparent from these data that outer layers for separate specimens had similar Δ^{14}C values, which is important when we attempt to establish the overall age for this animal.

The Δ^{14}C value for the tips sample from a third specimen (1278-3) was $+105 \pm 9\%o$. This Δ^{14}C value is higher than that previously reported (Griffin and Druffel, 1989) for a tips sample from the same specimen ($+58 \pm 13\%o$). This tips sample (Table 1) was slightly smaller in average diameter (1.0 mm) than that reported earlier (1.2 mm) and is more representative of the most recent Δ^{14}C value for the source carbon to the growth surface. We assume that the Δ^{14}C value for the tips of specimen 1273-2 would have been the same as those reported for 1278-3, as they both had healthy polyps growing on their skeletons.

3.2. Physical Structure of *Gerardia*

Scanning electron microscopy (SEM) was used to make detailed scans of a thin section from the *Gerardia* trunk (1273-2). Small bands of thicknesses 5–10 μm are observed in Fig. 2 near the center (100 μm scale shown). It is apparent that skeletal growth is by periodic deposition of a thin layer of protein. If these depositions are periodic, we can estimate an age for this animal.

3.3. Chemistry of *Gerardia*

The skeletal material has a C/N ratio of 2.8–3.0 (by weight), a value typical for other structural proteins such as bone collagen. The similarity extends beyond elemental composition. Of the eighteen amino acids detected in the amino acid analyses, $27.2 \pm 2.7\%$ of the amino acid residues are glycine; alanine is $9.7 \pm 0.7\%$. The corresponding values for bone collagen are about 33 and 11%, respectively. However, unlike collagen, the *Gerardia* protein does not contain a large amount of hydroxyproline, but a very unusual concentration of histidine ($18.3 \pm 3.0\%$). There are lesser amounts (4–6%) of the amino acids proline, tyrosine, cysteine, and leucine and trace amounts (<4%) of eleven others.

The glycine and perhaps the alanine provide structural strength to this skeleton by tightly binding the protein polymers through hydrogen-bonding, allowing *Gerardia* to withstand the strong currents (1–3 knots) surrounding the lithoherms in the Florida Current. The amino acid composition of a brittle star, another deep-sea organism, is similar to the *Gerardia* skeleton, again with the exception of histidine which is abundant in *Gerardia* but absent in brittle star.

We can only speculate on the reason for this high histidine concentration. Histidine is unusual, in that it is the only amino acid with a side-chain which can be variably charged under normal biological conditions, such that it can act as a catalyst in enzyme synthesis (Zubay, 1988). Perhaps the outer layer of the skeleton serves a metabolic as well as a structural role.

4. DISCUSSION

To obtain a radiocarbon age estimate for these *Gerardia* specimens we must assess the possible sources of carbon

TABLE 1. $\Delta^{14}C$ and $\delta^{13}C$ results for samples obtained from the three specimens of *Gerardia*. Also listed are glycine percent carbon values for the inner part of the trunk. ^{14}C ages are calculated using the true ^{14}C half-life of 5730 years. Corrected ^{14}C ages (*) are calculated using a reservoir age for surface ocean (ΔR) of 404 years, as recommended by Stuiver et al. (1986). ^ Indicates sample nos. for $\Delta^{14}C$ results obtained by gas counting at WHOI (Griffin and Druffel, 1989). ** Indicates AMS samples run at the McMaster Facility.

