

REPORT

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Effect of light and zooplankton on skeletal $\delta^{13}\text{C}$ values in the eastern Pacific corals *Pavona clavus* and *Pavona gigantea*

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Abstract Skeletal $\delta^{13}\text{C}$ levels in symbiotic reef corals are believed to be predominantly influenced by metabolic fractionation. Therefore, environmental variables influencing coral metabolism should also affect skeletal $\delta^{13}\text{C}$ levels. To test this hypothesis, we measured the effects of light (which drives photosynthesis) and relative zooplankton levels (heterotrophy) on skeletal $\delta^{13}\text{C}$ values in the corals *Pavona clavus* and *P. gigantea* at two depths (1 m and 7 m). For both species, decreases in light or increases in zooplankton resulted in significant decreases in skeletal $\delta^{13}\text{C}$ levels. A significant decrease in $\delta^{13}\text{C}$ values with depth was observed in *Pavona gigantea* only. Thus, light and zooplankton directly affect coral skeletal $\delta^{13}\text{C}$ values, supporting the hypothesis that metabolic fractionation significantly contributes to skeletal $\delta^{13}\text{C}$ levels. Simultaneous decreases in both light and zooplankton resulted in decreases in skeletal $\delta^{13}\text{C}$ values, reflecting decreases in light. In *Pavona clavus*, intra-annual variation in skeletal $\delta^{13}\text{C}$ values over one year correlated with seasonal changes in irradiance. Further study is needed to resolve how skeletal $\delta^{13}\text{C}$ values vary at intermediate levels of irradiance and zooplankton, and in other coral species.

Key words Skeletal $\delta^{13}\text{C}$ · Coral · Light
Zooplankton

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Introduction

Recent studies indicate that the stable isotope composition, and trace and minor elements content in scleractinian coral skeletons can be used to reconstruct high resolution paleoclimatic records from tropical latitudes (Table 1). While the stable coral oxygen isotopic signature in reef corals has proven to be a reliable recorder of sea surface temperatures and salinities, causes of variability in the stable carbon isotope signature ($\delta^{13}\text{C}$) are not well understood.

Aragonite deposited by scleractinian corals is usually depleted in ^{13}C and ^{18}O relative to equilibrium with ambient seawater as a result of kinetic and metabolic fractionation. Kinetic fractionation during CO_2 hydration and hydroxylation produces a simultaneous depletion of ^{13}C and ^{18}O (McConnaughey 1986, 1989a). Metabolic fractionation produces additional changes in skeletal $\delta^{13}\text{C}$ reflecting changes in photosynthesis and respiration (Swart 1983; Muscatine et al. 1989; McConnaughey 1989a, b; McConnaughey et al. 1997; Allison et al. 1996).

The two main sources of carbon for corals are dissolved inorganic carbon (DIC) in the surrounding seawater, which has a mean $\delta^{13}\text{C}_{\text{PDB}}$ of 0‰, and zooplankton with $\delta^{13}\text{C}_{\text{PDB}}$ values ranging from -14 to -25‰ or even more negative (Rau et al. 1989, 1990; Grottoli-Everett 1998). The two processes which potentially alter the carbon pool available to reef corals are photosynthesis and heterotrophy. Photosynthesis, a light driven metabolic reaction, affects fractionation (McConnaughey 1986, 1989a, b, McConnaughey et al. 1997; Muscatine et al. 1989). It is believed that as the rate of photosynthesis in zooxanthellae increases, the carbon pool becomes relatively depleted in ^{12}C relative to ^{13}C resulting in an increase in skeletal $\delta^{13}\text{C}$ levels (Swart 1983; McConnaughey 1986, 1989a; McConnaughey et al. 1997; Porter et al. 1989). Theoretically, increased heterotrophy should lead to a decrease in

Table 1 Summary of coral skeletal $\delta^{18}\text{O}$, mineral, $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$ tracers along with the environmental variable(s) they record. SST, sea surface temperature; SSS, sea surface salinity; $\Delta^{14}\text{C}$, radioactive carbon-14 relative to 19th century wood standard

| Tracer | Environmental variable | Reference |
|-----------------------|------------------------|---|
| $\delta^{18}\text{O}$ | SST | Weber and Woodhead 1972; Emiliani et al. 1978; Fairbanks and Dodge 1979; Dunbar and Wellington 1981; Weil et al. 1981; Druffel 1985; McConnaughey 1986; Carriquiry et al. 1988; Shen et al. 1992a; Klein et al. 1992; Quinn et al. 1993, 1996; Dunbar et al. 1994, 1996; Gagan et al. 1994; Wellington and Dunbar 1995; Leder et al. 1996, Tudhope et al. 1996; Wellington et al. 1996; Druffel 1997a; Fairbanks et al. 1997; Gagan et al. 1998 |
| $\delta^{18}\text{O}$ | SSS | Cole and Fairbanks 1990; Cole et al. 1993; Linsley et al. 1994; Tudhope et al. 1995, 1996; Wellington and Dunbar 1995; Swart et al. 1996a; Druffel 1997a; Fairbanks et al. 1997 |
| Sr/Ca | SST | Weber 1973; Beck et al. 1992; de Villiers et al. 1994; McCulloch et al. 1994; Alibert and McCulloch 1997 |
| Mg/Ca | SST | Mitsuguchi et al. 1996; Shen and Dunbar 1996 |
| Ur/Ca | SST | Min et al. 1996; Shen and Dunbar 1996 |
| Mn/Ca | Upwelling | Shen et al. 1991, 1992b; Delaney et al. 1993 |
| Cd/Ca | Nutrient levels | Shen et al. 1987, 1992a |
| $\Delta^{14}\text{C}$ | Ocean ventilation | Druffel and Griffin 1993; Druffel 1997a, b |
| $\delta^{13}\text{C}$ | Light (across depth) | Land et al. 1975; Weber et al. 1976; Fairbanks and Dodge 1979; Weil et al. 1981; McConnaughey 1989a; Muscatine et al. 1989; Aharon 1991; Leder et al. 1991; Bosscher 1992; Carriquiry et al. 1994; Julliet-Leclerc et al. 1997; Grottoli-Everett 1998 |
| $\delta^{13}\text{C}$ | Light (cloud cover) | Fairbanks and Dodge 1979; Pätzold 1984; Quinn et al. 1993; Tudhope et al. 1995; Grottoli-Everett 1998 |
| $\delta^{13}\text{C}$ | Light (seasonality) | Emiliani 1978; Fairbanks and Dodge 1979; McConnaughey 1986, 1989a; Cole and Fairbanks 1990; Shen et al. 1992a; Klein et al. 1992, 1993; Carriquiry et al. 1994; Gagan et al. 1994; Wellington and Dunbar 1995; Swart et al. 1996b |

skeletal $\delta^{13}\text{C}$ levels since zooplankton has a low $\delta^{13}\text{C}$ value relative to seawater. Some observational data strongly indicate that light affects $\delta^{13}\text{C}$ levels (Table 1). Skeletal $\delta^{13}\text{C}$ values in corals have been observed to decrease with depth (as light decreases) and with seasonal increases in cloud cover (Table 1).

