Oxygen and Carbon Isotopic Growth Record in a Reef Coral from the Florida Keys and a Deep-Sea Coral from Blake Plateau

Abstract. *Carbon and oxygen isotope analysis through a 30-year (1944 to 1974) growth of* Montastrea annularis *from Hen and Chickens Reef (Florida Keys) shows a strong yearly variation in the abundances of both carbon-13 and oxygen-18 and a broad inverse relationship between the two isotopes. Normal annual dense bands are formed during the summer and are characterized by heavy carbon and light oxygen. "Stress bands" are formed during particularly severe winters and are characterized by heavy carbon and heavy oxygen. The isotopic effect of Zooxanthellae metabolism dominates the temperature effect on the oxygen-18/oxygen-16 ratio. The isotopic results on the deep-sea solitary coral* Bathypsammia tintinnabulum, *where Zooxanthellae are nonexistent, indicates that the abundance of the heavy isotopes carbon-13 and oxygen-18 is inversely related to the growth rate, with both carbon and oxygen approaching equilibrium values with increasing skeletal age.*

The possible relationship of incremental banding in corals to environmental conditions was first investigated by Ma (*1*) and later by Wells (*2*) and Scrutton and Hipkin (*3*). The annual character of banding in *Montastrea annularis* has been established by both radiochemical methods (*4*) and direct field observations (*5*).

Weber and Woodhead (*6, 7*) showed that although hermatypic corals deposit their carbonate material in disequilibrium with seawater, the slope of the curve showing the relationship between oxygen isotopic composition and ambient temperature is the same as that given by the equation of Epstein *et al.* (*8*). These authors maintained that after a suitable, constant correction is applied, oxygen isotopic data from hermatypic corals can be used for paleoclimatological studies. Land *et al.* (*9*), however, showed that different parts of the same coral colony, and even different parts of the same corallite, may give different oxygen isotopic compositions. They found that faster-growing sites within a colony were further out of isotopic equilibrium than slower growing sites.

Weber and Woodhead (*6*) and Goreau (*10*) developed models to explain the oxygen and carbon isotopic composition of reef-building corals. According to the quantitative model developed by Goreau (*10, 11*) for carbon, skeletal carbon is derived from the organism's internal inorganic carbon pool, the isotopic composition of which is determined by the input of seawater HCO_3^- and respired metabolic CO_2 and by the output of excreted inorganic carbon and carbon fixed photosynthetically by symbiotic Zooxanthellae. It is expected that the carbon and oxygen isotopic composition of the skeletal parts will vary depending on the isotopic composition of the various contributors and sinks and their relative magnitudes. Because metabolic carbon is some 13 to 17 per mil lighter and metabolic oxygen some 10 per mil lighter than seawater carbon and oxygen (in HCO_3^-), the skeletons of reef-building corals are lighter in both carbon and oxygen isotopic composition. Rates of growth of skeletal elements and changes in Zooxanthellae activity also affect the isotopic composition. [Faster-growing corallites are isotopically lighter, and greater Zooxanthellae activity will increase the production of both lighter metabolic carbon and heavier seawater carbon (*6, 9, 10*).] These various parameters, variously operating in different environments and at different times of the year, complicate the simple relationship between oxygen isotopic composition and temperature observed by Weber and Woodhead (*7*).

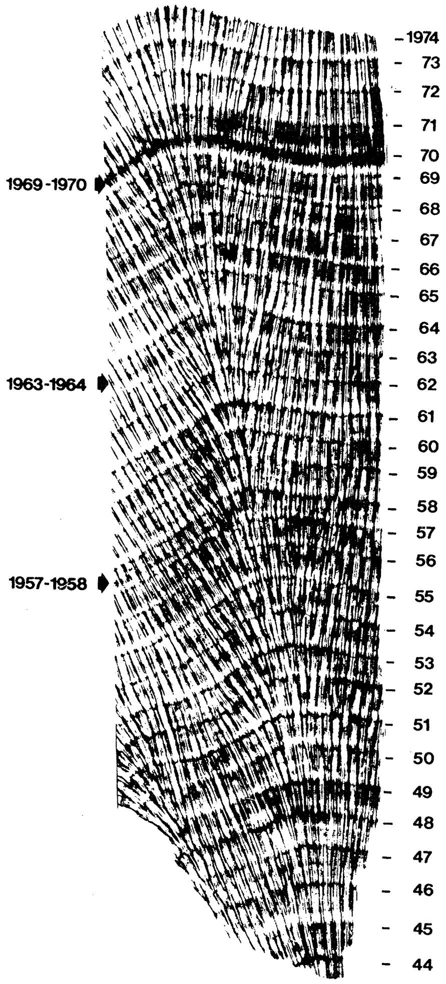

Fig. 1. X-radiograph of the section of *Montastrea annularis* analyzed isotopically. The numbers at the right indicate the year of deposition of the regular dense bands (months of August and September in each case). The numbers at the left identify abnormal dense bands deposited during particularly cold winters.

