

766. OXYGEN AND CARBON ISOTOPIC COMPOSITION IN THE  
SKELETON OF AN AHERMATYPIC SCLERACTINIAN CORAL,  
*DENDROPYLLIA JAPONICA* Rehberg\*

AKIO OMURA

Department of Earth Sciences, Faculty of Science,  
Kanazawa University

---

**Abstract.** The variation in oxygen isotope ratio ( $^{18}\text{O}/^{16}\text{O}$ ) shows the periodicity within a given corallite of an ahermatypic scleractinian coral, *Dendrophyllia japonica* Rehberg, which was collected at the depth of 140 m in the Toyama Bay, Central Japan. The variation in  $^{13}\text{C}/^{12}\text{C}$  ratio, however, is little observed in the same portion of the corallite. The annual growth rate of the corallite in this area is estimated to be 23—24 mm, the distance from peak to peak in the periodicity, on the bases of the temperature dependence of the  $^{18}\text{O}/^{16}\text{O}$  ratio in ahermatypic coral skeletons and of the seasonal change in local sea water temperature.

The distal part of the same corallite denotes much lower  $^{18}\text{O}/^{16}\text{O}$  and  $^{13}\text{C}/^{12}\text{C}$  ratios than those in the other parts. This observation suggests that metabolic oxygen and carbon are vigorously incorporated into the skeleton at the front of the growth of coral and that the proportion of skeletal  $\text{CO}_3^{2-}$  derived from metabolic  $\text{CO}_2$  to those from inorganic  $\text{HCO}_3^-$  taken from sea water is apparently varied in the process of skeletal calcification.

---

### Introductory Notes

Despite the widespread abundance in marine environment, the skeletons of scleractinian corals were not noted for a fairly long time with respect to the oxygen and carbon isotopes after the work of Epstein *et al.* (1951), by the reason of the isotopic disequilibrium with the ambient sea water. In the 1970's, studies on isotopic composition of scleractinian corals became active little by little, and then some noteworthy results have been reported one after another.

Weber and Woodhead (1970, 1972a, 1972b) and Weber (1973) examined the coelenterates from many places in respect to the stable isotope ratios of their skeletons. In a series of their research, they reached a conclusion that the most important factors causing isotope ratio

variations in the skeletal carbonate of corals are temperature and zooxanthellar activity. Moreover, they showed that the  $\delta^{18}\text{O}$  value versus temperature curves for various hermatypic scleractinian genera are parallel or nearly parallel to the isotopic paleotemperature scale determined by Epstein *et al.* (1953) and later modified by Craig (1965). In the case, the scleractinian curves are displaced toward more negative  $\delta^{18}\text{O}$  values. Such a temperature dependence of  $\delta^{18}\text{O}$  value in hermatypic genera was lately proved for *Montastrea annularis* from several locations by Emiliani *et al.* (1978) and Fairbanks and Dodge (1979). Weil *et al.* (1981) also substantiated the temperature dependence of coral skeletal  $\delta^{18}\text{O}$  values by their careful experiments on two hermatypic coral species, *Pocillopora damicornis* and *Montipora verrucosa*, which were cultured under various controlled temperature and light conditions. Meanwhile, carbon isotope ratios ( $\delta^{13}\text{C}$  values) in the skeleton of hermatypic

---

\* Received Aug. 14, 1982; read Jan. 26, 1980 at Tsukuba.

corals have been considered to change as a function of water depth (Weber *et al.*, 1976; Fairbanks and Dodge, 1979), because  $\delta^{13}\text{C}$  values are chiefly controlled by the activity of the symbiotic zooxanthellae which is associated with change in light intensity.

Developing the idea of Weber and Woodhead (1970), Goreau (1977) thought out a theoretical model to explain oxygen and carbon fractionation in process of the calcification of hermatypic corals, and then Erez (1978) verified experimentally the mechanism by which lighter carbon and oxygen isotopes ( $^{12}\text{C}$  and  $^{16}\text{O}$ , respectively) were selectively enriched into the skeleton of hermatypic corals.

Deep-sea ahermatypic corals have been known to be generally less depleted in  $^{13}\text{C}$  and  $^{18}\text{O}$  than hermatypic corals and to be temperature dependent for  $\delta^{18}\text{O}$  value of their carbonate skeletons (Weber, 1973). Emiliani *et al.* (1978) also discussed the possibility of a small-sized solitary coral *Bathypsammia tintinnabulum* as a temperature indicator, based on the fact that both oxygen and carbon isotopes in the distal part of corallite which was fully matured approached the equilibrium value with sea water.

The main aim of this study is to estimate the annual growth rate of an ahermatypic scleractinian coral *Dendrophyllia japonica* Rehberg by using the cyclic variation of  $\delta^{18}\text{O}$  value within a given corallite. The change of  $\delta^{18}\text{O}$  value must be periodical in the adequate part of the same corallite growing in the region where sea water temperature varies seasonally. Because little is known about their growth rate, this attempt may be significant to discuss the skeletal calcification rates of ahermatypic corals without any symbiont, which are living over the entire temperature range of present-day ocean as compared with the relatively narrow temperature range of hermatypes.