Although the aforementioned studies support the idea that light is a driving force in the variation of coral skeletal $\delta^{13}\text{C}$ composition, systematic experimental manipulations of light and zooplankton have not been done to assess the causes of variation in the carbon isotopic signature in corals. Some coral are very active heterotrophs (Yonge 1931; Coles 1969; Sorokin 1973, 1981; Lewis and Price 1975; Johnson and Sebens 1993; Helmuth and Sebens 1993; Sebens et al. 1996; Grottoli-Everett 1998) and zooplankton have significant effect on skeletal linear extension in some coral species (Wellington 1982; Sebens personal communication). Given that zooplankton and particulate organic material in seawater have low carbon isotopic values (Rau et al. 1989, 1990; Grottoli-Everett 1998), high levels of heterotrophic feeding in corals should be accompanied by a decrease in the $\delta^{13}\text{C}$ values of coral skeletons.

Here we evaluate the effect of solar irradiance and heterotrophy on $\delta^{13}\text{C}$ values in coral skeletons. We hypothesize that: (1) as light levels decrease, skeletal $\delta^{13}\text{C}$ values will decrease and (2) as heterotrophy decreases, skeletal $\delta^{13}\text{C}$ values will increase. These relationships could be used to reconstruct tropical paleoclimate changes related to cloud cover, water transparency and plankton rich upwelling events.

Methods

In this experiment, the corals *Pavona clavus* Dana and *P. gigantea* Verrill were grown in the field at 1 m and 7 m depths under ambient and low light conditions, and under ambient and reduced zooplankton conditions, from November 19, 1978 to November 5, 1979.

Study site

The study site was located on a fringing reef on the southwestern corner of Isla Contadora (8°37'23"N; 79°02'31"W), Perlas Archipelago in the Gulf of Panamá, Panamá (Fig. 1). The reef forms a veneer approximately 0.6 m thick and is approximately 3.2 ha in extent

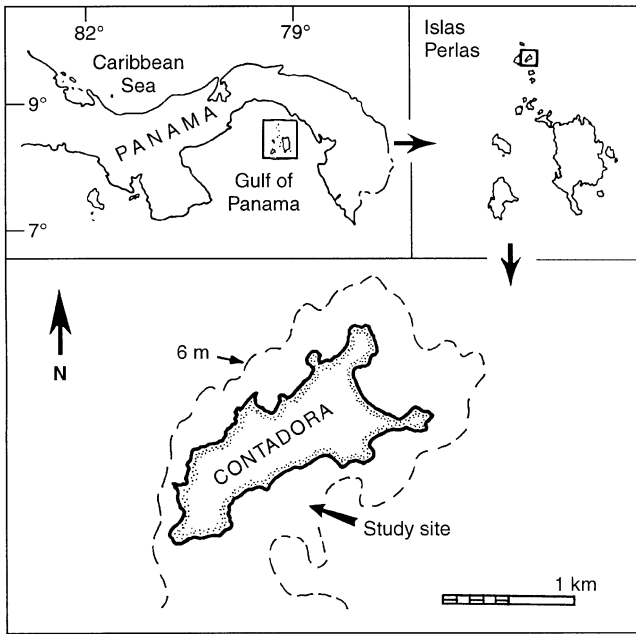


Fig. 1 Map showing the location of the study site on Isla Contadora (Gulf of Panamá), Panamá. From US Defense Mapping Agency Chart numbers 21605 and 21607, (reproduced from Wellington 1982)

(Wellington 1982). The branching coral *Pocillopora damicornis* forms a near-monotypic cover in shallow water from 0.5 to 6.0 m in depth while scattered colonies of massive *Pavona gigantea* corals are predominant at the reef base (7.0 to 10.0 m in depth). Although *Pavona clavus* was not common in the deep zone at the study site, it was abundant on nearby reefs within the same depth zone. Tides in the Gulf of Panamá are semi-diurnal with a mean spring range of 7.2 m (Wellington 1982). The dry season typically lasts from mid-

December through mid-April and is characterized by clear skies and upwelling of cool waters (3–4 °C drop below wet season average sea surface temperature of 28 °C) (Glynn 1977). Uniformly overcast skies occur over large parts of Panamá during the warm, wet season (Glynn 1977).

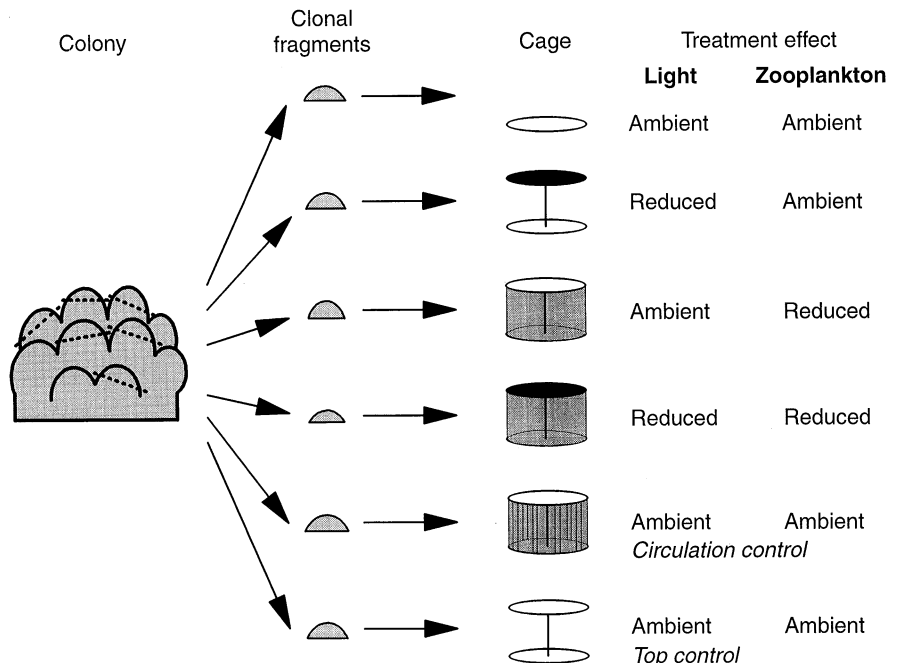
Experiment

Six individual colonies of *Pavona clavus* and six of *P. gigantea* were collected at each depth. Six fragments were removed from each parent colony and placed in one of 6 treatments for 11.5 months. The treatments were as follows: ambient light with ambient zooplankton, ambient light with reduced zooplankton, reduced light with ambient zooplankton, reduced light with reduced zooplankton, a circulation control (i.e., control for reduction in circulation caused by the mesh in the reduced zooplankton treatments; ambient light with ambient zooplankton), and a top control (i.e., control for the presence of the Plexiglas® tops; ambient light with ambient zooplankton) (Fig. 2). This use of replicate genotypes across treatments successfully reduced genotypic variation effects in the experiment.

