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Banded Corals: Changes in Oceanic Carbon-14 During the Little Ice Age

Ellen M. Druffel

Natural $^{14}$C is produced in the stratosphere by the action of cosmic rays on $^{14}$N. It is quickly oxidized to $^{14}$CO$_2$ and distributed into the troposphere, oceans, and land biota. During preindustrial times (before A.D. 1900), spatial variations in the $^{14}$C content of the troposphere resembles a partial sine wave with a period of about 11,500 years. This variation is attributed to a gradual change in intensity of the magnetic dipole moment of the earth (4). A strong dipole moment decreases the flux of galactic cosmic rays that reaches the earth's strato-

sphere, resulting in a lower production of $^{14}$C. Elasser et al. (5) determined that a 50 percent decrease of the geomagnetic field strength would increase the intensity of cosmic rays incident on the stratosphere by 10 percent (Fig. 1).

Superimposed on this major trend are minor fluctuations in the $^{14}$C/$^{13}$C ratio with a period of about 200 years (Fig. 1). These fluctuations are most likely caused by variations in solar activity (6, 7). The galactic cosmic-ray flux responsible for $^{14}$C production is modulated by changes in solar wind magnetic fields. As the intensity of the solar wind increases, more galactic cosmic rays are diverted from the earth's atmosphere, causing a decrease of the $^{14}$C production. From tree ring analyses, De Vries (8) deduced two recent episodes of unusually high atmospheric $^{14}$C concentration that occurred around A.D. 1500 (Spörer sunspot minimum) and A.D. 1700 (Maunder sunspot minimum). These periods of high $^{14}$C were coincident with decreased solar activity (9). Stuiver and Quay (10) determined the increase in the atmospheric $^{14}$C concentration that occurred around A.D. 1300 (Wolf sunspot minimum) (Fig. 2). These three periods of unusually high $^{14}$C production were coincident, although not directly correlated (11), with recorded intervals of especially severe winters in Europe (3), a period known as the Little Ice Age. Whether the Little Ice Age was the direct result of low solar activity or whether this was a coincidence has not yet been resolved.

It is possible, although not probable, that the observed increase in the atmospheric $^{14}$C concentrations during the Little Ice Age could also have been caused by decreased vertical mixing in the surface oceans or by large changes in the rate of CO$_2$ exchange between the air and the ocean. Neither of these changes is expected during periods of cooler average world temperature, such as that during the Little Ice Age. In order to eliminate these possibilities, however, it is necessary to acquire $^{14}$C records for this period in the oceans. I show here that banded, hermatypic corals can be used as recorders of $^{14}$C concentration in ocean waters during the Little Ice Age, just as tree rings are used to record $^{14}$C concentrations in the atmosphere. The atmospheric $^{14}$C record combined with the oceanic $^{14}$C record may be used to determine the causal relationship and the timing of the $^{14}$C variations observed in these two reservoirs during earlier times.

Corals as Oceanic Recorders

Hermatypic corals accrete aragonite, a crystalline form of calcium carbonate, with $^{14}$C/$^{13}$C ratios equal to those in the dissolved inorganic carbon (DIOC) in the seawater at the time of coral ring formation (12, 13). As the world's surface oceans are saturated with respect to aragonite, hermatypic coral skeletons do not dissolve with time. Nor does arago-
nite exchange its carbonate with any other source of carbon. Once accreted, coraline aragonite retains a permanent and unaltered record of the $^{14}\text{C}/^{12}\text{C}$ ratio present in surface seawater during the past.

Coral also record evidence within their skeletons of significant ecological conditions and changes that occurred during their lifetimes. Wells (14) studied middle Devonian fossil corals and interpreted fine ridges on the surface of the coral epitheca to be daily growth bands. He found approximately 400 ridges (days) per annum, which agrees with astronomical expectations of the deceleration of the earth’s period of rotation due to tidal friction.

The most conspicuous records contained within coral skeletons are annual density bands. These growth bands were first conclusively demonstrated as annual by Knutson et al. (15). The annual growth bands are primary skeletal characteristics that are exhibited as seasonal variations in the bulk density of the secreted skeleton (16). Many investigators have demonstrated the annual nature of density band pairs in hermatypic corals, using techniques such as alizarin staining, x-radiography, densiometry, autoradiography, and direct field observations (15, 17, 18).