Annual skeletal growth in *M. annularis* consists of a thin, dense layer followed by a thicker, less dense layer. The denser layer appears to be produced by a temporary thickening of dissepiment structures and closer bundling of sclerodermites. Although hermatypic corals are known to grow throughout the year, the obvious layering of *M. annularis* suggests the possibility of different growth rates during the year. Hudson *et al.* (*5*) and Goreau (*11*) published x-radiographs of slabs cut from colonies of *M. annularis* from, respectively, Hen and Chickens Reef in the Florida Keys (24°56′N, 80°33′W) and Discovery Bay in Jamaica. In the Jamaican specimens the dense layers appear to have been formed in November and December, if one assumes constant growth (*11*, figure 1a). On the other hand, direct field observation of the Hen and Chickens Reef specimens clearly demonstrates that the yearly dense layers were formed during the months of August and September (*5*, figure 2). The lowest temperature of the year occurs at both locations during January and February (*11*, figure 3). In either case, therefore, it appears that the dense layers are formed before the winter temperature minimum.

A portion of a coral head of *M. annularis* from a depth of 3.6 m at Hen and Chickens Reef, representing growth from 1944 to 1974 (Fig. 1), was analyzed for carbon and oxygen isotopes. About four samples were obtained from each yearly growth, using a small grinding wheel. The results (Fig. 2) show a very strong yearly variation in both isotopes. In almost all cases the dense layers have a high ^{13}C concentration and a low ^{18}O concentration. However, in most cases, the extremes in these two parameters were reached after the dense layers were deposited—that is, in the winter. There is a broad inverse correlation between ^{13}C and ^{18}O (Fig. 3), which is not in agreement with previous observations showing little (*11*, figure 3) or no (*7*, figures 1 to 3) correlation.

The enrichment in ^{13}C observed in the dense layers may have resulted from a temporary reduction in Zooxanthellae activity, requiring more seawater carbon

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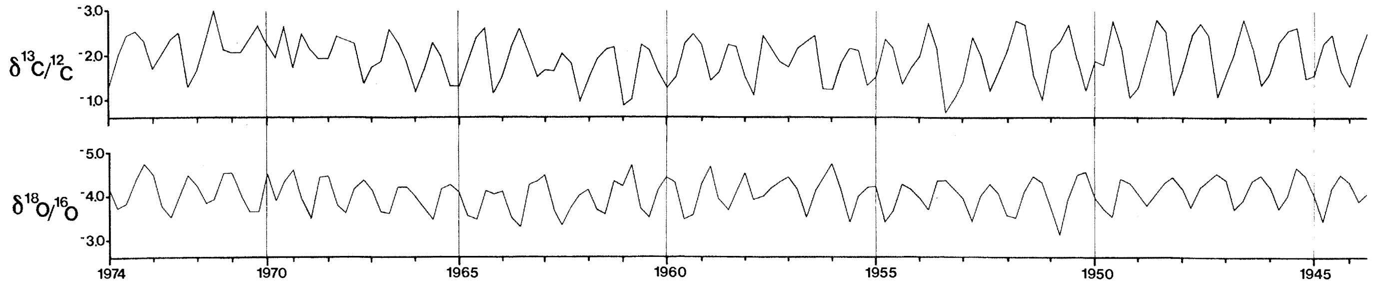
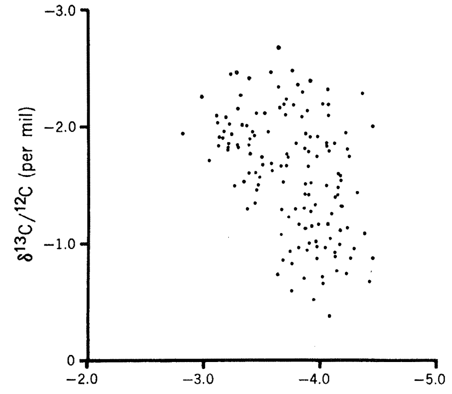
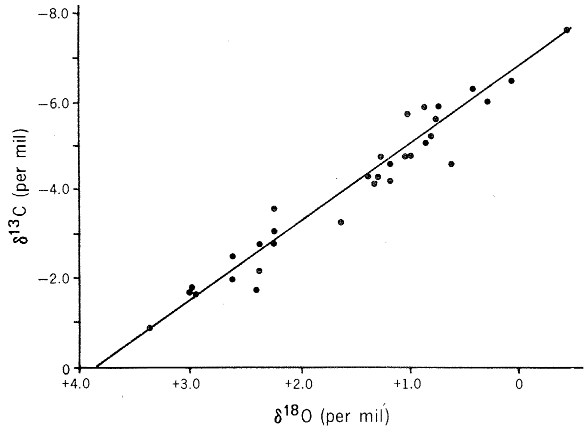