Fragments in each treatment were placed on a circular (30 cm diameter, 0.7 cm thick) clear plexiglas base. Tops of the same size were of clear or opaque Plexiglas placed 20 cm above the base. Only the ambient light with ambient zooplankton treatments did not have Plexiglas tops. In situ measurements of the light intensity within all treatments at both depths were made on January 21–22, 1978 under cloudless sky conditions between 10:00–14:00 hours. Lux (footcandles/m²) were recorded with a photometer (LI-185, Lambda Instrument Corporation, Nebraska) using an underwater photometric sensor Li-212S). Light levels were significantly lower at 7 m than at 1 m. Incident light levels were reduced by 90–95% from ambient by the opaque Plexiglas tops used in the reduced light treatments at both depths. Incident light measured under the clear Plexiglas control top did not significantly differ from ambient light levels. Although Plexiglas tops were transparent to ultraviolet radiation (UV), UV measurements were not made.

In the reduced zooplankton treatments, zooplankton greater than 95 µm were excluded with a 95 µm polyester netting (PeCap

Fig. 2 Schematic representation of the experimental design



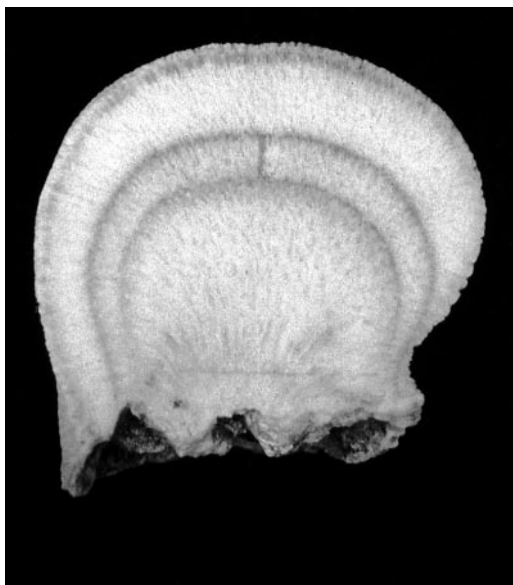


Fig. 3 Photograph of a cross-section of the coral *Pavona clavus*. The stain lines correspond to November, 1978 and April 1979 respectively. The skeletal samples were extracted along the major axis of growth as indicated by the resulting shallow long furrow. The coral fragment has a maximum width of approximately 9 cm

Mono-polyester HC7). This netting effectively excluded all mesoplankton (and organisms greater) in size as well as most of the microplankton. Nanoplankton and picoplankton were not excluded by the mesh but were reduced as a result of a 75% reduction in water circulation in the netted enclosures. Work by Sebens et al. (1996) showed that in the coral *Madracis mirabilis* (polyp diameter 1.5–2 mm), only 2% of heterotrophically acquired zooplankton was smaller than 500 μm . *Pavona clavus* and *P. gigantea* have polyp sizes of 2 and 3 mm, respectively. Therefore, the 95 μm netting in this experiment excluded the majority of zooplankton consumed by *Pavona* corals.

All non-netted cages were enclosed in stainless steel wire covers (5 cm mesh) to minimize grazing by corallivores. All materials used were non-toxic. The treatment enclosures were cleaned weekly to reduce fouling. Up to 6 enclosures were used per treatment at each depth with only one *Pavona gigantea* and one *P. clavus* fragment per enclosure. This allowed for independence between each fragment within a species.

The experiment was conducted at 1 m (using corals from 1 m) and 7 m (using corals from 7 m) depth. Corals were initially placed in the treatments and stained with Alizarin Red in November, 1978. Corals were re-stained in April, 1979 and collected in November, 1979 (Fig. 3). Six replicates were used for each treatment except the reduced light with reduced zooplankton treatment where only three colonies were used. In addition, four colonies were lost and five were unusable for the analysis due to missing stain lines. The total number of fragment used in the isotopic analyses was 122. A detailed description of the treatment design, methods and materials used in this field experiment is given in Wellington (1982). Seawater and zooplankton samples were not collected for isotopic analysis.

Controls

Plexiglas tops were placed over corals grown under the reduced light and reduced zooplankton treatments. To control for the presence of the top, corals were grown in treatments with Plexiglas tops (top control treatment). Polyester netting with 95 μm openings was used

to reduce zooplankton abundance in the reduced zooplankton treatments. Netting resulted in a 75% reduction in circulation inside the enclosure. To control for this, a control circulation treatment was used that allowed entrance of zooplankton yet reduced circulation to approximately the same level as in the netted, reduced zooplankton treatments. The control circulation treatment was constructed of 4 mm diameter mesh monofilament net (HC7-400) with 5 cm wide clear Plexiglas slates placed 2 cm apart all around the mesh. This allowed for 15% open area; sufficient for zooplankton passage while effectively reducing circulation.

Isotopic analysis

a Bulk samples: assessment of treatment effects

A 1 mm deep, homogenized bulk sample was extracted between the two stain lines (November 1978 and April 1979) of each coral fragment using a 1 mm dental drill with diamond tipped bits (Fig. 3). Skeletal material accreted from April 1979 to November 1979 were not extracted in order to avoid any potential contamination from the tissue layer. The skeleton was consistently sampled along the major axis of growth. Skeletal samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ by completely dissolving them individually in 100% H_3PO_4 then analyzing the resulting CO_2 gas with a VG Micromass 602E double-collecting mass spectrometer upgraded with SIRA series electronics. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were corrected for machine drift using a NBS-19 carbonate standard ($\delta^{18}\text{O} = -2.19_{\text{PDB}}$ and $\delta^{13}\text{C} = 1.93_{\text{PDB}}$). At least 10% of the samples were run in duplicate. The precision of replication for all samples was less than or equal to $\pm 0.1\text{‰}$. The effects of light, zooplankton and depth on skeletal $\delta^{13}\text{C}$ levels were statistically evaluated using a three-way, model III analysis of variance (ANOVA). Computations were done using Statistical Analysis Systems GLM program (SAS 1989). The null hypothesis was rejected when the probability level was less than 0.05. Change in the mean skeletal $\delta^{13}\text{C}$ values due to reduced light and/or zooplankton were calculated.

b High resolution samples: assessing intra-annual variation

In order to examine the intra-annual variation in skeletal $\delta^{13}\text{C}$ values and $\delta^{18}\text{O}$ within a coral fragment and among treatments, one fragment of *Pavona clavus* from each of the following three treatments from the 1 m depth was selected for more detailed analyses: ambient light with ambient zooplankton, ambient light with reduced zooplankton, and reduced light with ambient zooplankton. All fragments were of the same genotype. Skeletal samples were extracted at intervals of 1 mm or less along the major axis of growth starting at the first stain line to the base of the tissue line using a dental drill with diamond tipped bits.

