STABLE ISOTOPE COMPOSITION OF BENTHIC CALCAREOUS ALGAE FROM BERMUDA[1]

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ABSTRACT: Carbonate secreted by benthic algae from Bermuda (5 genera, 3 phyla) can be grouped into four types according to the $\delta^{18}O$ and $\delta^{13}C$ composition: a "heavy" and a "light" set for oxygen, and a "large-variability" and a "small-variability" set for carbon. The sets are not congruent. In one alga, different parts of the same skeleton belong to different oxygen sets. Vital effects, which are tied to developmental stages as well as to environmental response, are predominant in producing the observed isotopic variations.

INTRODUCTION

The isotopic composition of benthic calcareous algae is of interest in both biological and geological studies. These algae are important producers of both calcium carbonate and organic matter in many shelf areas from the tropics to temperate regions (Bathurst, 1971; Milliman, 1974). Estimates of regional algal contribution to shallow-water carbonate deposition range from 0 to 61 percent (Ginsburg, 1956; Milliman, 1972; Neumann and Land, 1975). Benthic algae have left a significant paleontologic record and have been responsible for the buildup of enormous masses of limestone. Their remains are useful in biostratigraphy and for paleo-environmental reconstructions (Johnson, 1961; Keith and Weber, 1965; Wray, 1977). Variations in the stable isotope composition of the algae may also be useful for the analysis of calcification processes (Borowitzka, 1977).

Our own studies were made to clarify some very elementary questions: 1) Granted that benthic algae deposit their skeletons outside of equilibrium (Keith and Weber, 1965), just how far from equilibrium does precipitation occur; 2) is the disequilibrium constant or variable within the same species; and 3) are there differences between the various kinds of benthic algae, regarding these parameters. This information is necessary for any kind of ecologic or paleoecologic assessment of the utility of stable isotopes in calcareous algae. We found very little information on the stable isotope composition of benthic calcareous algae in the literature. The data which exist are derived from the analysis of whole plants (Keith and Weber, 1965; Gross, 1964; Gross and Tracey, 1966), with the exception of those of Lowenstam and Epstein (1957), who distinguished between heads and stalks of *Rhipocephalus* and *Penicillus*.

Here we report the first detailed evidence on systematic relationships in the isotopic compositions within and between algal taxa from the same environment. The data are derived from the analysis of single *Halimeda* segments and from parts of single *Penicillus, Acetabularia, Padina,* and *Amphiroa* plants. Up to 18 samples were taken from one individual plant. In addition, the isotopic sequences are time-controlled, and they refer to exactly the same time-span in the various specimens analyzed. We find that vital effects on isotopic composition predominate and that these effects are tied both to developmental stages and to environmental change.

MATERIAL AND METHODS

The algae we chose to analyze are common representatives of modern Rhodophyta (red algae: *Amphiroa fragilissima*), Phaeophyta (brown algae: *Padina sanctae-crucis*), and Chlorophyta (green algae: *Halimeda incrassata, Penicillus*

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capitatus, and *Acetabularia crenulata*). All specimens were collected by diving in Harrington Sound, Bermuda, during September, 1978, from 2, 6, 8, and 10 m water depth. During the growth period the surface temperature varied between 26° C and 29° C at the pier of the Bermuda Biological Station (daily recordings). The specimens grew from the end of August to the end of September, 1978. Alizarin Red-S was used as a time marker. Algae were covered for one day by a clear plastic tent with a volume of about 3 m^3, into which the Alizarin stain was injected as a concentrated sea water solution. The alizarin was incorporated into the calcifying part of the algae while they were thus covered. The stain remains fixed as a visible red band in the skeleton as growth continues after removal of the cover, thus defining a "time line" in the skeleton. All skeletal carbonate deposited after staining appears above this time line. For the carbonate deposited between staining and sampling, we assumed linear growth. The "time line" in the skeletons allows us to compare the isotopic data with the environment during the deposition of the algal carbonate. The algae can grow one to several millimeters per day or in the case of *Halimeda* can produce up to one segment per day per branch on actively growing tips (Wefer, 1980). *Halimeda, Penicillus, Acetabularia*, and *Padina* are aragonitic, whereas Amphiroa precipitates Mg-calcite.