Layer No.	Average mm from growth edge	Thickness of layer (mm)	UCI#, AMS#	Δ14C (o/oo)	±	14C age (y BP)	Corrected 14C age * (y BP)	δ13C (o/oo)	Glycine (% of amino acids)	±
Specimen 1273-2										
Trunk										
1	0.5	1	197^	-76	4.0	700	295	-16.2		
2	1.5	1	198^	-96	3.0	880	475	-16.3		
3	2.5	1	199^	-111	4.0	1020	615	-15.9		
4	3.8	1.8	200^	-142	3.0	1310	905	-16.0		
5	5.6	1.7	201^	-189	3.0	1780	1380	-16.0		
6	7.5	2	**	-223	6.0	2140	1740		22.9	2.7
7	9.5	2	**	-249	4.0	2420	2010		26.8	2.7
8	11.5	2	**	-239	5.0	2310	1900		26.7	2.7
9	13.0	1	**	-257	6.0	2510	2100		29.5	2.7
Large Branch										
1	0.1	0.1	440, 12000	-58	6	450	45	-15.9		
2	0.25	0.5	441, 12001	-69	8	550	145	-15.7		
3	5.8	0.5	437, 11998	-231	5	2120	1720	-16.2		
4	10.2	1.5	442, 12002	-294	5	2820	2420	-16.6		
Base										
1	0.4	0.8	433, 11994	-68	6	520	120	-16.1		
2	3.3	0.5	436, 11997	-92	6	750	340	-16.2		
3	12.8	0.5	435, 11996	-170	6	1470	1070	-16.2		
4	21.0	1.0	434, 11995	-207	6	1860	1460	-16.2		
5	31.1	0.8	432, 11993	-257	5	2390	1980	-16.0		
Specimen 1274-2										
Medium Branch										
1	0.4	0.8	443, 12003	-66	7	520	115	-16.0		
2	2.25	0.5	439, 11999	-205	5	1840	1440	-16.4		
Specimen 1278-3										
Tips										
1	0.5	0.5	431, 11992	105	9			-16.0		
2	0.6	0.6	202^	58	13			-17.9		

available to the animal for skeletal construction. Since this skeleton is protein, the carbon pool must be organic, containing at least some amino acids which are essential to the animal. The possible carbon sources are surface-derived particulate organic carbon (POC), sedimentary organic carbon (SOC), and dissolved organic carbon (DOC) or a combination of these. Before we discuss these pools in turn, we should note the following: (1) The animals were alive when harvested. (2) The stable isotope results (Table 1) obtained for all layers are very similar, indicating that there were not large changes in the carbon source over the lifetime of the animal. (3) The nature of the material studied strongly suggests that little exchange could have taken place, and that the carbon in

the tissue is that which was originally deposited at tissue formation. The structural tissues of an animal is usually stable in the environment in which it is found (e.g., a saltwater-soluble skeleton would be rather maladaptive for this animal). Amino-acids in protein are strongly bound, and protein can persist for a very long time in stable conditions. (4) The outer tips include radiocarbon produced from nuclear weapons testing.

The characteristics of POC, SOC, and DOC are discussed in the context of origin, lability, and isotopic composition. POC is the material that is collected by a 1 μm filter during the filtration of seawater, and DOC is that fraction that passes the filter. POC originates mainly from the euphotic zone of
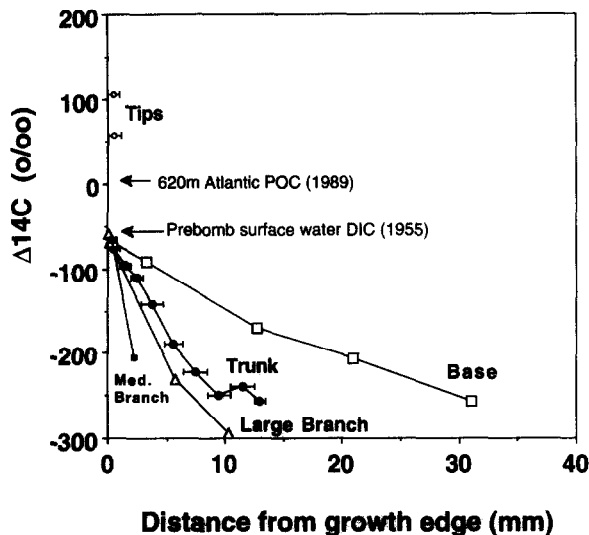
Fig. 1. $\Delta^{14}C$ measurements of samples from three specimens of *Gerardia* collected from 600 m depth off Little Bahama Bank. The trunk, base, and large branch layers were from specimen 1273-2, the medium branch from 1274-2, and tips from 1278-3. See Table 1 for isotope results and the text for detail.