#### Material Studied

During the KT-75-6 Cruise of the R/V "Tansei-maru", an ahermatypic scleractinian coral, *Dendrophyllia japonica* Rehberg, was

dredged at six locations in the Toyama Bay (Fig. 1). Most of all specimens were broken branches and it was rarely the case that the basal part was recovered. The bright yellowish-colored polyps were adhered originally to the distal part of each corallite and their color changed to dark brown after the collection, while some organisms encrusted compactly to the proximal part of branches.

It was the specimens collected at the locality named St-26 that were used in the present study, for the reason that the largest quantity of *Dendrophyllia* corallum were dredged with a lot of other benthos. The St-26 was situated at the depth of 140 m, about 10 km off Domi, Nanao City, Ishikawa Prefecture. Only the portion of the skeleton associated with the polyp was

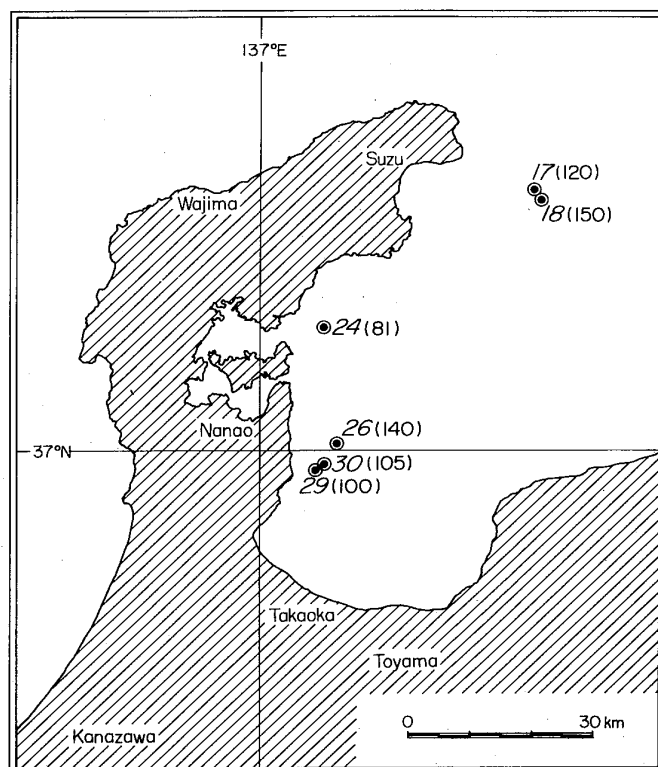


Fig. 1. Index map showing the localities where *Dendrophyllia* corallums were collected during the KT-75-6 Cruise of the R/V "Tansei-maru".

(Italic and parenthesized numbers represent the station number and water depth, respectively.)

analyzed for the purpose of determining the average isotopic composition of *Dendrophyllia* skeleton and of comparing the average isotopic composition between *Dendrophyllia* and shell samples. The shell samples used here were two species of molluscs, *Pycnodonte musashiana* (Yokoyama) and *Chlamys jousseaumei* Bavay, and one of brachiopod, *Terebratulina peculiaris* Hatai. These shell samples were entirely composed of calcite and were 16 mm in length and 15 mm in height, on the average.

A curved but the longest (about 19 cm) *Dendrophyllia* branch was selected in order to examine the variation in both oxygen and carbon isotope ratios within a corallite. The straight part was 6.3 cm in length from the tip. Soft tissues were attached to the distal part up to 14.2 mm in length. Some changes in diameter of the corallite could be observed but did not show any systematic periodicity. This corallite was elliptical in outline, and the maximum diameter attained 21.5 mm. The septa were in five complete cycles, arranged in the hexameral plan.

#### Experimental Methods

The main portion of septa was took away with a dentist's drill, after removal of polyp by immersion in 10% sodium hypochlorite solution. That is, only wall part of the corallite was used for examining the variation in isotope ratios. Because it was actually impossible to scrape along the isochronal surface inside of septa and special care was exercised to avoid the contamination of younger skeletal materials to older ones. The scraping of the specimen was carried out by use of a flat-shaped and fine-grained file. Both specimen and file were cleaned by blowing the compressed air as often as one sample was cut off. Each sample was finally ground to about 250 mesh (62  $\mu$  in diameter).

The powdered sample was roasted at 470°C for 30 min. in an atmosphere of flowing helium. Carbon dioxide was evolved under vacuum by reaction with 100% phosphoric acid and sub-

sequently extracted and purified as described before (Omura, 1977). Measurements were made on powder ranging in weight from 15 through 20 mg. The sample gas was extracted by standard techniques using trichloroethylene and liquid nitrogen cooled traps. The standardized analytical procedure involved a reaction time of about 15 hours and an extraction period of 20 min.