Specimens were subsampled using a scalpel to separate individual parts of capitulums, stalks, or segments. Depending on their size, 1 to 6 mm of brush-like capitulums or stalks (*Penicillus, Acetabularia*) or fronds (*Padina*) were used. In the case of *Halimeda*, between the entire and one-eighth (cut in vertical direction) of a segment was used for the analysis. To remove the organic matter attached to the skeletons, each subsample was soaked in 10 percent aqueous solution of H_2O_2 for one-half hour. Subsequently, it was washed five times with deionized water, dried at 60° C, and heated for 30 minutes at 300° C under vacuum. Procedures for the measurement of oxygen and carbon isotopes are described by Berger and Killingley (1977). Analytical precision was found to be 0.1‰ (one standard deviation). Results are given as deviation from PDB in per mil:

$$\delta^{18}O = [(^{18}O/^{16}O)\ \text{sample}/(^{18}O/^{16}O)\ \text{standard} - 1] \times 1000;\ \text{for}\ \delta^{13}C\ \text{use}\ ^{13}C/^{12}C.$$

The measured $\delta^{18}O$ values for different water depths in Harrington Sound were 1.05 ± 0.1‰ (Wefer et al., 1980). Kroopnick et al. (1972) reported a $\delta^{13}C$ of 1.94 permil in ΣCO_2 from a station (1 m water depth) in the North Atlantic.

OXYGEN ISOTOPES

Results

Clearly, there are two sets of data (Fig. 1 a–c; Table 1): one containing $\delta^{18}O$ values showing significant depletion in ^{16}O, the other showing similarly distinct depletion in ^{18}O, compared with those expected for equilibrium precipitation (calculation based on the initial water composition, daily temperature recordings, and the calcite paleoequation of Epstein et al., 1953; according to Tarutani et al. (1969) the aragonite equilibrium values should be 0.6‰ heavier than calcite equilibrium values). The "heavy" set includes *Penicillus* (except the stalk of the specimen from 8 m water depth), *Padina*, and *Acetabularia*. The "light" set consists of *Halimeda, Amphiroa*, and the stalk of *Penicillus* from 8 m water depth. The range of $\delta^{18}O$ variations within the algae is larger than expected from ambient temperature variations. Two types of "vital effects" (Urey et al., 1951) can be envisaged: those associated with programmed changes during growth ("stage" effects) and those which are environmentally induced ("response" effects). A striking example of a "stage" effect is given in the oxygen isotope composition of *Penicillus*. The stalk of the *Penicillus* from 8 m water depth is greatly depleted in ^{18}O while the capitulum is enriched. The same trend is visible in the *Penicillus* from 2 m depth although both stalk and capitulum are enriched in ^{18}O. The *Halimeda* segments from three water depths show similar changes through time. Here the variations would seem to be of the "response" type, as suggested by the parallelism of fluctuations in the three isotopic sequences from three separate specimens. Interestingly, the Halimeda from 10 m water depth shows the lightest values, the one from 6 m water shows the heaviest, and the one from 2 m water depth stays at strictly intermediate values.

The total range of the $\delta^{18}O$ in these algal carbonates is between 0.15 and −4.24‰. Similar ranges of isotopic composition of algal aragonites (whole algae) have previously been reported (Keith and Weber, 1965; Lowenstam and Epstein, 1957; Gross, 1964; Gross and Tracy,