Results

Coral health and growth

All coral fragments appeared healthy throughout the experiment. Fragments grown under reduced light conditions were consistently darker in pigmentation than fragments grown under ambient light conditions. This apparent photoadaptive response to decreases in light has been reported by many other researchers (Falkowski and Dubinsky 1981; Titlyanov 1981; Dubinsky et al. 1984; Barnes and Chalker 1990). Maximum linear

Table 2 Mean maximum linear extension (mm) (± 1 Standard Error) from November 1978 to November 1979 for *Pavona clavus* and *P. gigantea* at 1 m and 7 m depths. Sample size per treatment is indicated in brackets. ALRZ, ambient light with reduced zooplankton; ALAZ, ambient light with ambient zooplankton; CC, control circulation; TC, top control, RLRZ, reduced light with reduced zooplankton; RLAZ, reduced light with ambient zooplankton. All data from Wellington (1982) Appendix A.

| Coral | Depth (m) | Overall (33) | Treatments | | | | | |
|------------------------|-----------|------------------|------------------|------------------|------------------|-----------------|------------------|------------------|
| | | | ALAZ (6) | ALRZ (6) | RLAZ (6) | RLRZ (3) | TC (6) | CC (6) |
| <i>Pavona clavus</i> | 1 | 15.38 \pm 0.76 | 20.25 \pm 1.05 | 11.83 \pm 1.32 | 14.17 \pm 0.88 | 7.50 \pm 0.29 | 18.42 \pm 0.99 | 16.17 \pm 0.69 |
| | 7 | 12.39 \pm 0.72 | 16.08 \pm 1.32 | 11.08 \pm 1.00 | 10.25 \pm 1.41 | 4.67 \pm 0.66 | 14.92 \pm 0.95 | 13.50 \pm 1.18 |
| <i>Pavona gigantea</i> | 1 | 10.80 \pm 0.53 | 13.25 \pm 0.45 | 9.33 \pm 0.40 | 8.67 \pm 0.38 | 6.17 \pm 0.46 | 12.83 \pm 1.21 | 12.25 \pm 0.67 |
| | 7 | 8.05 \pm 0.67 | 11.33 \pm 1.23 | 6.42 \pm 0.81 | 3.58 \pm 0.49 | 3.23 \pm 0.10 | 11.67 \pm 1.09 | 9.50 \pm 0.66 |

Table 3 Mean $\delta^{13}\text{C}_{\text{pdb}}$ (± 1 Standard Error) and mean $\delta^{18}\text{O}_{\text{pdb}}$ (± 1 SE) for *Pavona clavus* and *P. gigantea* in each treatment at 1 m and 7 m depths. All isotope values are in ‰. Sample sizes indicated in brackets. D, depth. Other abbreviations as in Table 2.

| Coral | D (m) | Overall | Treatments | | | | | |
|--|-------|-----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| | | | ALAZ | CC | ALAZ | TC | RLRZ | RLAZ |
| Mean $\delta^{13}\text{C}_{\text{pdb}} \pm 1$ SE (n) | | | | | | | | |
| <i>Pavona clavus</i> | 1 | -2.02 \pm 0.16 (31) | -1.14 \pm 0.20 (6) | -1.76 \pm 0.24 (6) | -1.87 \pm 0.30 (6) | -1.82 \pm 0.20 (5) | -2.76 \pm 0.15 (2) | -3.23 \pm 0.26 (6) |
| | 7 | -2.30 \pm 0.14 (31) | -1.14 \pm 0.14 (6) | -1.90 \pm 0.12 (5) | -2.47 \pm 0.17 (6) | -2.73 \pm 0.17 (6) | -2.44 \pm 0.62 (2) | -3.13 \pm 0.19 (6) |
| <i>Pavona gigantea</i> | 1 | -1.87 \pm 0.12 (31) | -1.13 \pm 0.14 (6) | -1.88 \pm 0.26 (6) | -1.61 \pm 0.15 (6) | -2.00 \pm 0.16 (6) | -2.29 \pm 0.56 (2) | -2.74 \pm 0.12 (5) |
| | 7 | -2.46 \pm 0.12 (28) | -1.61 \pm 0.19 (5) | -2.12 \pm 0.28 (5) | -2.87 \pm 0.19 (6) | -2.65 \pm 0.16 (6) | -2.61 \pm 0.25 (2) | -2.98 \pm 0.22 (4) |
| Mean $\delta^{18}\text{O}_{\text{pdb}} \pm 1$ SE (n) | | | | | | | | |
| <i>Pavona clavus</i> | 1 | -4.59 \pm 0.05 (31) | -4.54 \pm 0.14 (6) | -4.60 \pm 0.07 (6) | -4.60 \pm 0.19 (6) | -4.45 \pm 0.06 (5) | -4.45 \pm 0.27 (2) | -4.62 \pm 0.07 (6) |
| | 7 | -4.39 \pm 0.04 (31) | -4.37 \pm 0.07 (6) | -4.39 \pm 0.11 (5) | -4.34 \pm 0.07 (6) | -4.52 \pm 0.09 (6) | -4.62 \pm 0.09 (2) | -4.27 \pm 0.14 (6) |
| <i>Pavona gigantea</i> | 1 | -4.37 \pm 0.04 (31) | -4.27 \pm 0.14 (6) | -4.43 \pm 0.02 (6) | -4.48 \pm 0.08 (6) | -4.44 \pm 0.12 (6) | -4.09 \pm 0.10 (2) | -4.32 \pm 0.20 (5) |
| | 7 | -4.44 \pm 0.06 (28) | -4.52 \pm 0.08 (5) | -4.45 \pm 0.27 (5) | -4.45 \pm 0.08 (6) | -4.43 \pm 0.09 (6) | -4.05 \pm 0.14 (2) | -4.48 \pm 0.09 (4) |

extension from November 1978 to November 1979, was greater in the shallow coral than in the deeper coral, for *Pavona clavus* than for *P. gigantea*, under ambient light than under reduced light treatments, and under ambient than under reduced zooplankton treatments (Table 2). Further details regarding the effects of light, zooplankton and depth on maximum linear skeletal extension are given in Wellington (1982).

Effect of light and zooplankton on skeletal $\delta^{13}\text{C}$ values

Skeletal $\delta^{13}\text{C}$ levels decreased with decreases in light levels and with increases in zooplankton (Table 3, Fig. 4). This relationship did not change with depth in *Pavona clavus*. A 3-way model III ANOVA of skeletal carbon isotopic levels in *Pavona clavus* yielded significant light and zooplankton effects and no significant depth nor interaction effects (Table 4). Results were similar for *Pavona gigantea* with the additional effect of depth (Table 4). Here, increased depth resulted in a decrease in coral skeletal $\delta^{13}\text{C}$ values.

A closer examination of the changes in skeletal $\delta^{13}\text{C}$ values with decreases in light and/or zooplankton are given in Table 5. Reduction in light conditions led to a decrease in the mean skeletal $\delta^{13}\text{C}$ values in *Pavona*

clavus and *P. gigantea* at both depths. This decrease was more pronounced in the shallower corals, especially in *Pavona clavus*. Reduction of zooplankton alone led to increases in mean skeletal $\delta^{13}\text{C}$ levels in both species at both depths. In deeper corals, the change in mean skeletal $\delta^{13}\text{C}$ values was always greater due to changes in zooplankton alone than due to changes in light alone. When both light and zooplankton were reduced, a decrease in the mean skeletal $\delta^{13}\text{C}$ values was observed in both species at both depths. This decrease was most pronounced in the shallow *Pavona clavus*.