Isotope ratios were determined with the McKinney type mass spectrometer in which sample and standard gases were alternately compared up to six times for 3 min. intervals. Isotope ratios are reported in the widely used delta notation with respect to PDB standard CO<sub>2</sub> as:

$$\delta^{18}\text{O} = \frac{R_x - R_s}{R_s} \times 1,000 (\text{‰, per mil})$$

where R is the <sup>18</sup>O/<sup>16</sup>O (or <sup>13</sup>C/<sup>12</sup>C for  $\delta^{13}\text{C}$ ) ratio, and x and s refer to sample and standard, respectively. The reproducibility of the measurement was less than 0.18 per mil for  $\delta^{18}\text{O}$  and about 0.11 per mil for  $\delta^{13}\text{C}$ . The isotopic composition of a working standard (CK-13) used in this study has already established with respect to PDB standard through interlaboratory calibration with H. A. Lowenstam and S. Epstein of the California Institute of Technology and R. N. Clayton of the Chicago University (Nakamichi *et al.*, 1969).

#### Results and Discussion

##### (1) Composition of *Dendrophyllia* skeleton versus shell samples.

The mean isotope ratios ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values) of *Dendrophyllia* skeleton and shell samples are summarized in Table 1.

The mean  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values of three species of shell samples are +0.91 ( $\pm 0.55$ ) and +2.15 ( $\pm 0.27$ ) per mil, respectively. However,  $\delta$  values of shell samples examined here cannot be used for the precise comparison with those of *Dendrophyllia* samples, because they are composed of the different mineral phase with each

Table 1. Mean oxygen and carbon isotope ratios of *Dendrophyllia japonica* Rehberg and three shell samples.

Sample	$\delta^{18}\text{O}^*$	$\delta^{13}\text{C}^*$
<i>Dendrophyllia japonica</i>	- 2.48(0.79)10	- 6.53(0.90)10
<i>Terebratulina peculiaris</i>	+ 0.67(0.33)5	+ 1.95(0.21)5
<i>Chlamys jousseaumei</i>	+ 0.70(0.63)5	+ 2.42(0.08)5
<i>Pyenodonte musashiana</i>	+ 1.36(0.30)5	+ 2.10(0.22)5

\* Format for data: mean delta value (standard deviation) number of specimens analyzed.