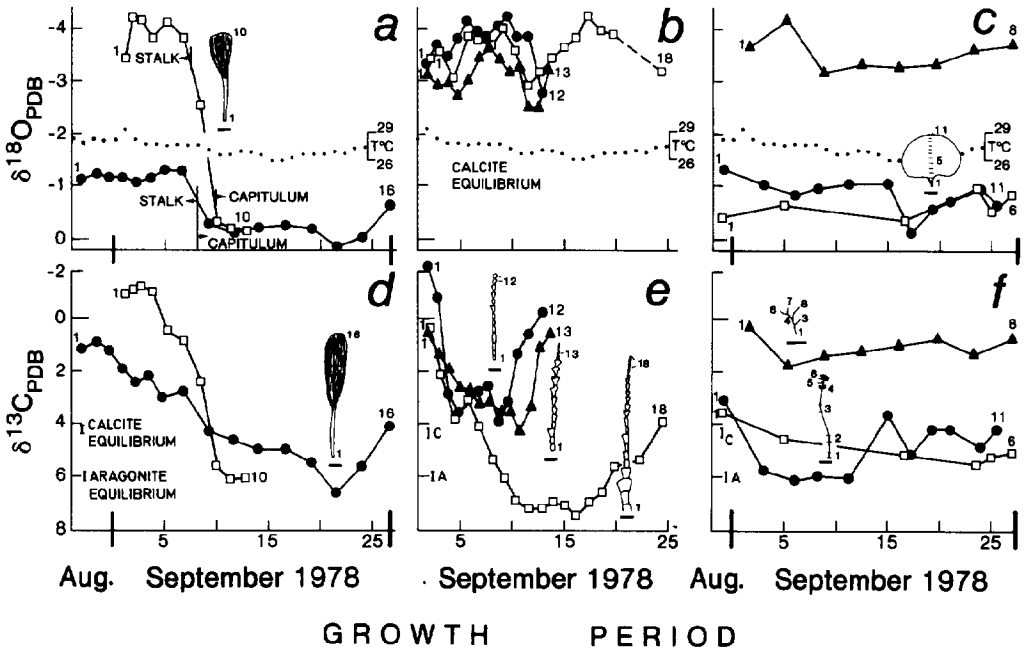

FIG. 1.—Isotopic composition of subsamples from benthic algae taken in Harrington Sound, Bermuda. The numbers on the curves refer to numbers on the drawings of the plants (scale is 1 mm). The growth period was estimated using Alizarin Red-S as a stain of a "time line" within the skeletons. Between staining and sampling, and for the skeletons' growth before the staining, linear growth was assumed. Temperature variations for the estimated growth period are shown as dotted lines. The temperature and isotope scale are matched using the "calcite" equations of Epstein et al. (1953) and the sea water composition data of Craig and Gordon (1965). The aragonite equilibrium values should be 0.6‰ heavier than calcite equilibrium values (Tarutani et al., 1969). a) $\delta^{18}O$ variations in two *Penicillus capitatus* from 2 m (circles) and 8 m (squares) water depth (16 and 10 subsamples, respectively). b) $\delta^{18}O$ variations in three *Halimeda incrassata* from 2 m (squares), 6 m (triangles), and 10 m (circles) water depth. c) $\delta^{18}O$ variations in *Amphiroa fragilissima* from 1.5 m (triangles), *Acetabularia crenulata* from 6 m (squares), and *Padina sanctae-crucis* from 2 m (circles) water depth. d) $\delta^{13}C$ variations in two *P. capitatus* (see 1a). e) $\delta^{13}C$ variations in three *H. incrassata* (see 1b). f) $\delta^{13}C$ variations in *A. fragilissima*, *A. crenulata*, and *P. sanctae-crucis* (see 1c).

1966) as has the fact that $\delta^{18}O$ values for *Penicillus* are lighter for the capitulum than for the stalk (Lowenstam and Epstein, 1957). Gross (1964) reported light $\delta^{18}O$ values for *Halimeda monile* and *Amphiroa*, which agrees with our data, but also reported $\delta^{18}O$ values about 2‰ heavier for two other *Halimeda* species from the same general environment.

