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REPORT

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# Implication of water depth on stable isotope composition and skeletal density banding patterns in a *Porites lutea* colony: results from a long-term translocation experiment

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**Abstract** This study investigates the effect of water depth on stable isotope composition and density-band formation in the skeletal material of the zooxanthellate coral *Porites lutea*. In February 1991, several colonies were stained with Alizarin red-S and then transferred from 6 to 40 m. Ten years later, in February 2001, one colony was retrieved and analyzed. This provided us with the unique opportunity to maintain the coral's genetic integrity and hence to isolate environmental factors affecting skeletal isotopic composition and density patterns. Despite extreme environmental changes experienced by the corals, the downward transplants showed no mortality after 10 years. Acclimatization of the coral to the deep-water environment involved changes in mean annual extension rates and colony morphology. The growth rate at 6 m was $5.66 \pm 0.47$ mm/year, almost twice the growth rate following transplantation to 40 m, which was $3.00 \pm 0.37$ mm/year. A significant difference in mean annual $\delta^{18}O$ between the shallow and deep growth phases ($-3.10 \pm 0.10$ and $-2.80 \pm 0.14$‰, respectively) and amplitude ($1.14 \pm 0.15$ and $1.49 \pm 0.20$‰, respectively) was detected. Mean annual $\delta^{13}C$ in the shallow growth phase was $-1.58 \pm 0.12$‰, significantly heavier than that of the deep growth phase which was $-1.92 \pm 0.14$‰. The phase relation between $\delta^{18}O$ and $\delta^{13}C$ was also depth dependent. These results suggest that the role of the kinetic effect in determining skeletal isotopic composition of deep-water hermatypic corals in the study site is greater than in that of shallow-water colonies. The timing of density-band formation was found to be depth independent. At both depths, low-density skeleton is produced during summer, and high-density skeleton is produced during winter, implying that it is intrinsically controlled rather than environmentally governed. The implications of these results on paleoclimate and sea level reconstruction are discussed.

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## Introduction

The sensitivity of scleractinian corals to their environment has long been recognized (Darwin 1842). The environmental setting in which an individual colony is growing has a major impact on the coral-algae symbiotic system and determines the characteristics of the colony. Massive coral colonies usually maintain the layered structure of the skeleton and can thus archive a continuous environmental record. Hence, time series of a variety of isotopes, geochemical tracers, and skeletal density have been developed as tools to reconstruct past climate and environmental variability (e.g. Klein et al. 1992; Swart et al. 1998).

Skeletal $\delta^{18}O$ is a well-established proxy, tracking both water temperature and the $\delta^{18}O$ of the surrounding seawater ($\delta^{18}O_{sw}$). In hermatypic corals, skeletal $\delta^{18}O$ is lighter than the expected $\delta^{18}O$ value of calcium carbonate accreted in isotopic equilibrium with seawater (McConnaughey 1989a). Thus, the efficacy of corals as temperature and precipitation proxies depends on the assumption that the departure from equilibrium is constant within a certain species. In addition to temperature and $\delta^{18}O_{sw}$, the rate of skeletal accretion also affects the skeletal $\delta^{18}O$. Low accretion rates produce $^{18}O$-enriched aragonite at the population, colony, and calyx levels (Land et al. 1975; McConnaughey 1989a, 1989b; de Villiers et al. 1995; Allison et al. 1996).

The environmental significance of skeletal $\delta^{13}C$ in scleractinian corals is controversial and results have led

to contradictory conclusions. Metabolic fractionation predominantly influences skeletal $\delta^{13}C$ (Swart 1983; McConnaughey 1989a, 1989b; Muscatine et al. 1989; Allison et al. 1996; McConnaughey et al. 1997; Grottoli and Wellington 1999; Grottoli 1999, 2002). Because sources and sinks of carbon within the coral and zooxanthellae are numerous, and its pathways are not fully understood, skeletal $\delta^{13}C$ is an intricate proxy reflecting numerous physiological and environmental variables, such as respiration and photosynthesis by the coral and zooxanthellae (Weber 1974; Goreau 1977a, 1977b; Erez 1977, 1978; Grottoli and Wellington 1999), light availability to the zooxanthellae (e.g. Weber and Woodhead 1970; Fairbanks and Dodge 1979; Guzman and Tudhope 1998; Grottoli 2002), the reproduction cycle of the colony (Gagan et al. 1994, 1995), and coral growth rate (Land et al. 1975; McConnaughey 1989a), although in some cases no correlation was recorded between growth rate and $\delta^{13}C$ (Grottoli 1999).