Controls

A comparison between the top control and ambient light with ambient zooplankton treatments revealed no significant difference in skeletal $\delta^{13}\text{C}$ levels (Table 6). The presence of a Plexiglas top did not significantly affect skeletal $\delta^{13}\text{C}$ levels in either species at either depth. A comparison between the top control treatment and the circulation control treatment revealed no significant difference in skeletal $\delta^{13}\text{C}$ levels in *Pavona gigantea* nor in shallow *Pavona clavus* (Table 6). However, a significant effect was detected in the deep

Fig. 4A, B The mean skeletal $\delta^{13}\text{C}_{\text{‰}}$ ($\pm 1\text{SE}$) of **A** *Pavona clavus* and **B** *Pavona gigantea* at the shallow (1 m = ●) and deep (7 m = ■) sites in each of the six treatments. Sample size in the shallow and deep treatments are indicated above and below each data point, respectively. ALRZ, ambient light with reduced zooplankton; CC, circulation control; ALAZ, ambient light with ambient zooplankton; TC, top control; RLRZ, reduced light with reduced zooplankton; RLAZ, reduced light with ambient zooplankton. In both **A** and **B**, the first four treatments have ambient light levels and the last two treatments have reduced light

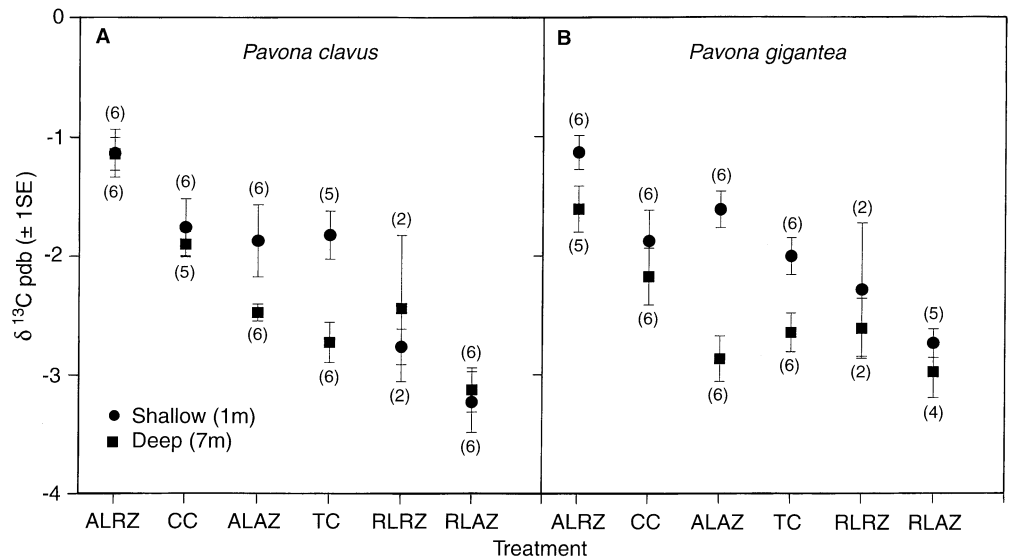


Table 4 Three-way model III ANOVA of light (ambient versus reduced), zooplankton (ambient versus reduced) and depth (1 m versus 7 m) effects on skeletal $\delta^{13}\text{C}$ values in the corals *Pavona clavus* and *Pavona gigantea*. Overall model *Pavona clavus*, $r^2 = 0.66$, $n = 62$, and *Pavona gigantea*, $r^2 = 0.59$, $n = 60$. (DF is degrees of freedom; SS, sum of squares; Zoop, zooplankton)

| Source | <i>Pavona clavus</i> | | | | <i>Pavona gigantea</i> | | |
|------------------|----------------------|--------|---------|----------|------------------------|---------|----------|
| | DF | SS | F Ratio | Prob > F | SS | F Ratio | Prob > F |
| Model | 7 | 28.798 | 15.023 | 0.0001** | 17.500 | 10.819 | 0.0001** |
| Light | 1 | 14.397 | 52.573 | 0.0001** | 6.279 | 27.173 | 0.0001** |
| Zooplankton | 1 | 5.344 | 19.514 | 0.0001** | 3.165 | 13.697 | 0.0005** |
| Depth | 1 | 0.014 | 0.051 | 0.822 | 1.632 | 7.062 | 0.010* |
| Light*Zoop | 1 | 0.337 | 1.230 | 0.272 | 0.364 | 1.577 | 0.215 |
| Light*Depth | 1 | 0.569 | 2.080 | 0.155 | 0.210 | 0.908 | 0.345 |
| Zoop*Depth | 1 | 0.353 | 1.290 | 0.261 | 0.016 | 0.068 | 0.795 |
| Light*Zoop*Depth | 1 | 0.069 | 0.253 | 0.617 | 0.061 | 0.264 | 0.610 |

* Significance at $P \leq 0.01$, ** $P \leq 0.0005$

Table 5 Change in skeletal $\delta^{13}\text{C}$ levels (‰) due to reduced light and/or reduced zooplankton levels in *Pavona clavus* and *Pavona gigantea* at 1 m and 7 m depths, relative to the appropriate control treatment. (Mean skeletal $\delta^{13}\text{C}$ levels in the reduced light with ambient zooplankton (RLAZ), ambient light with reduced zooplankton (ALRZ), reduced light with reduced zooplankton (RLRZ), top control (TC) and the circulation control (CC) treatments were used in the calculations). Negative values indicate a decrease in skeletal $\delta^{13}\text{C}$ levels and positive values an increase

| Species and depth (m) | *Change in skeletal $\delta^{13}\text{C}$ levels due to: | | |
|------------------------|--|----------------------------------|--|
| | Reduced light ^a | Reduced zooplankton ^b | Reduced light and reduced zooplankton ^c |
| <i>Pavona clavus</i> | | | |
| 1 | -1.40 | 0.62 | -1.01 |
| 7 | -0.40 | 0.76 | -0.54 |
| <i>Pavona gigantea</i> | | | |
| 1 | -0.73 | 0.74 | -0.41 |
| 7 | -0.33 | 0.51 | -0.49 |

^aRLAZ-TC

^bALRZ-CC

^cRLRZ-CC

Table 6 Paired t-test statistics for control treatments. (ALAZ, ambient light with ambient zooplankton; TC, top control; CC, circulation control; * $P < 0.005$)

| Treatment effect | Treatment | Species and depth | | | |
|------------------|----------------|----------------------|-------|------------------------|-------|
| | | <i>Pavona clavus</i> | | <i>Pavona gigantea</i> | |
| | | Shallow | Deep | Shallow | Deep |
| Top | ALAZ versus TC | -0.12 | 1.07 | 1.80 | -0.88 |
| Circulation | TC versus CC | -0.20 | 3.86* | -0.42 | -1.63 |

Pavona clavus (Table 6). This may be due to a slight decrease in zooplankton levels in the reduced circulation control treatment (due to the reduced flow and the limited number of 2 cm wide entrances to the enclosures) and not a circulation effect, for two reasons. First, the mean skeletal $\delta^{13}\text{C}$ level in the control circulation treatment was significantly greater than the mean $\delta^{13}\text{C}$ levels in both the top control treatment (Table 6, Fig. 4), and the ambient light with ambient zooplankton treatment (paired t-test $t = 2.73$, $P < 0.023$) (Fig. 4). Given that skeletal $\delta^{13}\text{C}$ levels increase as zooplankton decreases (see above), this supports the idea that zooplankton abundance is lower in the circulation control treatment of deep *Pavona clavus* corals. Second, decreases in water flow lead to decrease in photosynthesis (Lesser et al. 1994; Rex et al. 1995) which would lead to a decrease in $\delta^{13}\text{C}$ values (Swart 1983; McConnaughey 1986, 1989a; McConnaughey et al. 1997; Porter et al. 1989; Muscatine et al. 1989). We observed an increase in $\delta^{13}\text{C}$ values in the circulation control treatment corals, further indicating that circu-

lation had no significant affect on skeletal $\delta^{13}\text{C}$ levels. Thus, it is unlikely that reduced circulation was a contributing factor to skeletal $\delta^{13}\text{C}$ values in the deep-water *Pavona clavus*.