Discussion

Metabolic and Diffusional Effects.—Carbonates depleted in ^{18}O (*Halimeda, Amphiroa,* and *Penicillus* stalk) may indicate i) admixture of metabolic CO_2 at the site of calcification, or ii) fractionation of bicarbonate during transport to the calcification site. Sites of calcification are commonly separated from the external medium by a layer of cells so that there is a relatively long diffusion path (Borowitzka, 1977). These depletion mechanisms presumably apply to *Halimeda, Amphiroa,* and the stalks of *Penicillus*. In *Penicillus*, especially, fractionation during transport of bicarbonate taken up in the capitulum of the plant and delivered to calcification sites at the stalk would appear to be a likely cause for the isotopic differences between stalk and capitulum.

While depletion in ^{18}O is not unusual in biogenic carbonates and has been described for foraminifera (Duplessy et al., 1970; Buchardt and Hansen, 1977; Erez, 1978; Wefer et al., 1980) and corals (Erez, 1978; Weber, 1973; Land et al., 1975; Goreau, 1977; Land et al., 1977), enrichment in ^{18}O is unexpected. It was previously reported for some ahermatypic corals (Land et al., 1977) and large tropical foraminifera (Wefer and Berger, 1980). Dudley and Goodney (1979)

TABLE 1.—*Isotopic composition of calcareous algae, in per mil (‰) relative to the PDB standard. The subsample numbers refer to numbers on the drawings in Figure 1*

Subsample No.	$\delta^{18}O$	$\delta^{13}C$
Penicillus capitatus, 2 m water depth		
1	−3.44	−0.94
2	−4.21	−1.14
3	−4.15	−1.20
4	−3.82	−1.04
5	−4.11	0.51
6	−3.82	0.87
7	−2.51	2.41
8	−0.31	5.60
9	−0.22	6.13
10	−0.16	6.09
Penicillus capitatus, 8 m water depth		
1	−1.13	1.19
2	−1.23	0.90
3	−1.16	1.23
4	−1.17	1.93
5	−1.07	2.51
6	−1.16	2.38
7	−1.30	2.96
8	−1.28	2.69
9	−0.30	4.31
10	−0.12	4.61
11	−0.23	4.94
12	−0.26	4.95
13	−0.20	5.54
14	0.15	6.67
15	−0.03	5.69
16	−0.63	4.13
Halimeda incrassata, 2 m water depth		
1	−3.42	0.37
2	−3.57	2.11
3	−3.04	3.86
4	−3.83	3.12
5	−3.75	4.12
6	−3.68	5.40
7	−4.00	6.09
8	−3.57	6.91
9	−2.90	7.25
10	−3.17	7.29
11	−3.43	6.94
12	−3.62	7.11
13	−3.81	7.49
14	−4.21	7.01
15	−3.95	6.60
16	−3.88	5.68
17	−5.32	5.38
18	−3.16	4.00
Halimeda incrassata, 6 m water depth		
1	−3.13	0.53
2	−2.90	1.33
3	−2.95	1.93
4	−2.72	2.59
5	−2.98	2.70
6	−3.42	3.25
7	−3.61	3.21
8	−3.41	3.55
9	−3.16	3.58
10	−3.25	4.33
11	−2.49	3.34
12	−2.53	1.15
13	−3.18	0.61

Subsample No.	$\delta^{18}O$	$\delta^{13}C$
Halimeda incrassata, 10 m water depth		
1	−3.34	−1.98
2	−3.67	−0.79
3	−3.45	2.85
4	−3.80	3.56
5	−4.14	3.26
6	−3.94	2.77
7	−3.83	2.55
8	−4.04	3.95
9	−4.24	3.15
10	−3.83	1.35
11	−3.83	0.60
12	−2.77	−0.25
Amphiroa fragilissima, 1,5 m water depth		
1	−3.63	0.28
2	−4.14	1.36
3	−3.16	1.74
4	−3.24	1.21
5	−3.31	1.30
6	−3.30	0.97
7	−3.60	0.74
8	−3.71	0.74
Padina sanctae-crucis, 1,5 m water depth		
1	−1.30	3.08
2	−1.02	5.75
3	−0.86	6.08
4	−0.96	5.96
5	−1.04	6.04
6	−1.05	3.65
7	−0.11	5.12
8	−0.56	4.18
9	−0.71	4.20
10	−0.94	4.85
11	−0.63	4.17
Acetabularia crenulata, 6 m water depth		
1	−0.39	3.58
2	−0.64	4.54
3	−0.35	5.15
4	−0.94	5.52
5	−0.51	5.20
6	−0.83	5.05

showed on coccoliths grown in culture that the isotopic composition of at least some algal carbonate is influenced by growth rate.