Several models have been suggested in an attempt to explain the carbon fractionation mechanism in which corals precipitate their skeleton (Weber and Woodhead 1970; Goreau 1977a, 1977b; Erez 1978; Swart 1983; McConnaughey 1989a, 1989b). The original model was described by Weber and Woodhead (1970). They proposed that photosynthesis preferably fixes $^{12}C$ relative to $^{13}C$; therefore as photosynthesis increases, fractionation decreases and the ratio of skeletal $^{13}C$ to $^{12}C$ ($\delta^{13}C$) would increase. Erez (1978) proposed an opposite model that suggested that increased photosynthesis was linked to increased isotopic fractionation, resulting in an isotopically light skeleton.

All of the above variables are directly influenced by the depth at which the coral is growing and consequently are bound to affect skeletal $\delta^{13}C$ composition. The photosynthetic light requirements of the symbiotic zooxanthellae restrict reef corals to the euphotic zone. Light intensity and light spectrum are the major environmental factors that change along this depth gradient. Coral colonies living in the upper 10–20 m of the euphotic zone experience higher light intensity with a broader light spectrum available for photosynthesis than deep-water colonies living at depth greater than 30 m. Consequently, deep-water hermatypic corals differ from shallow-water corals in energy-requiring physiological functions, such as growth rate (Hubbard and Scaturo 1985), fecundity (Kojis and Quinn 1984), respiration (Davies 1977), and colony morphology (Riegl and Piller 1999). Water temperature, physical stress, abundance of sediment, and water chemistry may also change along a depth profile. It appears that light is the dominant factor controlling coral abundance and all other parameters have a secondary influence (Achituv and Dubinsky 1990). Ecological parameters such as competition, predation, and symbiosis are also depth dependent and consequently water depth strongly influences the habitats of zooxanthellate corals.

For an improved coral-based paleoclimate reconstruction it is important to determine the effect of water depth on isotopic and density banding patterns. Overall, skeletal $\delta^{13}C$ values gradually decrease with depth (Weber et al. 1976; Fairbanks and Dodge 1979; Swart and Coleman 1980; McConnaughey 1989a; Muscatine et al. 1989; Aharon 1991; Leder et al. 1991; Juillet-Leclerc et al. 1997; Grottoli 1999; Grottoli and Wellington 1999), whereas in some cases a maximum $\delta^{13}C$ was recorded at intermediate depths (Land et al. 1975; Erez 1977, 1978; Swart et al. 1996; Guzman and Tudhope 1998; Grottoli 1999). Depth profiles of coral $\delta^{18}O$ are rare. In Hawaii and Panama, across an 8.3-m depth gradient, $\delta^{18}O$ values were not significantly different (Grottoli 1999; Grottoli and Wellington 1999), whereas in the Great Barrier Reef a 0.4‰ difference was reported across a 12-m depth gradient (Juillet-Leclerc et al. 1997). The timing of density-band formation was found to be depth dependent, with opposite patterns in shallow (3 m) and deep (51 m) water (Klein et al. 1993). A *Porites* sp. colony living in shallow water (3 m) in the Gulf of Eilat, Red-Sea, deposited high-density bands during winter and low-density bands during summer, while a *Porites* sp. colony living in deep water (51 m) deposited high-density bands during summer and low-density bands during winter (Klein et al. 1993).

Studies of the effect of water depth on stable isotope composition and density-band formation have always used distinct colonies sampled along a depth gradient. Two major factors may contribute to the patterns observed along the depth gradient. The first is the actual change in environmental and physiological conditions with depth, and the second is the genetic variation among the sampled colonies. Here, we present results of a long-term transplantation experiment in which an individual coral colony experienced two depth environments for several years at each depth. This provided us with the unique opportunity to maintain the coral's genetic integrity and hence to isolate environmental factors affecting skeletal isotopic composition and density patterns.