Various radioisotopes, such as bomb-produced $^{14}\text{C}$ (12, 13, 19, 20), $^{87}\text{Sr}$ (21), and $^{226}\text{Ra}$ (22) have been used to corroborate the annual nature of growth bands in various corals. Seasonal variations in the $^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$ ratios have been illustrated by Emiliani et al. (23), Fairbanks and Dodge (24), and Dunbar and Wellington (25). They concluded that corals accrete aragonite with a constant displacement of $^{18}\text{O}/^{16}\text{O}$ ratios from isotopic equilibrium with seawater and that these stable isotope ratios are records of changes in the seawater temperature.

**Sample Collection and Growth Analyses**

Two coral cores (TRI and TRII) of *Montastrea annularis* were collected from The Rocks reef (24°57'S, 80°33'W) at a depth of 4 meters in the Florida Straits (Fig. 3). They were drilled and recovered by J. Harold Hudson (U.S. Geological Survey) and me. The Rocks reef is located 1 kilometer offshore from Plantation Key and lies on the fringes of the Florida Current (Fig. 3). The corals examined in this work were from an area that was constantly flushed by open ocean waters, specifically the Florida Current which is part of the Gulf Stream system. The corals were collected with a hydraulic drill, fitted with a diamond bit and core barrel. The drill was powered by a small hydraulic pump that was operated from aboard a small boat (18, 26).

Both coral cores were obtained from the same coral head at The Rocks reef. There is a partial void in both of these cores (around A.D. 1800) that represents the absence of no more than 5 years of coral growth (27).

Hudson et al. (18) used alizarin-staining techniques and x-radiography to depict annual density bands in *Montastrea annularis* from the Florida Straits. These investigators noticed that dense aragonitic bands accreted during the warm summer months of July through September and that thicker, less dense bands accreted during the cooler months of October through June. The most convincing evidence that these bands are annual is the presence of stress bands in the coral record. These bands form during unusually severe winters and are thicker than the annual dense bands of summer. These events, referred to locally as cold fronts, are the result of cold weather that originates in the northwest and passes over the reef in a southeastern direction. There is excellent correlation between the stress band record and all recorded cold fronts (late 1856, 1885, 1894, 1898, 1941, 1957, 1963, and 1969) (Fig. 4) (18).
Coral slabs (4 millimeters thick) were cut along the vertical growth axes of both cores. Upon x-radiographic analyses (18) of the slabs, it was determined that TRI grew from A.D. 1642 to 1975 (Fig. 4) and TRII grew from A.D. 1692 to 1978. Subjection of these samples to x-ray diffraction analyses revealed pure aragonite and showed no traces of calcite. Each core was sectioned into samples that consisted of one to ten consecutive years of growth. Radiocarbon analyses were carried out at the La Jolla Radiocarbon Laboratory (28) on a total of 135 samples from both cores. Druffel and Linick (12) reported 65 of the results from TRI for the period 1800 to 1974. The 14C measurements were carried out by standard gas proportional counting techniques (12).

All measurements were corrected for isotope fractionation (to a δ13C relative to PDB-1 = −25.0 per mil) (29) and for decay since the time of formation (to A.D. 1950). The standard used was 95 percent of the net National Bureau of Standards oxalic acid count rate, corrected to δ13C = −19.0 per mil. All results are reported in terms of Δ14C, which is the deviation (per mil) from the activity of 19th-century wood:

$$\Delta^{14}C = \delta^{13}C - 2(\delta^{13}C + 25) \left(1 + \frac{\delta^{14}C}{1000}\right)$$

Stable isotope measurements ($\delta^{18}O$) (29) were performed by W. G. Mook at the University of Groningen on 79 coral samples from TRI for the period A.D. 1700 to 1790. Samples of coralline aragonite (10 milligrams) were baked (400°C) under vacuum to remove organic matter. They were acidified with 100 percent orthophosphoric acid, and the isotopes were measured on a V. G. Micromass 903 mass spectrometer. Results are reported with standard δ (per mil) notation relative to the PDB-1 standard. The precision for isotopic measurement of these samples was ±0.05 per mil for $\delta^{18}O$.