Variations in the $\delta^{18}O$ composition in the sea water appear to have been negligible for the duration of the experiment. The expected salinity variation in September 1978 was not larger than 0.3‰ (v. Bodungen, pers. comm.), which would have caused a $\delta^{18}O$ variation of no more than 0.1‰ (Craig and Gordon, 1965). Therefore, the apparent disequilibrium is not an artifact of uncontrolled variation in the $\delta^{18}O$ of seawater. At least in these algae, therefore, and under the conditions studied, there are metabolic processes which lead to enrichment of ^{18}O. The fact that our data show two distinct sets of $\delta^{18}O$ values suggests that ^{18}O enrichment processes and ^{18}O depletion processes are strong and unbalanced in the plants studied. Data on deposition rates of calcium-isotopes in various calcareous algae from Bermuda (Böhm, 1978) suggest slower growth rates for *Cymopolia, Padina,* and *Amphiroa,* but about the same rates for *Halimeda* and *Penicillus*. Thus, growth rate per se does not seem to be responsible for the partitioning into a "heavy" and "light" set. Both photosynthesis and calcification rates are highest in the upper, younger segments of *Halimeda* plants. The younger segments also have a higher light-to-dark ratio in calcification than the older, mature segments (Borowitzka and Larkum, 1976). These differences do not result in different fractionation of oxygen (Fig. 1b).

Mineralogy.—There is no apparent relationship between isotopic composition and mineralogy of the skeletons. As mentioned, *Halimeda* and *Penicillus* are aragonitic, whereas *Amphiroa* precipitates Mg-calcite (in this case with 17.5 mol per cent $MgCO_3$). The mol percent $MgCO_3$ in $CaCO_3$ was determined by X-ray diffraction (using the data of Goldsmith and Graf, 1958). All analyzed specimens show about the same depletion in ^{18}O relative to expected values. For *Amphiroa* with a $MgCO_3$ content of 17.5 mol percent, an enrichment in ^{18}O of about 1‰ should be expected (0.06‰ per mol percent $MgCO_3$; see Tarutani et a., 1969). If this calculation is correct, $\delta^{18}O$ values of *Amphiroa* are 2.5 to 3.5‰ lighter than the expected equilibrium values.

Response Effects.—It is tempting to invoke environmental factors in explaining ^{18}O enrichment or depletion, such as light and nutrient supply. We believe these are important in explaining the variations about the general level ("response" effect seen in Halimeda). In the case of *Halimeda,* response effects may be largely irrelevant to the level itself, as suggested by the similar overall level of the different *Halimeda* plants growing at different depths (Fig. 1b). However, in *Penicillus* the two distinct records come from specimens from different depths (2 m and 8 m); hence an environmental effect in producing the distinctness cannot be excluded.

In the case of *Penicillus* we can postulate an "irradiation" effect (the 8 m specimen has about 3‰ lighter $\delta^{18}O$ values in the stalk than the 2 m specimen, Fig. 1a). At noon, light intensities at 2 m are between 130 and 160 Watt m^{-2}, at 6 m between 25 and 60 Watt m^{-2}, at 8 m between 10 and 30 Watt m^{-2}, and at 10 m between 7 and 15 Watt m^{-2}, depending on clouds. The temperature range between 0 and 10 m was less than 0.3° C, the salinity range less than 0.2‰. The nutrients showed about the same level within the uppermost 10 m (v. Bodungen, pers. comm.). Only a statistical study could show whether such an "irradiation" effect exists.