the ocean and sinks or is suspended in seawater. SOC is particulate organic carbon that is contained within sediment on the ocean floor and can be resuspended in the near-bottom waters by currents and biotic activity (i.e., fish, burrowing organisms). Of these three organic carbon sources, POC contains the highest abundance of labile organic compounds, i.e., amino acids, sugars, and lipids (50–80%), and DOC contains the least (<10%). $\Delta^{14}C$ of suspended POC collected in 1989 using in situ pumps off Bermuda (32°N, 64°W) decreased from post bomb values in the surface (+138‰ at 85 m depth) to 8 ± 10‰ at 600 m depth (Druffel and Williams, 1990); the average $\delta^{13}C$ of suspended POC within this depth range was $-20.8 \pm 0.4(SD)‰$ ($N = 7$). The $\Delta^{14}C$ values of sinking POC also collected off Bermuda were 179 ± 8‰ and 66 ± 7‰ at 1500 m and 3200 m depth, respectively (Druffel et al., 1992); $\delta^{13}C$ of total amino acids separated from sinking POC collected at 650 m above bottom (3600 m depth) off the coast of California in May 1992 was −17.6‰ (X. Wang and E. R. M. Druffel, unpubl. data). The DOC had a $\Delta^{14}C$ value of −210 ± 6‰ at 20 m depth, and decreased to −356 ± 6‰ by 600 m depth (Druffel et al., 1992); average $\delta^{13}C$ of DOC was −21.1 ± 0.2‰ ($N = 8$). The $\Delta^{14}C$ of SOC from surface sediment at a depth of 990 m off the eastern United States coast was −170‰ in 1988 (Anderson et al., 1994). The average $\delta^{13}C$ values of SOC from 0–1 cm depth in three cores from the North Central Pacific (5600 m water depth) is −19.6 ± 0.6‰.

First, suppose the $\Delta^{14}C$ decrease measured in *Gerardia* reflects a shorter lifetime than that determined from the half-life of ^{14}C. Could we be observing the slow input of bomb ^{14}C into the animal's skeleton over most of its lifetime? If we were to assume that the early, prebomb growth of *Gerardia* ($\Delta^{14}C = -267‰$) was a combination of SOC and DOC (average $\Delta^{14}C = < -280‰$) and sinking POC (−50‰), a mass balance calculation reveals that less than 6% of the carbon

source would have originated from POC. In order to obtain the post-bomb value in the tips (105‰) from SOC and DOC (−280‰) and sinking POC (179‰), 84% of the carbon would have been from POC. This would have required a huge shift in the balance of the POC-DOC-SOC mixture over the organism's life to explain the large $\Delta^{14}C$ gradient (Fig. 1). The high $\Delta^{14}C$ values obtained for the tips clearly demonstrate a surface-derived food source (i.e., POC) most recently for *Gerardia*, not SOC or DOC. In addition the similarity of $\delta^{13}C$ values for *Gerardia* and amino acids from the deep sea (X. Wang and E. R. M. Druffel, unpubl. data) suggests that an amino acid–rich material (i.e., POC) is the primary food source. Further, the sediment in this area is nearly 100% calcitic sand and silt, with very low abundance of SOC and is an unlikely source of food for *Gerardia*. Also, one wonders why *Gerardia* would choose DOC, as its nutritional value is low.