Fig. 2. $\delta^{18}O/^{16}O$ and $\delta^{13}C/^{12}C$ (per mil, with respect to the Chicago standard PDB-1) for the period 1944 to 1974, obtained from the section of *M. annularis* illustrated in Fig. 1. Divisions on the abscissa refer to the months of August-September of each year.





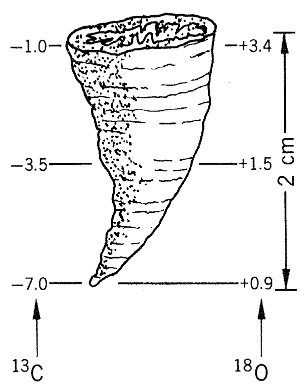


Fig. 3 (left). Relationship between carbon and oxygen isotopic composition in the time series illustrated in Fig. 2. Fig. 4 (middle). *Bathypsammia tintinnabulum* from the Blake Plateau escarpment: relationship between carbon and oxygen isotopic composition of samples taken along growth lines at different intervals from the base (upper right) to the top (lower left) of the calyxes of different adult specimens. Fig. 5 (right). *Bathypsammia tintinnabulum* from the Blake Plateau escarpment showing isotopic change during growth.

to enter the skeleton and increased deposition of sclerodermites (thereby producing the dense layers themselves) to eliminate the carbon normally removed by the Zooxanthellae. The ensuing slower growth would also favor the concentration of ^{13}C in the skeleton (*9*). The oxygen isotopic composition is affected not only by various physiological parameters mentioned but also by the ambient temperature. Thus, the ^{18}O depletion in the dense layers is undoubtedly in part due to the higher temperature at which these layers were formed. Three-year water temperature averages at Hen and Chickens Reef ranges from 20.9°C (January) to 29.4°C (July), which corresponds to a change of 2.1 per mil in the equilibrium oxygen isotopic composition. As shown in Fig. 2, the isotopic range is only about 1 per mil. It is apparent, therefore, that the temperature effect is masked by oxygen isotopic changes caused by variations in physiological activity.

Hudson *et al.* (*5*) find a correlation between some wide, high-density bands and severe environmental stress. More particularly, they consider that these bands (called stress bands to distinguish them from the normal yearly dense bands) were formed during the especially cold winters of 1941 to 1942, 1957 to 1958, 1963 to 1964, and 1969 to 1970. Of these unusually cold winters, those of 1957 to 1958 and 1969 to 1970 were the most severe (*5*, figure 3). Figure 2 shows that at these times the regular periodicity of the curve is broken, suggesting interruption of growth.

In ahermatypic corals living below the euphotic zone, Zooxanthellae are missing and the relationship between oxygen and carbon isotopes is much clearer. Weber (*12*) demonstrated that deep-sea ahermatypic corals are generally less depleted in ^{13}C and ^{18}O than hermatypic corals. We have analyzed incrementally several skeletons of the solitary coral *Bathypsammia tintinnabulum*, collected from a depth of 850 m on the Blake Plateau escarpment (32°33′N, 76°59′W), where Zooxanthellae do not exist and the yearly temperature range is small (4.5° to 6.0°C). This deep-sea solitary coral, whose skeleton seldom exceeds 2.5 cm in height, exhibits regular and irregular growth rings. These epithecal rings may represent a longer growth period and a greater amplitude than those of *M. annularis*. Although the yearly temperature range is negligible or nonexistent in the dark and seasonless deep water, it is possible that endogenous physiological rhythms may govern the growth patterns. We can only conclude on the basis of the isotopic data that the growth rate in this deep-sea solitary coral decreases from the base up, reaching zero when maturity is attained. The isotopic results (Fig. 4) reflect the growth pattern, with both carbon and oxygen approaching equilibrium values with increasing skeletal age (Fig. 5). Ahermatypic corals of this type can therefore be used for paleotemperature studies.