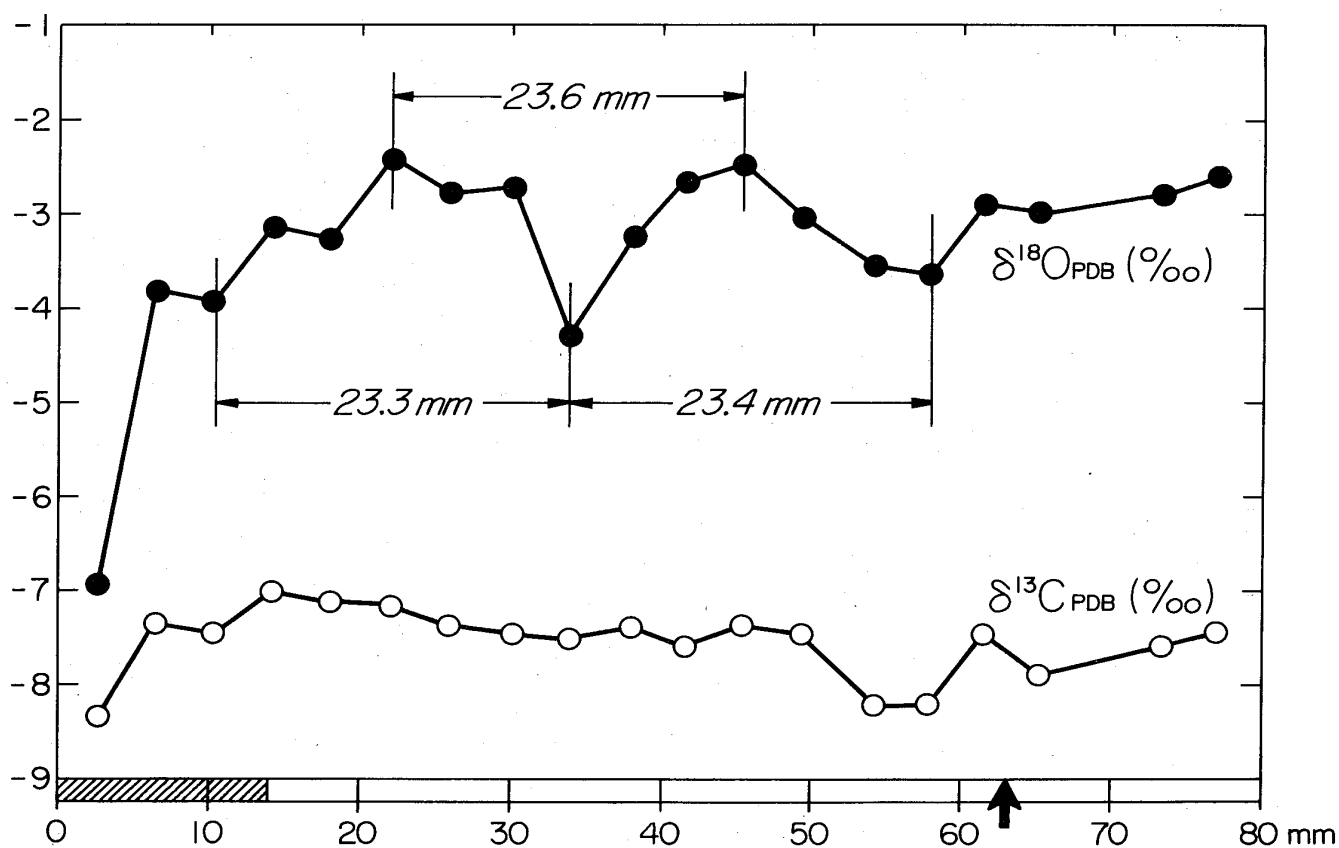


Fig. 2. Variations in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values within a corallite of *Dendrophyllia japonica* Rehberg. (Shaded part denotes the region where polyp was attached; the arrow shows the curvature point of the corallite.)

other. It is possible to estimate the  $\delta$  value of the aragonitic material in isotopic equilibrium with sea water. Such an aragonite is expected to give the  $\delta^{18}\text{O}$  value of +1.8 per mil relative to the PDB standard, by using the equation of Horibe and Oba (1972). Accordingly, *Dendrophyllia* skeleton is thought to be approximately 4.3 per mil lower in  $\delta^{18}\text{O}$  value than the aragonite in isotopic equilibrium with sea water. Depending on the data of Weber and Woodhead (1972a), the difference in  $\delta^{18}\text{O}$  value between skeletons of hermatypes and the aragonite in isotopic equilibrium is not exceeding 3 per mil at a given temperature. Therefore, it can be conclusively said that the above observations support the strong "bital effect" of ahermatypic corals, as mentioned by Weber (1973).

(2) Variations in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values within a corallite.

Variations in oxygen and carbon isotope ratios within a given corallite are illustrated in Fig. 2.

$\delta^{13}\text{C}$  value does not vary systematically and its variation is characterized by the limited ranges, particularly in the straight-elongated part of the corallite. On the other hand, Fig. 2 denotes clearly the cyclic variation of  $\delta^{18}\text{O}$  value in the corallite up to about 6 cm in length from the tip. The range of variation in  $\delta^{18}\text{O}$  value is 1.17 to 1.91 per mil. The distance from peak to peak in the periodicity is 23 to 24 mm.

If the salinity of the ambient sea water changed seasonally, apparent  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values alike should be influenced and show the same pattern of their variations. The limited range in variation of  $\delta^{13}\text{C}$  value suggests that the chemistry of the sea water is little varied by the seasonal change in influx of fresh water. If the variation in  $\delta^{18}\text{O}$  value within the corallite depends substantially on temperature curve is parallel or nearly parallel to the paleotemperature scale, as pointed out by Weber and Woodhead (1972a), the variation from 1.17 to 1.91 per mil in  $\delta^{18}\text{O}$  value means that the seasonal change in sea water temperature is approximately 5 to 8°C at the sampling location. So far some data at the location tell us about the change in

temperature and salinity of the sea water through the year (Figs. 3 and 4). Such data seem to support that the temperature range of 5 to 8°C is not irrelevant as the seasonal variation in sea water temperature even at the depth of 140 m near the location where the samples analyzed were collected.

For those reasons, the cyclic variation in  $\delta^{18}\text{O}$  value is considered to be caused by the seasonal change of sea water temperature. In other words, the distance from peak to peak seen in the periodicity is regarded as an annual growth rate of *Dendrophyllia japonica* Rehberg. The *Dendrophyllia* specimen used here was a broken branch, and hence it is quite hard to infer what part in a dendroid corallum was examined. It may, however, be said that the