Effect of light and zooplankton on skeletal $\delta^{18}\text{O}$

The mean $\delta^{18}\text{O}$ values (± 1 Standard Error) for each treatment, coral species and depth are given in Table 3. A 3-way model III ANOVA showed no significant light, zooplankton, depth nor interactive effects on $\delta^{18}\text{O}$ in *Pavona clavus* (Model $df = 7$, $n = 62$, $F = 1.424$, $P < 0.215$) nor *Pavona gigantea* (Model $df = 7$, $n = 60$, $F = 1.576$, $P < 0.164$).

Intra-annual variation in $\delta^{13}\text{C}$ values

A detailed examination of intra-annual variation in skeletal isotopes revealed that $\delta^{18}\text{O}$ varies seasonally, reflecting cooler temperatures from mid-December through June and warmer temperatures over the remainder of the year (Fig. 5, Table 7). This pattern was clearest in both ambient light treatments. The 2–2.5‰ range in $\delta^{18}\text{O}$ over the course of the year was similar in all three treatments and reflects seasonal changes in sea-water temperature of approximately 10 °C (Dunbar and Wellington 1981). In the case of skeletal $\delta^{13}\text{C}$, three main features emerge. First, skeletal $\delta^{13}\text{C}$ values at any given time of the year are always highest under reduced zooplankton with ambient light treatment and lowest under reduced light with ambient zooplankton treatment (Fig. 5). This is consistent with the analyses of the bulk samples.

Second, intra-annual variation in skeletal $\delta^{13}\text{C}$ values in the two ambient light treatments seems to

Fig. 5 Time series of skeletal $\delta^{13}\text{C}_{\text{pdtb}}$ values (◆) and $\delta^{18}\text{O}$ (●) from November 1978 to November 1979 in shallow *Pavona clavus* from three treatments (ambient light with reduced zooplankton, ambient light with ambient zooplankton and reduced light with ambient zooplankton) over the course of the experimental time period. Data are plotted with $\delta^{13}\text{C}$ values and $\delta^{18}\text{O}$ on separate y-axes and time along the x-axis. The time frame was established using the two stain lines and the base of the tissue line as reference frames

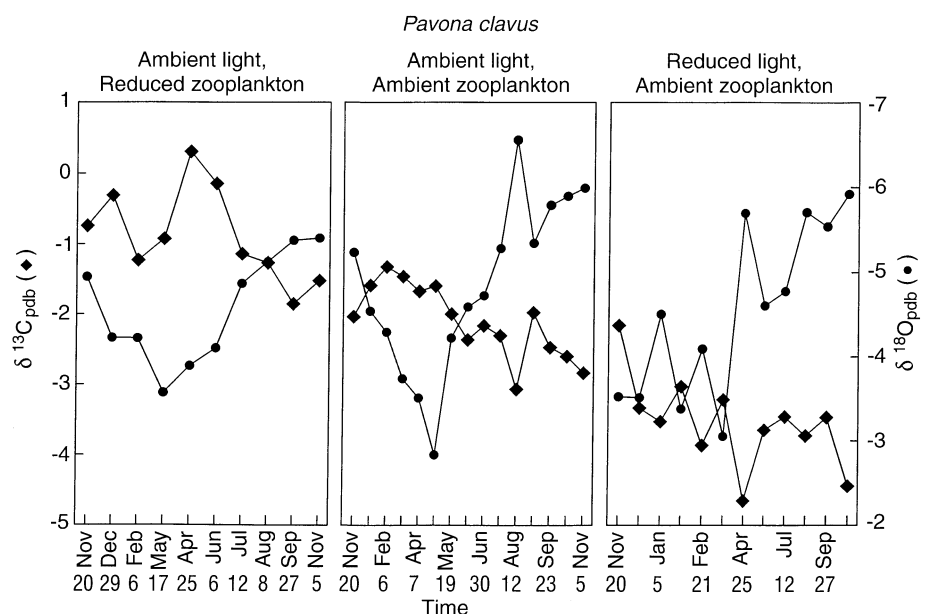


Table 7 Intra-annual variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for *Pavona clavus* (genotype 2) from November 1978 to November, 1979. Samples were drilled every 1 mm or less. Dates are given as month-day-year. Bold dates indicate the stain lines

| Treatment | Sample | Date | $\delta^{13}\text{C}$ ‰ PDB | $\delta^{18}\text{O}$ ‰ PDB |
|---|--------|-----------------|-----------------------------|-----------------------------|
| Ambient light with ambient zooplankton | 1 | 11-20-78 | -2.03 | -5.27 |
| | 2 | 12-29-78 | -1.58 | -4.57 |
| | 3 | 02-06-79 | -1.32 | -4.32 |
| | 4 | 03-17-79 | -1.46 | -3.77 |
| | 5 | 04-07-79 | -1.67 | -3.54 |
| | 6 | 04-28-79 | -1.59 | -2.86 |
| | 7 | 05-19-79 | -1.99 | -4.24 |
| | 8 | 06-09-79 | -2.36 | -4.62 |
| | 9 | 06-30-79 | -2.16 | -4.75 |
| | 10 | 07-22-79 | -2.30 | -5.31 |
| | 11 | 08-12-79 | -3.06 | -6.59 |
| | 12 | 09-02-79 | -1.97 | -5.37 |
| | 13 | 09-23-79 | -2.47 | -5.82 |
| | 14 | 10-14-79 | -2.60 | -5.93 |
| | 15 | 11-05-79 | -2.83 | -6.02 |
| Ambient light with reduced zooplankton | 1 | 11-20-78 | -0.74 | -4.97 |
| | 2 | 12-29-78 | -0.31 | -4.25 |
| | 3 | 02-06-79 | -1.23 | -4.25 |
| | 4 | 03-17-79 | -0.93 | -3.60 |
| | 5 | 04-25-79 | 0.30 | -3.92 |
| | 6 | 06-03-79 | -0.15 | -4.13 |
| | 7 | 07-12-79 | -1.14 | -4.89 |
| | 8 | 08-20-79 | -1.27 | -5.15 |
| | 9 | 09-27-79 | -1.85 | -5.41 |
| | 10 | 11-05-79 | -1.52 | -5.43 |
| Reduced light with ambient zooplankton | 1 | 11-20-78 | -2.16 | -3.55 |
| | 2 | 12-13-78 | -3.33 | -3.54 |
| | 3 | 01-05-79 | -3.53 | -4.53 |
| | 4 | 01-29-79 | -3.03 | -3.41 |
| | 5 | 02-21-79 | -3.87 | -4.12 |
| | 6 | 03-17-79 | -3.22 | -3.08 |
| | 7 | 04-25-79 | -4.65 | -5.73 |
| | 8 | 06-03-79 | -3.65 | -4.63 |
| | 9 | 07-12-79 | -3.46 | -4.80 |
| | 10 | 08-20-79 | -3.73 | -5.74 |
| | 11 | 09-27-79 | -3.47 | -5.57 |
| | 12 | 11-05-79 | -4.44 | -5.95 |