## Methods

In order to understand the effect of water depth on the patterns of density banding, $\delta^{18}O$ and $\delta^{13}C$ composition of a coral skeleton, we transplanted several *Porites lutea* colonies from a depth of 6 to 40 m (downward transplantation). An upward transplant was also conducted, but these corals did not survive the transplantation procedure. The study site was located at the northern tip of the Gulf of Aqaba (Eilat), in front of the H. Steinitz Marine Biology Laboratory. The Gulf of Aqaba is surrounded by desert, with negligible precipitation and runoff. The mean net evaporation (~350 cm/year) greatly exceeds precipitation (~3 cm/year) (Genin et al. 1995) and is the main driving force of the Gulf circulation. The excess evaporation over precipitation causes a northward surface inflow from the Red Sea through the shallow Straits of Tiran and a southward deep outflow back to the Red Sea. Two seasons characterize the Gulf of Aqaba, winter (December–April) and summer (May–November). The mean seasonal SST amplitude is 6 °C at the study site, with a minimal value during February (21 °C) and a maximal value in August (27 °C) (Paldor and Anati 1979). The vertical stratification is weak and is driven mainly by temperature rather than salinity

variations (Wolf-Vecht 1992; Berman 2000). The heating of surface water mass during summer causes stratification of the water column with the main thermocline at a depth of about 200 m. Winter cooling of surface water mass results in deep water mixing that can reach up to 800 m (Genin et al. 1995). Dataloggers were placed next to the transplanted corals at depths of 6 and 40 m in order to accurately record local temperature variability during a full annual cycle.

In February 1991, five *P. lutea* colonies were dislodged from their natural substrate at a depth of 6 m and prepared for transplantation. The colonies were glued onto pre-labeled ceramic tiles. The outermost skeleton layer was stained underwater in the original habitat by placing the colonies in a plastic bag containing a 20-ppm solution of the vital calcification indicator Alizarin red-S, for 24 h. The shallow colonies were then transferred to the deep-water habitat and vice versa. To follow acclimatization processes of the colonies to their new environment, observations were made annually. Ten years after the transplantation procedure, in February 2001, one downward transplanted colony was retrieved. The living tissue was thoroughly removed using a Water-Pik system, and the skeleton was dried at 60 °C for 24 h. A 5-mm thick skeleton slice was cut along the coral's major axis of growth with a circular, diamond-tipped masonry blade and was x-rayed to reveal the annual growth bands. The x-radiograph was optically scanned and the skeleton's optical density was measured along a profile parallel to the axis of growth using image analysis software (Scion Image for Windows, Beta 4.0.2, Scion Corporation). Skeletal optical density within the core is reported in arbitrary units. Skeletal optical density was measured along exactly the same path and in the same resolution as the stable isotope composition of the skeleton, thus enabling alignment of isotopic and skeletal density values for correlation analyses.

Two sampling techniques were employed in order to accomplish the same sampling resolutions in the two growth phases within the coral core. In the shallow-water growth phase, where skeletal extension rate is relatively high, the skeleton was drilled along the growth axis using a 0.5-mm diameter dental drill at 0.6-mm increments. In the deep-water growth phase, where skeletal extension rate is relatively low, the skeleton was milled along the growth axis using a Silesium-Carbide sanding disc (Proxxon GmbH) at 300-μm increments. Consequently, between 10 and 12 samples per annual band were collected and measured from both shallow and deep growth phases of the coral. About 100 μg of $CaCO_3$ were reacted in 100% orthophosphoric acid to produce $CO_2$ for mass spectrometric analyses on a GasBench II connected on-line to a Finigan MAT 252. All $\delta^{13}C$ and $\delta^{18}O$ measurements are the ratio of $^{13}C/^{12}C$ and $^{18}O/^{16}O$, respectively, reported in per mil units relative to the international Vienna-Peedee Belemnite Limestone Standard (V-PDB). Calibration was maintained by routine analyses of internal and international standards. The long-term precision of replicated analysis of our internal laboratory standard is 0.06 and 0.10‰ for carbon and oxygen, respectively.