Results for Coral Growth from A.D. 1642 to 1800

The Δ14C values for banded corals from TRI that had grown from A.D. 1642 to 1800 and all of those from TRII are listed in Table 1. Results for TRI for the period 1801 to 1974 are listed in (12).

The Δ14C measurements of Florida coral that grew during preindustrial times are shown in Fig. 5. There are significant variations in the Δ14C record for this period. The 15 Δ14C values for coral that grew between A.D. 1642 and 1706 averaged −49 ± 4 per mil (Fig. 5a). There was a deviation from this average (to −43 ± 3 per mil) in a coral sample that grew from 1656 to 1660. The Δ14C measurements of coral that grew after 1706 were significantly higher than −49 per mil. Of the 16 Δ14C results for coral that grew from 1709 to 1740, almost 90 percent were higher than −49 per mil. A least-squares analysis of these 16 measurements reveals a significant slope; the fit of these data is shown in Fig. 5a. The 14C concentrations increased rapidly from −49 to −42 per mil in a relatively short period (1706 to 1712). The values decreased slowly during subsequent years (1712 to 1750), from −42 to −49 per mil. The trends that are apparent in Fig. 5a are also shown to be statistically significant on the basis of a spline function (third-order polynomial) fitted to the Δ14C data from Florida and Belize (19) corals (Fig. 6). Thus, it is apparent from these data that an increase in Δ14C of 7 per mil had occurred in the surface waters of the Florida Current (Gulf Stream system) during the early 1700’s. During
the second half of the 18th century the 
$^{14}$C concentrations remained unchanged; 
the average of 19 $\Delta^{14}$C values is $-49 \pm 3$ 
per mil.

The increase in $^{14}$C in oceanic DIOC 
during the early 1700's was most likely 
the result of increased $^{14}$C concentrations 
in the atmospheric CO$_2$ during that 
time. Figure 2 shows two $^{14}$C maxima 
that were observed in tree rings from the 
early 16th and 18th centuries (10). These 
maxima, which coincide with the Little 
Ice Age, are almost certainly the result 
of decreased solar activity (7). As CO$_2$ is 
 exchanged between the atmosphere and 
the oceanic carbon, an increase in the 
 atmospheric $^{14}$CO$_2$ concentration would 
also appear in the DIOC of the surface 
ocean. There is a lag time of three to four 
decades between the onset of the in- 
crease in the atmosphere and that in 
the ocean (Fig. 7). Part of this delay can 
be attributed to the residence time (10 
to 15 years) for $^{14}$CO$_2$ in the atmosphere 
(2, 12). The $^{14}$C increase in the atmos- 
phere was about 20 per mil by the 
beginning of the 18th century, whereas 
the increase observed in corals during 
this time was only 7 per mil (Fig. 7). The 
attenuation of the $^{14}$C peak in the surface 
 ocean was caused by vertical exchange 
of older subsurface waters, which contain 
less $^{14}$C, with surface waters (2). The 
isolation of subsurface waters from the 
 atmosphere for extended periods of 
time causes $^{14}$C to be lost as a result of 
in situ radioactive decay (2).

It is possible that the increase of $\Delta^{14}$C 
in the surface waters of the Florida 
Straits during the Little Ice Age could 
also have been caused by a decrease in 
the rate of vertical exchange in the upper 
few hundred meters of the water column; 
this could have been caused by warmer 
surface water temperatures, which 
would not have been expected during an 
 Ice age. However, the $\delta^{18}$O values from 
these banded corals (Fig. 8) indicate 
that the average temperature in Gulf 
Stream surface waters was slightly lower during 
the latter stage of the Little Ice Age 
(about 1700). A least-squares analysis of 
the $\delta^{18}$O values reveals an overall de-
crease of 0.2 per mil from 1700 to 1790 
(dashed line, Fig. 8), which corresponds 
to a warming of about 1°C (24, 25) 
from the latter part of the Little Ice Age to 
the end of the 18th century. A closer look 
at these data reveals a maximum $\delta^{18}$O value 
of $-4.0$ per mil around 1725 and a 
sharp decrease to $-4.4$ per mil in the 
1740's, which represents a rise in 
temperature of 2°C over this time period. 
There also appears to be a somewhat 
smaller maximum (about 4.1 per mil) around 
1760. These maxima (solid lines, Fig. 8) 
represent periods when the surrounding 
seawater was 1° to 2°C cooler than 
during the earlier periods. Cooler surface 
water temperatures during the early 
1700's imply that there was an increase in 
vertical mixing between surface and 
subsurface waters, not decreased verti-