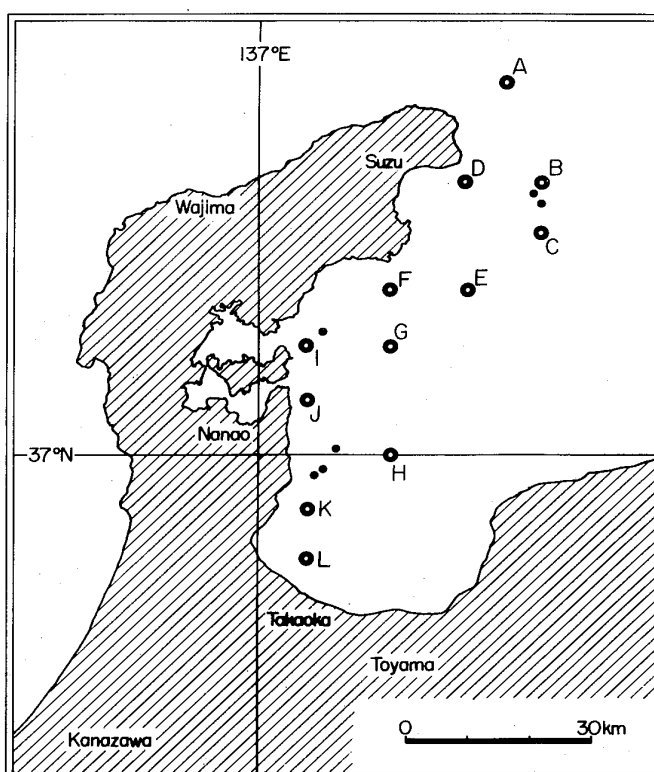


Fig. 3. Map showing some locations where fixed point observation is carried out for temperature and salinity of sea water by the Fisheries Experiment Station of Toyama Prefecture.

(Small black circles show the localities where *Dendrophyllia* corallums were found to inhabit at present.)

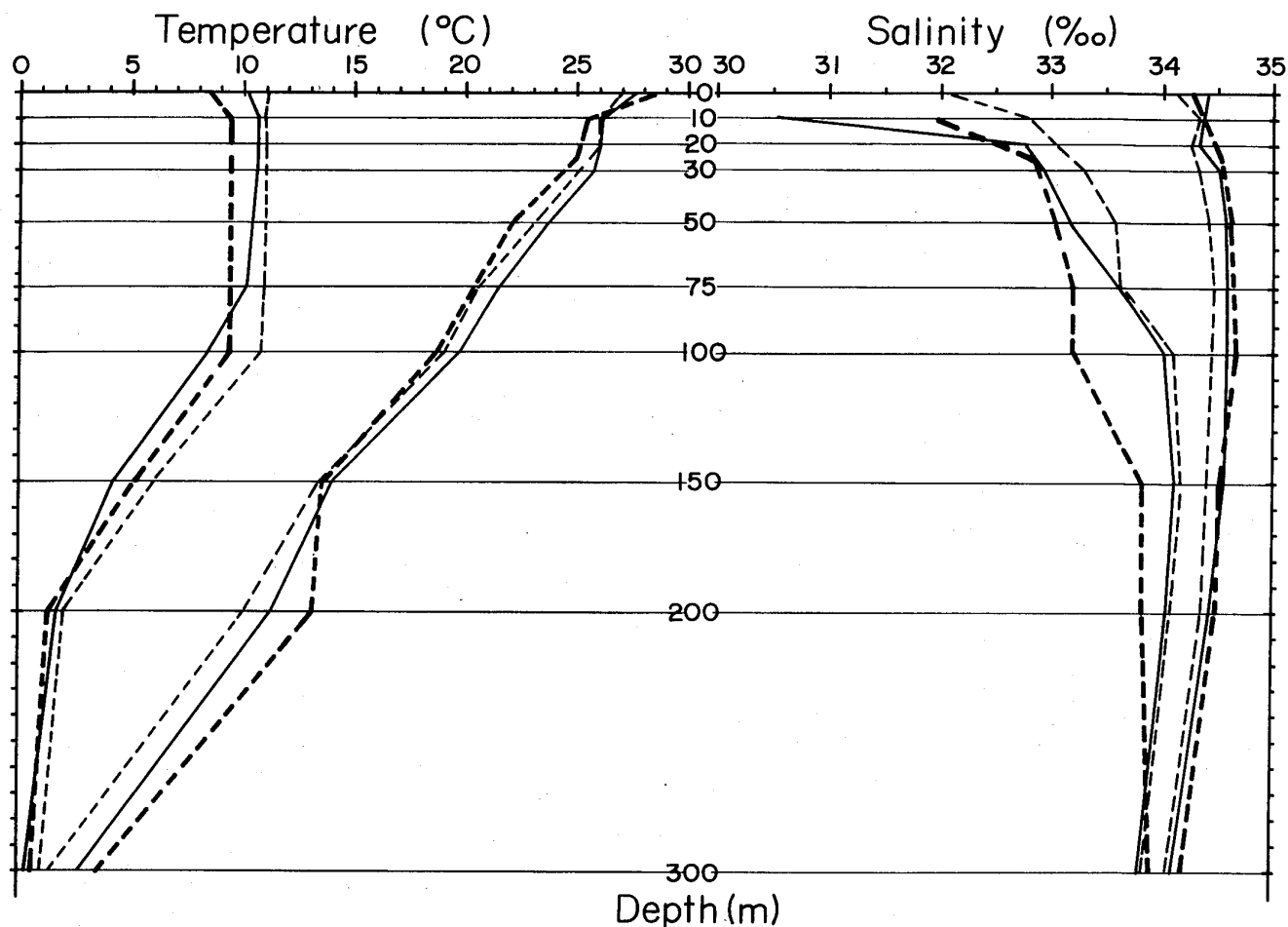


Fig. 4. The range of variation in temperature and salinity of sea water in the Toyama Bay. (Thick dotted lines are drawn on fifty data at twelve locations from points A to L, from April, 1953 through March, 1958; while thin solid and dotted lines on ten data from November, 1978 through November, 1979, at twelve locations and point H, respectively.)