CARBON ISOTOPES

Results

The $\delta^{13}C$ values also can be grouped into two sets: one with large variability in $\delta^{13}C$, another with a small variability (Fig. 1d, e, f; Table 1). These two sets are not congruent with the oxygen isotope sets. The "large variability" set includes *Penicillus* and *Halimeda* (max. range 8‰), and the "small variability" set consists of *Amphiroa, Acetabularia,* and *Padina* (range 2 to 3‰). Actual ranges of $\delta^{13}C$ in the skeletal carbonates must be larger than those found because each data point represents a mixture. In the three *Halimeda* and in *Penicillus* from 2 m water depth, we found light $\delta^{13}C$ values both in the older and younger parts of the skeletons, with heavier values in between (Fig. 1d, e). In both *Acetabularia* and *Padina,* there may be a tendency to heavier values in the middle part of the algal structure although the data are inconclusive. The expected equilibrium $\delta^{13}C$ values for calcite are between 4 and 4.5‰ and for aragonite are between 5.8 and 6.3‰. For the $\delta^{13}C$ values of the water, data from Kroopnick et al. (1972) (derived from a open ocean station near Bermuda) were used, and the $\delta^{13}C$ $CaCO_3$ equilibrium (calcite) values were calculated using the fractionation relationships of Emrich et al. (1970). For aragonite, equilibrium values were estimated using a re-

ported calcite/aragonite fractionation difference (Rubinson and Clayton, 1969). The *Halimeda* from 2 m water depth shows values which are both lighter and heavier than aragonite equilibrium, while those of *Penicillus, Padina,* and *Acetabularia* are lighter than aragonite equilibrium values. The *Amphiroa* $\delta^{13}C$ values are 4 to 5‰ lighter than calcite equilibrium. In *Halimeda,* a tendency to lighter values with increasing water depth and lesser availability of light is seen. In *Penicillus,* the same trend is found only in the stalks, not in the capitulums of the plants.

Discussion

Metabolic and Diffusional Effects.—The light-heavy-light cycle in *Halimeda* and *Penicillus* is intriguing. Two types of processes must be considered: i) admixture of carbon from metabolic pathways, and ii) fractionation during the various stages of calcification proper.

The fractionation associated with metabolism is quite complicated. A three-step process (light-heavy-light) in the carbon isotope fractionation was proposed by Park and Epstein (1960) and by Wheelan et al. (1973) for vascular plants. For a summary of these processes see Faure (1977). For the present purposes it suffices to state that if $\delta^{13}C$ values of the carbonates precipitated are controlled by admixture from metabolic carbon reservoirs, it is necessary to know the pathways involved in order to explain the variations seen.

Fractionation also could occur during calcification proper. Detailed investigations on the ultrastructure of carbonate skeletons were performed on the green alga *Halimeda* (Wilbur et al., 1969; Flajs, 1977). In the typical case, three stages of calcification can be distinguished: i) an impregnation of filament walls with very fine-grained aragonite, followed by the formation of small granular crystals, ii) the growth of long aragonite needles normal to the surface of filaments, and iii) a filling out of the remaining spaces with irregularly arranged aragonite needles. This type of calcification is common in aragonitic *Chlorophyta* and also in *Phaeophyta* (Flajs, 1977). Presumably these various steps are associated with fractionation of various intensity. The importance of the various factors, fractionation of carbon isotopes in the organic matter, and fractionation associated with precipitation of the various types of carbonate crystals can only be assessed by parallel analysis of organic matter and carbonate types.

CONCLUSION

In a general way, and subject to the usual caveats, it appears that the oxygen and carbon isotopes in calcareous algae reflect metabolic processes to a very large degree so that environmental signals are subdued or (as in the case of oxygen in *Halimeda*) amplified to an unknown degree. The conclusion seems safe that no simple explanation can be given for the observed oxygen and carbon variations, which would apply across different phyla of calcareous algae. The level at which the taxa are close enough to show similar patterns remains to be discovered.

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