## Results

### Measured temperature

Mean monthly temperatures measured at 6- and 40-m depth by data loggers exhibit the full annual cycle, which is almost identical to the long-term average surface temperatures at the northern part of the Gulf (Fig. 1). At 6-m depth, temperature reaches a maximum of 27.0 °C during August and a minimum of 21.0 °C during February. At 40-m depth, maximal summer temperature during August is 1.5 °C lower than at 6 m and is only 25.5 °C. However, winter temperatures are the same at both depths.

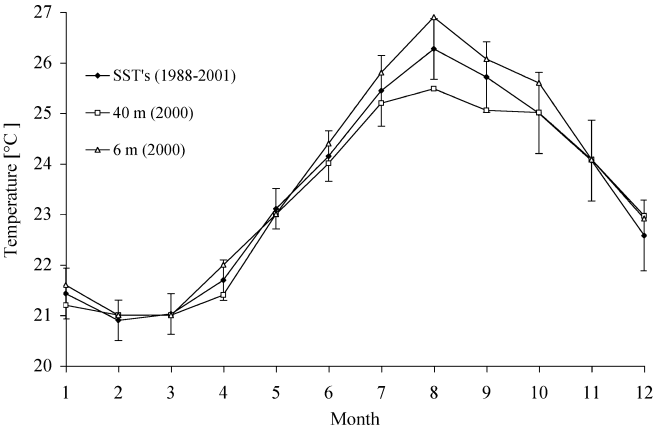


**Fig. 1** Long-term (1988–2001) mean monthly SST (±SD) at the study site (Genin, personal communication) and mean monthly seawater temperature during 2000 as recorded by two data loggers placed next to the studied corals at 6- and 40-m depth

### Acclimatization

Observations made 3 months after the coral transplantation (in May 1991) and a year later (in May 1992), revealed that the corals at 40 m, were in poor condition, exhibiting acute stress signs (tissue retraction and partial mortality). Further observations of the transplanted colonies were made annually. These observations revealed that the downward transplanted colonies gradually recovered and regained their natural appearance 2 years after transplantation. In February 2001, all five downward transplanted colonies were alive. Here we present results based on the first downward transplanted colony, which was retrieved, sliced, and analyzed (Fig. 2). The remaining four downward transplanted colonies still remain in the field. The Alizarin red-S staining line is visible in the coral slice, dividing the skeleton into two parts: (A) the inner skeleton, deposited during the time the coral lived at 6 m (shallow growth phase), and (B) the outer skeleton, deposited during the time the coral lived at 40 m (deep growth phase). Part of the skeleton formed during the shallow growth phase that was studied consists of five distinct pairs of high and low density bands. Younger density bands were not analyzed, due to indistinct banding patterns. The skeleton formed during the 10 years (Feb. 1991 to Feb. 2001) following transplantation to 40 m, exhibits only eight pairs of distinct density bands. $\delta^{18}O$ annual cycles confirmed the number of density band pairs observed (Figs. 2 and 3).

### Morphology and growth rate

The colony height-to-width ratio was 1.0 for the shallow growth phase and 1.1 for the deep growth phase. The change in height-to-width ratio of the transplanted colony indicates that the coral grew in a massive form at 6 m and slightly changed its morphology toward a