partial annual growth rate of *Dendrophyllia* corallum attains 23 to 24 mm at this place. It has often been said that growth rates of ahermatypic corals are much lower than hermatypes. Because they do not have a favorable influence upon the symbiotic zooxanthellae in their calcification process. Further elucidation on the cyclic variation in  $\delta^{18}\text{O}$  value will require more detail observations. The growth rate of *Dendrophyllia* should be reconfirmed with a radiochemical technique by use of short-lived radioactive isotopes.

(3) Oxygen and carbon isotope ratios at the tip of a corallite.

Another interesting result was obtained in the variation of oxygen and carbon isotope ratios

within a corallite. It is the low  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values observed at the tip of the corallite (Fig. 2). In order to make sure whether such an extremely low  $\delta$  value is a characteristic common to all of *Dendrophyllia* corallite, only the wall part of three portions in a corallite was taken out from the other four corallite specimens as shown in Fig. 5 and were examined for isotopic composition.

As a result, it is clear that all of the examined corallite show the same pattern without exception (Table 2). Because metabolic carbon is some 12 to 17 per mil lighter and metabolic oxygen is some 10 per mil lighter than those derived from  $\text{HCO}_3^-$  in sea water (Weber and Woodhead, 1970; Land *et al.*, 1975; Goreau, 1977; Emiliani *et al.*,

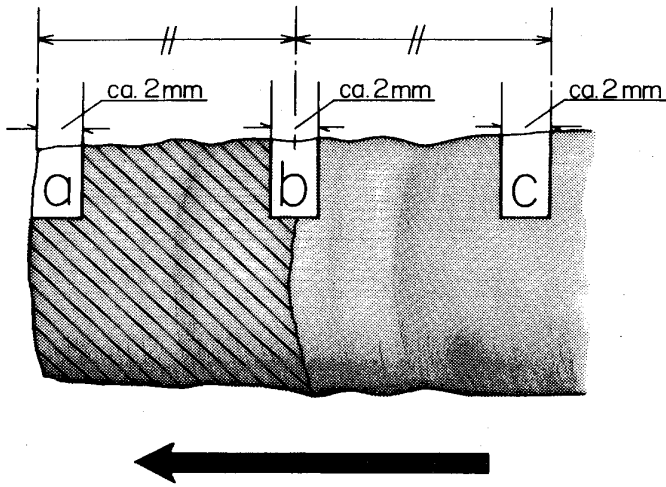


Fig. 5. Simplified sketch of *Dendrophyllia* specimen showing three portions to examine the variation in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values within a corallite.

(Shaded part and black arrow represent the limit of adherent polyp and growth direction, respectively.)

1978), it is very likely that metabolic carbon and oxygen are vigorously incorporated into the skeleton which is secreted at the front of growth. That is, the proportion of skeletal  $\text{CO}_3^{2-}$  derived from metabolic  $\text{CO}_2$  to that from inorganic  $\text{HCO}_3^-$  taken from sea water seems to vary in the process of the skeletal calcification by hermatypic scleractinian coral. Such an apparent variation in isotopic composition is summarized in Fig. 6. In the case of *Dendrophyllia* skeletons, it does never approach the value in isotopic equilibrium with sea water, as shown for a small-sized solitary coral *Bathypsammia tintinnabulum* by Emiliani *et al.* (1978). These facts are suggestive of the followings: (1) *Dendrophyllia* grow infinitely at the same growth rate if circumstances permit, whereas ahermatypic simple corals like *Bathypsammia* cannot exceed certain limit in size; (2) The higher  $\delta$  values in a corallite except the tip may be resulted from reformation of the isotopic composition due to the secondary thickening or the secondary deformation of fine skeletal structure during the life time of scleractinian coral as observed in rugosa by Kato (1963).