reflect seasonal changes in irradiance (Fig. 5). Skeletal $\delta^{13}\text{C}$ values are highest during the cool dry season (approximately mid-December to May) and lowest during the warm, cloudy, rainy season. No seasonal changes were observed in the $\delta^{13}\text{C}$ values in the reduced light treatment. This may be attributable to a narrow range in light variation for corals grown under highly reduced light treatments. Third, within a coral fragment, variation in $\delta^{13}\text{C}$ associated with seasonal changes in zooplankton concentration (associated with upwelling from December to April) is not apparent.

Discussion

Carbon isotopic composition in reef corals is believed to be predominantly affected by metabolic fractiona-

tion (McConnaughey 1986, 1989ab, McConnaughey et al. 1997; Muscatine et al. 1989). Therefore, the physiological processes of photosynthesis (light driven) and heterotrophy should influence the skeletal carbon isotopic composition. While some observational data support this prediction (Table 1), results from the manipulative field experiment presented here confirm that both light and zooplankton contribute significantly to the skeletal $\delta^{13}\text{C}$ composition. By growing corals under the same environmental conditions and manipulating both light and zooplankton levels (while controlling for changes in circulation and the presence of the Plexiglas tops), the effects on skeletal $\delta^{13}\text{C}$ values could be isolated. While skeletal carbon isotopes may vary due to changes in the isotopic composition of the dissolved inorganic carbon (DIC) in the seawater (Swart 1996b), dissolved organics and bacteria (Sorokin 1973; Muscatine and Porter 1977) or spawning (Gagan et al. 1994, 1996) these factors were constant across all treatments

and therefore did not interfere with the interpretation of the present data. In addition, skeletal $\delta^{13}\text{C}$ may vary due to changes in kinetic fractionation. However, examination of the skeletal $\delta^{18}\text{O}$ data reveals that kinetic fractionation did not interfere with the interpretation of the present $\delta^{13}\text{C}$ data (see below).

Effects of light and zooplankton on skeletal $\delta^{13}\text{C}$ values

In situ, both *Pavona clavus* and *P. gigantea*, grown under decreased light conditions, showed a significant decrease in skeletal $\delta^{13}\text{C}$ values (Tables 3 and 4, Fig. 4). When zooplankton levels were reduced, both species of coral showed significant increases in skeletal $\delta^{13}\text{C}$ values (Tables 3 and 4, Fig. 4). The results support both proposed hypotheses: (1) as light levels decrease skeletal $\delta^{13}\text{C}$ values decrease due to reduced photosynthesis, leading to an increase in ^{12}C in the available carbon pool and, (2) as heterotrophy decreases skeletal $\delta^{13}\text{C}$ levels increase due to the removal of zooplankton with low $\delta^{13}\text{C}$ values.

Recent work by Swart et al. (1996b) suggests that changes in skeletal $\delta^{13}\text{C}$ values are not necessarily due to changes in photosynthesis but rather to changes in respiration. They reported that $\delta^{13}\text{C}$ levels decreased in *Montastrea annularis* as the ratio of photosynthesis to respiration (P/R) decreased and that this decrease was attributable to increases in respiration rather than decreases in photosynthesis. We would expect increases in respiration to lead to increases in $\delta^{13}\text{C}$ values via metabolic fractionation, however, the lack of a correlation between photosynthesis and $\delta^{13}\text{C}$ values is unexpected. The results reported by Swart et al. (1996b) may be influenced by low sample size (data from only four corals were reported and intraspecific variation of the physiological parameters measured at any given time was high thus reducing the power of the statistical analyses) and choice of statistical analyses (the data points used in the correlation analyses consisted of

repeated measurements of the same four corals and thus were not independent). We re-analyzed their raw published data using the mean of each variable for each coral and offer an alternative interpretation of their data (Table 8). Although Swart et al. (1996b) used $\Delta^{13}\text{C}$ values in their analyses ($\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{coral}} - \delta^{13}\text{C}_{\text{DIC}_{\text{seawater}}}$), we chose to use the original $\delta^{13}\text{C}$ data instead to minimize the error associated with additional calculations and to increase the size of the data set ($\delta^{13}\text{C}_{\text{DIC}_{\text{seawater}}}$ was not available for the first three sampling intervals). In any case, results were similar when the reanalyses were performed using the $\Delta^{13}\text{C}$ or $\delta^{13}\text{C}$ means. This is attributable to the fact that $\Delta^{13}\text{C}$ and $\delta^{13}\text{C}$ are positively correlated ($r = 0.939$, $P < 0.061$).

Upon reanalysis of Swart et al.'s (1996b) data, we found a significant positive correlation between $\delta^{13}\text{C}$ values and respiration and a marginally non-significant positive correlation between $\delta^{13}\text{C}$ values and photosynthesis (Table 8). While the correlation of respiration (R) versus $\delta^{13}\text{C}$ values had a slightly greater slope than photosynthesis (P) versus $\delta^{13}\text{C}$ values, the resulting negative slope of P/R versus $\delta^{13}\text{C}$ levels was not significant. In fact, photosynthesis and respiration vary almost directly in proportion to each other ($r = 0.967$) (Table 8). No other variables were significantly correlated (Table 8). This reanalysis of the data leads us to conclude that it is not possible to unequivocally attribute changes in $\delta^{13}\text{C}$ to changes in respiration; they could just as easily be the result of changes in photosynthesis, or alternatively, to some combination of the two processes. This is in agreement with our results, where changes in light had a direct effect on skeletal $\delta^{13}\text{C}$ values in *Pavona clavus* and *P. gigantea*. In addition, Swart et al. (1996b) recognize seasonal variation in $\delta^{13}\text{C}$ values that corresponds to seasonal changes in irradiance. Peak skeletal $\delta^{13}\text{C}$ values occurred during the cool, cloudless, dry months and minimum $\delta^{13}\text{C}$ values occurred during the warm, cloudy months. These findings also further support our

Table 8 Re-analysis of raw published data by Swart et al. (1996b). Correlation of the mean skeletal $\delta^{13}\text{C}$ value, ratio of photosynthesis/respiration (P/R), calcification, linear extension, photosynthesis (P) and respiration (R) of each coral are shown. Pearson correlation coefficients and probability of a non-zero slope are given. $N = 4$ in all cases

| | $\delta^{13}\text{C}$ | R | P | P/R | Calcification | Linear extension |
|-----------------------|-----------------------|--------|--------|--------|---------------|------------------|
| $\delta^{13}\text{C}$ | 1.000 | 0.971 | 0.895 | -0.718 | 0.035 | 0.177 |
| - | | 0.029* | 0.105 | 0.282 | 0.965 | 0.823 |
| R | 1.000 | 0.967 | -0.721 | 0.171 | -0.044 | |
| - | | | 0.033* | 0.279 | 0.829 | 0.956 |
| P | | | 1.000 | -0.564 | 0.127 | -0.281 |
| - | | | | 0.436 | 0.873 | 0.719 |
| P/R | | | | 1.000 | -0.645 | -0.293 |
| - | | | | | 0.355 | 0.708 |
| Calcification | | | | | 1.000 | -0.216 |
| - | | | | | | 0.784 |
| Linear extension | | | | | | 1.000 |
| - | | | | | | |

* $P < 0.05$

hypothesis that light is a driving factor that influences the coral skeletal $\delta^{13}\text{C}$ composition.