cal mixing as would have been the case 
if there were changes in seawater temperature but 
the cause of the $^{14}$C increase in the 
1700's. An increase of the $^{14}$C/$^{12}$C in the 

| Sample No. | Year Range | $\delta^{14}$C (per mil) | $\Delta^{14}$C (per mil) |
|-------------|-------------|--------------------------|--------------------------|
| 4432        | 1642 to 1645 | $-1.3$                   | $-50 \pm 3$              |
| 4409        | 1646 to 1655 | $-0.6$                   | $-46 \pm 3$              |
| 4404        | 1656 to 1660 | $-0.4$                   | $-43 \pm 3$              |
| 4431        | 1661 to 1665 | $-0.7$                   | $-47 \pm 3$              |
| 4406        | 1666 to 1670 | $-0.4$                   | $-50 \pm 4$              |
| 4450        | 1671 to 1675 | $-0.4$                   | $-49 \pm 3$              |
| 4428        | 1691 to 1698 | $-0.8$                   | $-46 \pm 3$              |
| 4891        | 1694 to 1695 | $-1.6$                   | $-53 \pm 4$              |
| 4851        | 1696 to 1697 | $-1.4$                   | $-49 \pm 4$              |
| 4894        | 1698 to 1699 | $-1.3$                   | $-49 \pm 5$              |
| 4832        | 1700 to 1701 | $-1.1$                   | $-41 \pm 5$              |
| 4472        | 1702 to 1703 | $-0.7$                   | $-53 \pm 3$              |
| 4479        | 1699 to 1705 | $-0.3$                   | $-46 \pm 3$              |
| 4479        | 1704 to 1706 | $-0.2$                   | $-56 \pm 3$              |
| 4479        | 1706 to 1707 | $-0.4$                   | $-46 \pm 3$              |
| 4479        | 1708 to 1710 | $-0.1$                   | $-50 \pm 3$              |
| 4479        | 1708 to 1710 | $-1.0$                   | $-41 \pm 5$              |
| 4479        | 1710 to 1715 | $-0.6$                   | $-32 \pm 5$              |
| 4479        | 1711 to 1713 | $-0.8$                   | $-41 \pm 4$              |
| 4479        | 1716 to 1720 | $-0.7$                   | $-44 \pm 3$              |
| 4479        | 1717 to 1719 | $-0.5$                   | $-45 \pm 4$              |
| 4479        | 1720 to 1722 | $-0.3$                   | $-43 \pm 4$              |
| 4479        | 1723 to 1725 | $-0.4$                   | $-48 \pm 3$              |
| 4479        | 1725 to 1727 | $-0.1$                   | $-45 \pm 3$              |
| 4479        | 1726 to 1728 | $-0.3$                   | $-45 \pm 3$              |
| 4479        | 1729 to 1731 | $-0.2$                   | $-46 \pm 4$              |
| 4479        | 1731 to 1735 | $-0.6$                   | $-46 \pm 3$              |
| 4479        | 1732 to 1734 | $-0.5$                   | $-43 \pm 3$              |
| 4479        | 1735 to 1737 | $-0.0$                   | $-40 \pm 3$              |
| 4479        | 1737 to 1739 | $-0.3$                   | $-45 \pm 5$              |
| 4479        | 1739 to 1740 | $-0.2$                   | $-51 \pm 7$              |
| 4479        | 1741 to 1742 | $-0.8$                   | $-53 \pm 3$              |
| 4479        | 1742 to 1744 | $-1.1$                   | $-42 \pm 8$              |
| 4479        | 1746 to 1750 | $-0.3$                   | $-48 \pm 7$              |
| 4479        | 1747 to 1749 | $-0.3$                   | $-42 \pm 4$              |
of CO₂ in surface waters cooled 1°C would be insignificant.