Corallite No.	a		b		c	
	$\delta^{18}\text{O}_{\text{PDB}}$	$\delta^{13}\text{C}_{\text{PDB}}$	$\delta^{18}\text{O}_{\text{PDB}}$	$\delta^{13}\text{C}_{\text{PDB}}$	$\delta^{18}\text{O}_{\text{PDB}}$	$\delta^{13}\text{C}_{\text{PDB}}$
1	- 6.94	- 8.35	- 3.13	- 7.00	- 2.81	- 7.38
2	- 7.45	- 8.63	- 2.48	- 7.10	- 2.84	- 7.37
3	- 6.04	- 8.06	- 3.00	- 6.18	- 4.25	- 5.82
4	- 6.06	- 7.81	- 3.31	- 5.74	- 3.53	- 6.20
5	- 4.66	- 8.79	- 3.63	- 7.33	- 3.43	- 7.04
Mean delta value	- 6.23	- 8.36	- 3.11	- 6.67	- 3.37	- 6.76
Standard deviation	( $\pm 1.06$ )	( $\pm 0.41$ )	( $\pm 0.42$ )	( $\pm 0.68$ )	( $\pm 0.59$ )	( $\pm 0.71$ )

Table 2.  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values in different three portions within the same corallite.

(See Fig. 5 for the portion analyzed.)

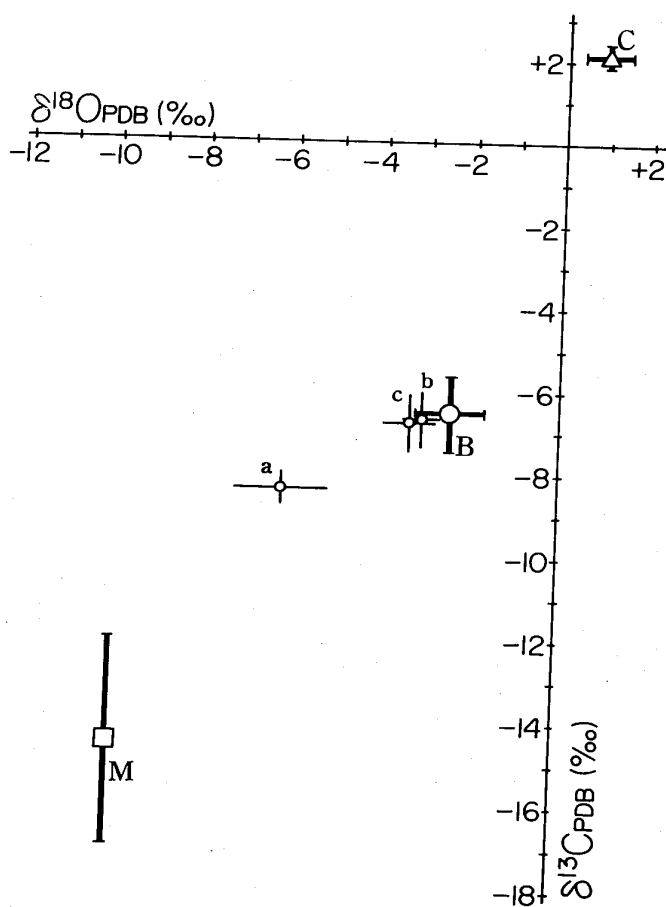


Fig. 6.  $\delta^{18}\text{O}$  versus  $\delta^{13}\text{C}$  diagram of the samples examined in this study.

(B and C show mean  $\delta$  values of bulk *Dendrophyllia* skeleton and shell samples, respectively; a, b and c, mean  $\delta$  values of three portions illustrated in Fig. 5; M,  $\delta$  value of metabolic carbon and oxygen in coral skeleton, mentioned by Weber and Woodhead, 1970; Land *et al.*, 1975; Goreau, 1977; and Emiliani *et al.*, 1978.)

#### Acknowledgments

I wish to thank Prof. K. Konishi of the Department of Earth Sciences, Faculty of Science, Kanazawa University, for his continuous encouragement throughout this study. Coral and shell samples used in this work were identified by Drs. K. Mori and K. Ogasawara of the Institute of Geology and Paleontology, Faculty of Science, Tohoku University. My thanks are also due to the KT-75-6 crew of the R/V

“Tansei-maru” of the Ocean Research Institute, University of Tokyo, for collecting the samples and to members of the Fisheries Experiment Station of Toyama Prefecture for their permission to cite the data on temperature and salinity of sea water in the Toyama Bay.