It is apparent from this study that strong yearly isotopic variations occur in the growth of the reef coral *M. annularis* (Fig. 2). These variations are deeply affected by the presence of Zooxanthellae, as indicated by previous studies (*6, 7, 9–11*). It appears that much work remains to be done before an unequivocal interpretation of the carbon and oxygen isotopic results is obtained in terms of basic environmental parameters.

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Structural Control of the Rapids and Pools of the Colorado River in the Grand Canyon

Abstract. *Most of the major rapids along the 450-kilometer course of the Colorado River in the Grand Canyon are within fracture zones that run perpendicular to the river. Steep tributaries flowing within the zones of bedrock weakness move large debris to the Colorado, forming the rapids. Accelerated flow through the rapids scours the deep pools that are located below them.*

The Colorado River in the Grand Canyon slopes from an elevation of about 1000 m near Lee's Ferry, Arizona, to less than 300 m at Lake Mead 450 km downstream. The 161 rapids along the route are responsible for most of the elevation change; in fact, 50 percent of the decrease takes place in 9 percent of the distance (*1*). With few exceptions, the rapids are produced by tributary debris fans that partially obstruct the main channel (Fig. 1). These rapids are the premier white water in North America and one of the major attractions in Grand Canyon National Park (*2*).

In his 1969 U.S. Geological Survey (USGS) report, Leopold (*1*) concluded that the longitudinal profile of the Colorado River was in a state of quasi-equilibrium of which the alternating deep pools and rapids are a necessary part and that the occurrence of rapids and pools is independent of the bedrock types and the valley characteristics associated with the bedrock types. In this report we present evidence that many of the pools and rapids in the Grand Canyon are located where the river crosses regional and local fracture zones.

The USGS expedition down the Grand Canyon in 1965 included the first measurements of water depths along the length of the Colorado River. Leopold's measurements, taken before construction of the Glen Canyon Dam, were made with a nonrecording Fathometer at 5-second intervals as their boat progressed down the river. We made a similar set of measurements in 1976 with a recording Fathometer, using the same method for determining the locations of the boat as we progressed downstream (*1*).

There is a problem in recording exact locations from a boat that is moving downstream at varying speed; however, we minimized the location problem by using a powerboat, and there was a fairly constant discharge (~450 m^3/sec) during our trip. Locational errors are limited to the sections of the river between points that were keyed to aerial photographs. Since our concern was regional-scale patterns over a distance of 450 km, locational errors of up to 100 m were not disturbing. The continuous records provide excellent profiles of the riverbed at a vertical resolution of ±0.3 m.

Our profile data show that although the average depth of the river is about 10 to 12 m, the longitudinal profile is highly irregular. We defined a deep pool as any place where the water depth exceeded twice the average depth of the river (20 m). On this basis we found 86 deep pools within the 360-km section sampled (mile 0 to mile 225 below Lee's Ferry), but the number would almost double if we chose 15 m as the depth. Ten pools equal in depth to the deepest reported by Leopold (about 35 m) were found when we corrected for the difference in discharge between the two data sets (~450 compared to ~1500 m^3/sec). Most of the deep pools occur in pool-and-rapid sequences. Three are located just upstream of the rapids and the others are immediately (within ~150 m) downstream.

Sixty-eight of the 86 deep pools occur in close association with "rated rapids"; this is a subjective classification ranging from 1 to 10, with 1 a riffle and 10 a large and extremely dangerous rapid (*3*). Sixteen of the 86 deep pools occur in sections of the river without rapids. Of the 40 largest rapids (rated 4 and higher), 31 have deep pools. Of the nine remaining, three have pools at least 14 m deep, and six occur along the river where the bedrock is weakest and the canyon widest (mile 50 through mile 90). We were not able to record water depths at 13 rapids because of equipment problems and extreme turbulence. Water depths for the deep pools closely associated with the ten steepest rapids (*1*) are House Rock, 24 m; Horn Creek, 20 m; 75-Mile Rapid, 13 m; Badger Creek, no record; Zoroaster Creek, 25 m; 76-Mile Rapid, no record; Unkar, no record; Tuna Creek, 25

Fig. 1. One of the many side canyon tributaries to the Colorado River in the Grand Canyon. Since the tributaries have steeper gradients than the river, they transport larger debris than the river. This large debris forms the alluvial fans and thus the rapids.