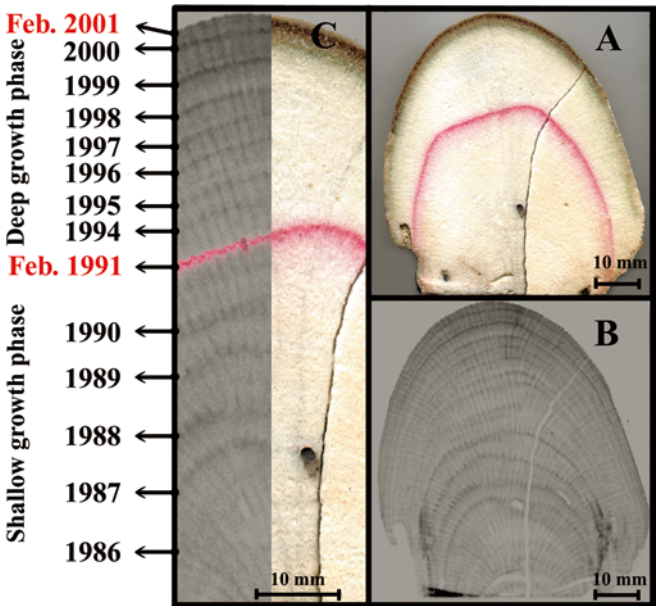


**Fig. 2** A colony of *P. lutea* stained with Alizarin red-S was transferred from 6- to 40-m depth on February 1991 and retrieved on February 2001. **A** Photo of a slab cut out along the maximal growth axis of the colony. The pink Alizarin red-S stain line separates between the shallow and deep growth phases of the colony. **B** X-radiographic positive illustrating skeletal high- and low-density banding pattern. **C** Composite image of the coral slab (right) and the x-radiograph (left), indicating the position of the Alizarin red-S stain line in relation to the x-radiograph. The two definite time markers (i.e., transplantation and retrieval dates) are indicated in *red*. Note the marked differences in growth rates between the shallow and deep growth phases and the growth hiatus following transplantation

columnar growth at 40 m by adding more skeletal material to the top of the colony in comparison to the amount of skeleton added to it's side (Fig. 2). Annual growth rates were determined from the seasonal cycle of the $\delta^{18}O$ (Fig. 3). The growth rate at 6 m was $5.66 \pm 0.47$ mm/year, almost twice the growth rate following transplantation to 40 m, which was $3.00 \pm 0.37$ mm/year (Table 1).

### Stable isotopes

$\delta^{18}O$ and $\delta^{13}C$ show a clear pattern of annual periodicity in both shallow and deep growth phases (Fig. 3). The mean annual $\delta^{18}O$ of the shallow growth phase skeleton is significantly lighter by 0.30‰ (Fig. 4A; Table 1). The mean annual $\delta^{13}C$ demonstrates an opposite trend; the shallow growth phase skeleton is significantly heavier by 0.34 ‰ than the deep growth phase skeleton (Fig. 4B; Table 1).

The mean seasonal $\delta^{18}O$ amplitude (i.e., the difference between minima and maxima in each annual cycle) in the shallow growth phase skeleton is significantly lower than in the deep growth phase by 0.35‰ (Fig. 4A; Table 1). An opposite trend is detected in the mean $\delta^{13}C$ where the deep growth phase skeleton has a significantly smaller seasonal amplitude than the shallow growth phase by 0.33‰ (Fig. 4B; Table 1).

No significant linear correlation was found between $\delta^{18}O$ and $\delta^{13}C$ during the time the coral grew in shallow water (Fig. 5A; $y = -0.15x - 2.02$; $r = -0.2$; $p = 0.2$). The skeleton became depleted in $^{18}O$ and enriched in $^{13}C$ during the season of high water temperatures and high light intensity (summer), and vice versa during wintertime. A cross-correlation analysis reveals that the maximal correlation between $\delta^{18}O$ and $\delta^{13}C$ during the shallow growth phase ($r = -0.71$; $p < 0.05$) is achieved when $\delta^{18}O$ time series lag $\delta^{13}C$ series by 3 months. However, this phase shift is not observed in the deep skeleton. $\delta^{13}C$ and $\delta^{18}O$ are positively correlated with a maximum correlation at a time lag of zero months (Fig. 5B; $y = 0.50x - 0.55$; $r^2 = 0.65$; $p < 0.05$).

### Density bands

Two definite time markers are evident in this record (Fig. 2). The first is the Alizarin red-S stain line marking the transplantation date (February 1991) and the second is the outermost skeleton layer representing the retrieval date (February 2001). Both time markers correspond to high-density bands, although one was formed during the shallow phase and the other during the deep phase of the coral growth. A cross-correlation between skeleton optical density and $\delta^{18}O$ shows that maximum correlation occurs at a time lag of zero for the two growth phases. Low-density skeleton is produced during summer and high-density skeleton is produced during winter, in both shallow and deep growth phases of the coral ($r = 0.52$; $p < 0.05$ for shallow growth phase and $r = 0.54$; $p < 0.05$ for deep growth phase).