#### References Cited

- Craig, H. (1965): The measurement of oxygen isotope paleotemperature. In Tongiorgi, E. (ed.): *Stable Isotopes in Oceanographic Studies and Paleotemperatures*. p. 161–182, Spoleto.
- Emiliani, C., Hudson, J. H., Shinn, E. A. and George, R. Y. (1978): Oxygen and carbon isotopic growth record in a reef coral from the Florida Keys and deep-sea coral from Blake Plateau. *Science*, vol. 202, p. 627–629.
- Epstein, S., Buchsbaum, R., Lowenstam, H. and Urey, H. C. (1951): Carbonate-water isotopic temperature scale. *Bull. Geol. Soc. Amer.*, vol. 62, p. 417–426.
- , ———, ——— and ——— (1953): Revised carbonate-water isotopic temperature scale. *Bull. Geol. Soc. Amer.*, vol. 64, p. 1315–1326.
- Erez, J. (1978): Vital effect on stable-isotope composition seen in foraminifera and coral skeletons. *Nature*, vol. 273, p. 199–202.
- Fairbanks, R. G. and Dodge, R. E. (1979): Annual periodicity of the  $^{18}\text{O}/^{16}\text{O}$  and  $^{13}\text{C}/^{12}\text{C}$  ratios in the coral *Montastrea annularis*. *Geochim. Cosmochim. Acta*, vol. 43, p. 1009–1020.
- Goreau, T. J. (1977): Carbon metabolism in calcifying and photosynthetic organism: theoretical models based on stable isotope data. *Proc. 3rd Int. Coral Reef Symp.*, vol. 2, p. 395–401.
- Horibe, Y. and Oba, T. (1972): Temperature scales of aragonite-water and calcite-water systems. *Fossils*, nos. 23/24, p. 69–79. (in Japanese with English abstract)
- Kato, M. (1963): Fine skeletal structures in rugosa. *Jour. Fac. Sci. Hokkaido Univ.*, Ser. 4, (Geol. & Mineral.), vol. 11, p. 571–630.
- Land, L. S., Lang, J. C. and Smith, B. N. (1975): Preliminary observations on the carbon



- isotopic composition of some reef coral tissues and symbiotic zooxanthellae. *Limnol. Oceanogr.*, vol. 20, p. 283—287.
- Nakamichi, O., Konishi, K. and Sakai, H. (1969): On the isotopic analyses of oxygen and carbon of marine biogenic carbonates such as corals and pelecypods. *Mass Spectroscopy*, vol. 17, p. 500—508. (in Japanese with English abstract)
- Omura, A. (1976): On the measurement of oxygen and carbon isotope ratios of biogenic carbonates. *Bull. Japan Sea Res. Inst., Kanazawa Univ.*, no. 8, p. 15—25. (in Japanese with English abstract)
- Weber, J. N. and Woodhead, M. J. (1970): Carbon and oxygen isotope fractionation in the skeletal carbonates of reef-building corals. *Chem. Geol.*, vol. 6, p. 93—117.
- and ——— (1972a): Temperature dependence of oxygen-18 concentration in reef coral carbonates. *Jour. Geophys. Res.*, vol. 77, p. 463—473.
- and ——— (1972b): Stable isotope ratio variations in non-scleractinian coelenterate carbonates as a function of temperature. *Mar. Biol.*, vol. 15, p. 293—297.
- (1973): Deep-sea ahermatypic scleractinian corals: isotopic composition of the skeleton. *Deep-Sea Res.*, vol. 20, p. 901—909.
- , Deines, P., Weber, P. H. and Baker, P. A. (1976): Depth related changes in the  $^{13}\text{C}/^{12}\text{C}$  ratio of skeletal carbonate deposited by the Caribbean reef-frame building coral *Montastrea annularis*: further implications of a model for stable isotope fractionation by scleractinian corals. *Geochim. Cosmochim. Acta*, vol. 40, p. 31—39.
- Weils, S. M., Buddmeier, R. W., Smith, S. V. and Kroopnik, P. M. (1981): The stable isotopic composition of coral skeletons: control by environmental variables. *Geochim. Cosmochim. Acta*, vol. 45, p. 1147—1153.

非造礁性サンゴ *Dendrophyllia japonica* Rehberg 骨格中の酸素・炭素同位体組成: 石川県七尾市百海東方約 10 km・水深 140 m の地点からドレッジされた非造礁性サンゴの一種 *Dendrophyllia japonica* Rehberg 骨格中の酸素・炭素同位体比 ( $^{18}\text{O}/^{16}\text{O}$ ・ $^{13}\text{C}/^{12}\text{C}$ ) を求めた。その結果、炭素同位体比の変動がほとんど見られないのに対し、同一 corallite の成長方向に沿って酸素同位体比の周期的変動が明らかになった。 $\delta^{18}\text{O}$  値の変動巾は 1.2~1.9‰ で、周期性にみられる各ピーク間の距離は 23~24 mm であった。このことは、非造礁性サンゴ骨格中の酸素同位体比の温度依存性から、生息環境における水温の季節変化を示すと考えられ、周期性にみられた各ピーク間の距離から採集地付近の同種のサンゴの成長率が 20 mm/yr 以上に達すると結論できる。

また、corallite の最先端部における酸素・炭素同位体比がともに上記の周期性にみられた変動巾をこえて、著しく低い  $\delta$  値を示すことが明らかになった。この事実から、とくに成長の最前線でサンゴ固有の代謝作用で作られる、いわゆる metabolic な酸素および炭素がさかんに取込まれていること、またサンゴ骨格の石灰化過程で、導入される酸素・炭素のうち、海水中の重炭酸イオン ( $\text{HCO}_3^-$ ) 由来のものと metabolic なものとの割合が変化するように思われる。

大村 明雄