Most of the water in the Gulf Stream comes from the Sargasso Sea (2), a subtropical gyre in the North Atlantic that circulates in a clockwise (anticycloonic) direction. The circulation in the surface mixed layer is wind-driven (Ekman transport), and that in the deep water is a result of geostrophic forces. Ekman transport is convergent in a subtropical gyre, which forces water downward from the mixed layer. There is a complex process at work that selects only late winter water for actual net downward pumping, called Ekman pumping, into the geostrophic regime below (30). As the surface waters in the Gulf Stream were 1° to 2°C cooler during the early 1700’s, it is probable that Sargasso Sea surface waters were also cooler during this period. It is likely that cooler surface water temperatures during the latter part of the Little Ice Age enhanced the downward penetration of waters in the Sargasso Sea during the late winter and perhaps induced prolonged convection that extended from early winter to spring.

Results for Subsequent Coral Growth, A.D. 1800 to 1952

The 1⁴C concentrations in Florida coral that grew subsequent to 1800 also appear to reflect 1⁴C changes in the atmosphere. The Δ¹⁴C measurements of Florida coral that grew during the 19th century (12) are shown in Fig. 5b. From 1800 to 1820, Δ¹⁴C values remained unchanged from the previous 50-year period (-49 ± 5 per mil). However, further ¹⁴C analyses since the publication of (12) reveal a significant decrease from about 1815 to 1865.

This decrease of 4 to 5 per mil in the Δ¹⁴C of the surface ocean during the early and mid-1800’s was coincident with a decrease of 9 per mil observed in the atmosphere (10) (Figs. 2 and 7). As was the case for the data from the early 1700’s, the magnitude of the ¹⁴C variation in the atmosphere was at least twice that in the surface ocean (Table 2). It is probable that the 4 to 5 per mil decrease observed in ocean waters was caused by declining atmospheric ¹⁴CO₂ concentrations. It is unlikely that this decrease was caused by enhanced vertical mixing in the upper layers of the ocean in view of preliminary δ¹⁸O measurements which show a slight increase in the average surface water temperature from 1800 to 1900 (31).

A recent decrease in the ¹⁴C concentration from A.D. 1900 to 1952, known as the Suess effect, has been noticed both in the atmosphere (32) and in the surface waters of the Gulf Stream (12, 19) and in the Peru Current (20). Concentrations of ¹⁴C in the atmosphere decreased 20 to 25 per mil as a result of a dilution with ¹⁴C-free CO₂ that results from the burning of fossil fuels (33, 34). The change in the surface waters of the Gulf Stream during this period (-12 per mil) (Fig. 6) was about half that in the atmosphere.

Table 2 lists data on the three variations in ¹⁴C that were observed in the atmosphere and in the ocean from A.D. 1642 to 1952. The ratio of the observed variations (atmosphere/ocean) ranges from 1.7 to 2.8. The ratio predicted by the box-diffusion model of Oeschger et al. (35) for the Suess effect, a perturbation of the ¹⁴C/¹²C that was introduced
initially into the atmosphere, is 2.5. The ratios listed in Table 2 are comparable, as the duration of each $^{14}$C/$^{12}$C change is approximately the same (50 years). The agreement between the observed and calculated ratios is further evidence that the variations of $^{14}$C observed in Florida corals during the Little Ice Age and during the mid-1800’s were induced by changes of $^{14}$C that occurred initially in the atmosphere. Had the $^{14}$C variations originated in the ocean, for example, by the reduction or cessation of mixing between surface and subsurface waters, a ratio (atmosphere/ocean) of $\pm 1$ would have been expected.

**Conclusions**

Analysis of the amplitude of the $^{14}$C increase in the surface waters of the Florida Straits and that in atmospheric CO$_2$ during the Little Ice Age indicates that $^{14}$C concentrations rose first in the atmosphere, probably as a result of reduced solar activity during the Maunder sunspot minimum. Analyses of the stable isotopic measurements ($^{818}$O) of these corals show that slightly cooler surface water temperatures (by 1°C) were present in the Gulf Stream during the latter part of the Little Ice Age. This cooling suggests that ocean mixing patterns may have been different in the Gulf Stream during this period. A likely scenario may have included enhanced convection in the Sargasso Sea of late winter water (30) together with the downward penetration of cooler spring and early winter water into the geostrophic flow below.