A second, more reasonable treatment of the data, is to use the radiocarbon half-life of 5730 years to calculate an apparent ^{14}C age for each of the layers of *Gerardia* examined (see Table 1). As there is a "reservoir age" of the carbon in surface ocean waters due to mixing with aged carbon from subsurface depths, a correction of −404 years as per convention (Stuiver et al., 1986) is applied to the reported ^{14}C ages (see Table 1). Corrected ^{14}C ages of the samples are plotted in Fig. 3. To estimate the growth period for the trunk, large branch, and base samples, we subtract the corrected ^{14}C age of the outer layers from that of the innermost layers. If we assume that the $\Delta^{14}C$ of prebomb carbon supplied to *Gerardia* was −76‰ (corrected age = 295 yBP) and take the average of the three innermost $\Delta^{14}C$ values as −267‰ (corrected age 2110 y BP), then an average estimate for the growth period of this animal is 1820 ± 300 years.

This age estimate is based on three assumptions: (1) The source of carbon to *Gerardia* is surface-derived POC from the western North Atlantic, and its pre-bomb $\Delta^{14}C$ signature (−76‰) remained constant over its lifetime; (2) Its skeleton remained unaltered and there was no exchange with other carbon sources or selective remineralization that would cause

Fig. 2. Scanning electron micrograph (SEM) for a thin section near the center of the *Gerardia* trunk. Distance scale of 100 μm is shown in bottom right corner.
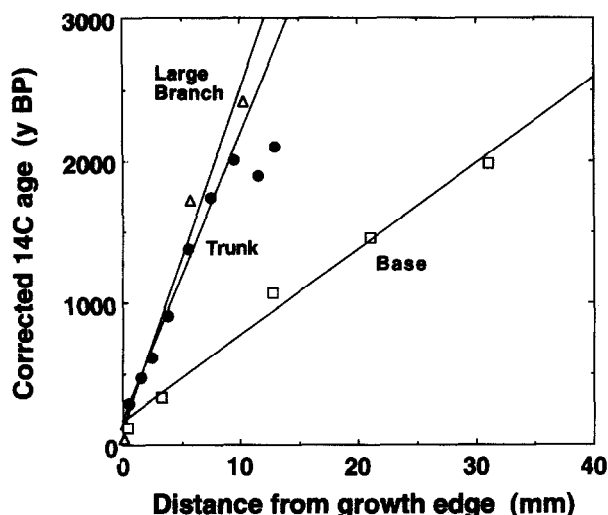
FIG. 3. Apparent ^{14}C ages for layers of *Gerardia* trunk (closed circles), base (open squares), and large branch (open triangles). Ages have been calculated as in Table 1 and corrected for reservoir effects (see text). Least-squares fits are indicated by the three lines, where correlation coefficients r^2 are 0.980, 0.933, and 0.992 for large branch, trunk (layers 1–7 only), and base, respectively.

changes in Δ^{14}C; and (3) the linear growth rates of the trunk, base, and large branch are constant with time. Regarding the first assumption, the presence of bomb-^{14}C in the tips clearly illustrates the presence of mostly surface-derived, bomb ^{14}C to *Gerardia*. A time-history of surface DIC Δ^{14}C values from banded corals off the Florida Keys reveals values of +105‰ or greater after 1965. An average integrated Δ^{14}C value of +110–120‰ is obtained from 1957–1982 for surface carbon off Florida (Druffel and Linick, 1978). This provides a maximum estimate of 25 years for the growth period of the tips (UCI#431), as the suspended POC at depth has a lower Δ^{14}C value than that in the surface (Druffel et al., 1992). Second, the skeleton likely remained unaltered with respect to exchange with other sources of carbon. The skeleton is extremely hard and impermeable to water, and it is unlikely that exchange could take place. Third, our assumption of constant linear growth rates of the trunk, large branch and base of *Gerardia* is based on the near-linear trends of the ^{14}C-age data (Fig. 3). The tailing off of the ^{14}C ages in trunk layers 7 through 9 is likely the result of a higher rate of growth early in the animal's life.