Changes in skeletal $\delta^{13}\text{C}$ values due to light and zooplankton

In order to determine the degree to which light and zooplankton contributed to skeletal $\delta^{13}\text{C}$ values, we calculated the change in skeletal $\delta^{13}\text{C}$ values due to each variable relative to the appropriate control for each species at each depth (Table 5). Decreases in light resulted in decreases in skeletal $\delta^{13}\text{C}$ values in both species, with decreases in $\delta^{13}\text{C}$ values being most pronounced in the shallower corals. Decreases in zooplankton resulted in increases in $\delta^{13}\text{C}$ values of at least 0.51‰ in all cases. For deeper corals, the effect of zooplankton alone resulted in a greater change in $\delta^{13}\text{C}$ values than did the effect of light alone. Simultaneous reductions in both light and zooplankton led to decreases in $\delta^{13}\text{C}$ values, reflecting decreases in light. In particular, the decrease in the $\delta^{13}\text{C}$ value in the shallow *Pavona clavus* was almost two times greater than the decrease in $\delta^{13}\text{C}$ values measured in the deep *P. clavus* and in *P. gigantea* at both depths. In general, skeletal $\delta^{13}\text{C}$ values in *Pavona clavus* changed more with respect to decreases in light or zooplankton levels than did *P. gigantea*. This is in keeping with the faster growth rate (hence greater metabolic demands with decreased fractionation) of the former species (Wellington 1982) (Table 3) and emphasizes species specific differences in skeletal $\delta^{13}\text{C}$ variation.

Effect of light and zooplankton on skeletal $\delta^{18}\text{O}$ values

Since oxygen isotopes are not believed to be metabolically fractionated in corals, light and zooplankton were not expected to have any significant effect on the skeletal $\delta^{18}\text{O}$ composition of corals. In situ, neither light, zooplankton, nor depth had a significant effect on skeletal $\delta^{18}\text{O}$ values of *Pavona clavus* (model $df = 7$, $n = 62$, $F = 1.424$, $P < 0.215$) or *P. gigantea* (model $df = 7$, $n = 60$, $F = 1.576$, $P < 0.164$).

Some researchers have demonstrated a relationship between skeletal $\delta^{18}\text{O}$ values and maximum linear skeletal extension, supporting the idea that kinetic fractionation is influenced by growth rate (Land et al. 1975; McConnaughey 1989; Allison et al. 1996). Whereas light, zooplankton and depth do not significantly affect skeletal $\delta^{18}\text{O}$ in our data set, these same variables do significantly affect maximum linear skeletal extension (Table 2) (Wellington 1982). This lack of a correlation between skeletal extension and skeletal $\delta^{18}\text{O}$ demonstrates that skeletal extension does not have a major effect on isotope fractionation. This implies that changes in skeletal $\delta^{13}\text{C}$ values in this experiment are

predominantly due to treatment effects and are not being influenced by variation in skeletal extension rates and kinetic fractionation.

Applications for paleoclimate reconstruction

Given the significant effect light and zooplankton have on coral skeletal $\delta^{13}\text{C}$ values combined with the species-specific and depth-dependent responses, our findings have several implications for paleoclimate reconstruction. First, skeletal $\delta^{13}\text{C}$ in shallower corals should be an effective recorder of changes in irradiance, whereas in deeper corals it may better reflect changes in zooplankton. Coral cores taken from shallow sites will best reflect changes in light levels and hence provide better records of seasonal cloud cover variability. Coral from deeper sites may be better recorders to changes in zooplankton levels and may provide a record of seasonal changes in productivity. These predicted patterns could be confounded when high nutrient levels lead to significant reductions in downwelling irradiance. Theoretically, examination of the $\delta^{13}\text{C}$ record from a shallow and deep coral from the same species and location might provide a simultaneous reconstruction of the seasonal variation in both irradiance and productivity. Second, the degree of response in $\delta^{13}\text{C}$ values to environmental changes varies between species and depths. In general, coral species with a greater range in $\delta^{13}\text{C}$ response to environmental variables will provide a clearer isotope record.

Our examination of the intra-annual variation in $\delta^{13}\text{C}$ values reveals seasonal changes in solar irradiance (Fig. 5). However, variation in $\delta^{13}\text{C}$ associated with seasonal changes in zooplankton concentration (associated with upwelling from December to April) was not apparent.

Future research

Results from this experiment, an initial attempt at reconstructing environmental changes in irradiance and zooplankton, provide optimism for using coral records for paleoclimate studies. A broad measure of the degree of skeletal $\delta^{13}\text{C}$ sensitivity to these variables has been defined: (1) as light levels decrease, skeletal $\delta^{13}\text{C}$ decrease and, (2) as zooplankton levels decrease, skeletal $\delta^{13}\text{C}$ increase. Additional experiments are now needed to fine tune the interpretation of skeletal $\delta^{13}\text{C}$ values. First, to compare corals from different sites with different seasonal patterns in seawater $\delta^{13}\text{C}_{\text{DIC}}$, or to compare data from different years, will require close monitoring of seawater $\delta^{13}\text{C}_{\text{DIC}}$ to establish its relative contribution to the overall skeletal $\delta^{13}\text{C}$ levels. Second, only the relative isotopic contribution of zooplankton greater than 95 μm was accounted for in these experiments. Corals are known to feed on smaller

zooplankton size fractions (Sebens 1996) as well as dissolved and particulate organic material in the water column (Sorokin 1973; Muscatine and Porter 1977). In order to fully determine the relative effect of all plankton on skeletal $\delta^{13}\text{C}$ values, close monitoring of all size fractions of plankton and their isotopic composition is required. Third, in this experiment we measured the direct effect of large reductions in irradiance on skeletal $\delta^{13}\text{C}$ values. Reduction in light to 5% of ambient at 1 m is biologically significant because it is roughly equivalent to 100% of ambient light at 20 m depth. However, seasonal changes in light levels attributable to changes in cloud cover or water clarity for a given coral at a given depth, are likely to be less dramatic. Finally, paleoclimate records are reconstructed from coral cores from many different species and locations. To validate our current findings for general application in coral-based climate reconstruction, additional similar experiments involving different species and locations should be conducted.

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