**References and Notes**

1. J. C. Lerman, W. G. Mook, J. C. Vogel, in Radiocarbon Variations and Absolute Chronology, I. Olsson, Ed. (Wiley, New York, 1970), pp. 275-302.
2. E. M. Druffel and H. E. Suess, J. Geophys. Res., in press.
3. H. E. Suess, Radiocarbon 22, 100 (1980).
4. V. Buxa, Nature (London) 213, 1005 (1967).
5. W. E. Neyes, F. P. Ney, J. R. Winckler, ibid. 178, 1226 (1956).
6. M. Suwcr, J. Geophys. Res. 66, 273 (1961).
7. H. E. Suess, in Radiocarbon Variations and Absolute Chronology, I. Olsson, Ed. (Wiley, New York, 1970), pp. 595-605.
8. H. De Vries, Proc. K. Ned. Akad. Wet. B 61 (No. 2), 94 (1958).
9. M. Waldmeier, The Sunspot Activity in the Years 1610-1960 (Schmirlitz, Zurich, 1961); J. A. Eddy, Science 192, 1189 (1976).
10. M. Suwcr and P. D. Quay, Science 207, 11 (1980).
11. M. Suwcr, Nature (London) 286, 868 (1980).
12. E. M. Druffel and T. W. Linick, Geophys. Res. Letts. 5, 913 (1978).
13. Y. Nogaki, D. M. Rye, K. K. Turekian, R. E. Dodge, ibid., p. 825.
14. J. W. Wells, Nature (London) 197, 948 (1963).
15. D. W. Kauwton, R. W. Baddemeier, S. V. Smith, Science 177, 270 (1972).
16. R. W. Baddemeier, J. E. Macas, D. W. Kauwton, J. Esp. Mar. Biol. Ecol. 14, 179 (1974).
17. I. G. MacIntyre and S. V. Smith, in Proceedings of the Second International Symposium on Coral Reefs (Great Barrier Reef Commission, Brisbane, 1974), vol. 2, pp. 277-287.

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**Table 2. Observed $\Delta^{14}C$ changes in Florida coral and in trees as compared to those calculated by Oeschger et al. (35), using a box-diffusion model.**

| Time period (A.D.) | Variation of $\Delta^{14}C$ (per mil) | Ratio of atmospheric to surface ocean value |
|--------------------|-------------------------------------|----------------------------------------|
|                    | Atmosphere                          | Surface ocean (Gulf Stream)            |                                      |
| 1650 to 1710 (Little Ice Age or Maunder Minimum) | +20 (10)                            | +7*                                    | 2.8                                  |
| 1820 to 1870       | -9 (10)                             | -4 to -5*                              | 1.8 to 2.2                           |
| 1900 to 1950 (Suess effect) | -20 to -25 (10, 54)                 | -11 to -12 (12, 19)                    | 1.7 to 2.3                           |
| 1900 to 1950, Oeschger et al. (35) | -14.5                               | -5.7                                   | 2.5                                  |

*This study.
The activities, values, and behavior of an individual that are acquired through instruction or imitation will be termed "cultural." Such phenomena are not exclusively human (1) but are mostly highly selection has produced the complexity and diversity of living systems is the cornerstone of interpretation in the biological sciences. Observed genetic variation is the result of interactions between technological innovations. Our concern here is not with the comparison of mutation and selection in biological and cultural situations, but with another ingredient in the process of evolution—transmission. Although well studied and quantified in biology, transmission is poorly understood in its cultural context. The study of quantitative aspects of cultural transmission can, we believe, create a foundation for the study of cultural evolution and, in the quantitative theoretical development upon which we have embarked, modeling of cultural transmission has a central place (2). To date quantitative studies of cultural transmission have been limited, although there already exist theories, such as mathematical epidemiology (5), which could augment the study of diffusion of innovations (6). In this article we suggest some of the possible applications of our general theory, in an empirical investigation of quantitative aspects of our general theory.

Models of Transmission

Cultural transmission is the process of acquisition of behaviors, attitudes, or technologies through imprinting, conditioning, imitation, active teaching and learning, or combinations of these. A quantitative theory of the evolution of a culturally transmitted trait requires modeling who transmits what to whom,