If the bands shown in the SEM image (Fig. 2) are interpreted as annual, then a crude but independent estimate of *Gerardia*'s age can be calculated. Based on band widths of 5–10 μm with annual periodicity and a total radius of 13.5 mm, the age is calculated as 1350–2700 years. A detailed analysis of the band structure of *Gerardia* needs to be done to confirm these preliminary results. Annual variability is present in deep-sea POC flux in the North Atlantic (Deuser and Ross, 1980), with high flux occurring during the late winter and spring when nutrients are in high concentration and primary productivity rates are large. Thus, we would expect to see seasonal variability in the POC flux at our site, and presumably similar periodicity in the skeletal matrix of *Gerardia*.

Why were the Δ^{14}C values of the recent growth of trunk, branches, and base (−58 to −76‰) so much lower than those in the tips (105 and 58‰)? The Δ^{14}C data (and inferences from the SEM data) indicate the growth rates of the trunk, large branch, and base appear to have been very low (~5 μm/y), with the outer layers of 0.1 and 0.5 mm thickness representing time spans of 20 and 100 years, respectively. The time span of the tips ($\leq$1 mm diameter) is likely much less, similar to the higher growth rate observed in the center of the trunk. Thus, the difference between the Δ^{14}C of the tips and the outer layers of the trunk, large branch, and base supports our assertion that the organism is very old.

Potential promise exists to use *Gerardia* for paleoenvironmental reconstruction on millennial time scales. As *Gerardia* appears to accrete POC derived mainly from the upper ocean, it is feasible that records of surface productivity, perhaps new production, are stored within its skeleton. Characteristics of the flux of POC in the water column may be monitorable by studying carbon and nitrogen isotopes in thin layers of *Gerardia*. For example, the uniformity of the *Gerardia* δ^{13}C data (Table 1) suggests that the isotopic fractionation associated with the uptake of carbon by the marine biota and the POC pool formed from it was constant over the past 1800 years. This may imply that the factors influencing isotopic fractionation of surface POC, i.e., surface water CO_2 (aq) concentrations (Popp et al., 1989), remained constant (within the resolution of the *Gerardia* layers) over the past two millennia in the northwestern Atlantic. If such measurements were made on 5–50 μm thin bands, then isotopic information on decade time scales might be obtained. It is also conceivable that the composition and lability of the POC falling through the water column is contained within the amino acids incorporated in *Gerardia*'s skeleton. High-resolution sampling and subsequent amino acid analyses of the layers may reveal decadal variations of the abundance of the most labile organic compound class present in particulate matter. Correlation between certain amino acid abundances and the change by a factor of three in water mass renewal rate previously observed in the upper layers of the Sargasso Sea during the past thirty years (Jenkins, 1982; Druffel, 1989) could be an initial test of this hypothesis.

A limitation for using *Gerardia* as a paleoenvironmental tool is that, from data presented here, it appears to be a recorder of surface water chemistry; thus, its usefulness as an integrator of deep-sea processes narrows. In addition, radiocarbon is not the ideal time clock for this animal due to past variability of DIC Δ^{14}C in the surface ocean (Druffel and Griffin, 1993) and to limited resolution thus far obtainable. Comparisons between ^{14}C ages and those using another isotope, perhaps [230]Th, may provide more accurate dating of *Gerardia*, though this is presently untested.

It is not known whether relict specimens can be found to extend the paleoreconstructions of surface productivity and POC fluxes back to the early Holocene or the last glacial period. Field studies on lithoherms and other sites where *Gerardia* are known to grow are needed to help resolve this issue. It is important to note that due to their old age, proper monitoring and protection of *Gerardia* are essential if they are to maintain their present place in the deep-sea biota.

5. CONCLUSIONS

We conclude that the $\Delta^{14}C$ data presented here support an age for *Gerardia* of 1800 $\pm$ 300 years. There is potential for *Gerardia* to serve as millennial-scale paleointegrators of upper ocean POC flux, by measuring stable isotope signatures and amino acid composition of high-resolution (5–50 μm thick) bands. In this way, *Gerardia* may be a useful tool for discerning decade timescale changes of productivity in the surface ocean.

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REFERENCES

Anderson R., Rowe G., Kemp P. F., Trumbore S., and Biscaye P. E. (1994) Carbon budget for the mid-slope depocenter of the Middle Atlantic Bight. *Deep-Sea Res. II* **41**(2/3), 669–703.

Bell F. J. (1891) Contributions of our knowledge of Antipatharian corals. *Trans. Zoological Society of London* **13**, 141–142.

Broecker W. S., Gerard R., Ewing M., and Heezin B. (1960) Natural Radiocarbon in the Atlantic Ocean. *J. Geophys. Res.* **65**, 2903–2931.

Cohen S. A. et al. (1989) *The Pico-Tag Method.* Millipore Corporation, Bedford, MA.

Deuser W. G. and Ross E. H. (1980) Seasonal change in the flux of organic carbon to the deep Sargasso Sea. *Nature* **283**, 364–365.

Druffel E. R. M. (1989) Decade time scale variability of ventilation in the North Atlantic determined from high precision measurements of bomb radiocarbon in banded corals. *J. Geophys. Res.* **94**, 3271–3285.

Druffel E. R. M. and Griffin S. (1993) Large variations of surface ocean radiocarbon: Evidence of circulation changes in the southwestern Pacific. *J. Geophys. Res.* **98**, 20,249–20,259.

Druffel E. M. and Linick T. W. (1978) Radiocarbon in annual coral rings from Florida. *Geophys. Res. Lett.* **5**, 913–916.

Druffel E. R. M. and Williams P. M. (1990) Identification of a deep source of particulate organic carbon using bomb ^{14}C. *Nature* **347**, 172–174.

Druffel E. R. M. et al. (1992) Cycling of dissolved and particulate organic matter in the open ocean. *J. Geophys. Res.* **97**, 15,639–15,659.

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

Emiliani C. et al. (1978) Oxygen and Carbon Isotopic Growth Record in a Reef Coral from the Florida Keys and a Deep-Sea Coral from Blake Plateau. *Science* **202**, 627–629.

Griffin S. M. and Druffel E. R. M. (1985) Woods Hole Oceanographic Institution Radiocarbon Laboratory: Sample treatment and gas preparation. *Radiocarbon* **27**(1), 43–51.

Griffin S. and Druffel E. R. M. (1989) Sources of carbon to deep-sea coral skeletons. *Radiocarbon* **31**, 533–542.

Grigg R. (1977) Fishery Management of Precious Corals in Hawaii. *Third International Coral Reef Symposium, Miami, Florida, University of Miami*, 609–616.

Jenkins W. J. (1982) On the climate of a subtropical ocean gyre: Decade timescale variations in water mass renewal in the Sargasso Sea. *J. Mar. Res.* **40**(suppl.), 265–290.

Ostlund H. G. and Grall C. (1987) Transient Tracers In The Ocean, North and Tropical Atlantic Tritium and Radiocarbon. *Tritium Laboratory Data Report No. 16.* University of Miami.

Popp B. N., Takigiku R., Hayes J. M., Louda J. W., and Baker E. W. (1989) The post-paleozoic chronology and mechanisms of ^{13}C depletion in primary marine organic matter. *Amer. J. Sci.* **289**, 436–454.

Stuiver M., Pearson G. W., and Braziunas T. (1986) Radiocarbon age calibration of marine samples back to 9000 cal yr BP. *Radiocarbon* **28**(2B), 980–1021.

Suess H. E. (1980) The radiocarbon record in tree rings of the last 8000 years. *Radiocarbon* **22**(2), 200–209.

Vallentyne J. R. (1964) Biogeochemistry of Organic Matter. *Geochim. Cosmochim. Acta* **28**, 157–188.

Vogel J., Nelson D. E., and Southon J. R. (1987) ^{14}C background levels in an accelerator mass spectrometry system. *Radiocarbon* **29**, 323–333.

Zubay G. (1988) *Biochemistry.* MacMillan.