## Discussion

### Measured temperature and acclimatization

The two data loggers show that the mean annual temperature difference between 6 and 40 m is less than 0.25 °C, with a maximum of 1.5 °C difference in summer and no difference during winter. This temperature decline along the 40-m depth gradient is negligible in comparison to the annual mean temperature amplitude of 5.5 °C. On the other hand, light spectrum and light intensity change rapidly along this depth gradient and largely dictate the coral abundance (Achituv and Dubinsky 1990). In addition to the general light attenuation, colonies living in shallow water receive proportionally more red and ultraviolet radiation (UVR) and less blue and green radiation than deep-water corals. This results in the presence of high-light- and low-light-adapted ecotypes of corals and zooxanthellae along a depth gradient (Rowan et al. 1997; Jokiel et al. 1997; Lesser 2000).

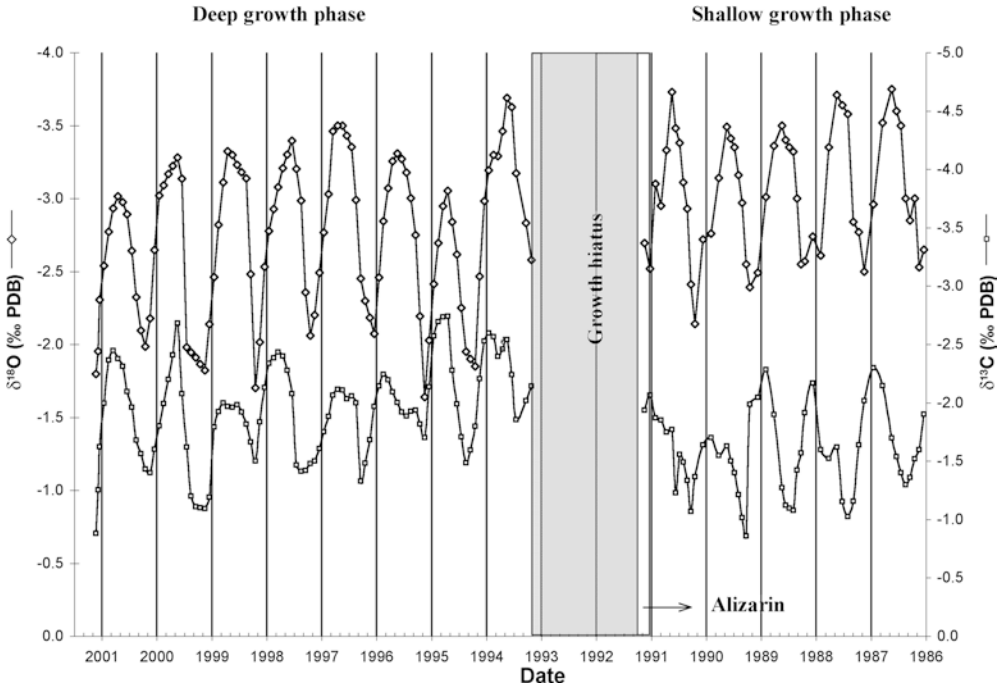


**Fig. 3** *P. lutea* skeletal $\delta^{18}O$ and $\delta^{13}C$ composition recorded in the deep and shallow growth phases of the transplanted colony. *Vertical gray lines* indicate January of each year. The two time markers are the collection date in February 2001 (*top of the record*) and the transplantation date in February 1991 (*Alizarin red line*). The *gray bar* represents the growth hiatus inferred from the missing 2 years in the deep growth phase and from observations made after the transplantation

**Table 1** Results of a Kolmogorov-Smirnov test comparing growth rate and isotopic variables as calculated in the shallow ($n = 5$ years) and deep ($n = 8$ years) growth phases of the colony

| Variable | Shallow | | | Deep | | | |
|---|---|---|---|---|---|---|---|
| | *n* | Avg. | STDV | *n* | Avg. | STDEV | P value |
| Growth rate (mm/year) | 5 | 5.66 | 0.47 | 8 | 3.00 | 0.37 | < 0.05 |
| Mean annual $\delta^{18}O$ (‰) | 5 | −3.10 | 0.10 | 8 | −2.80 | 0.14 | < 0.05 |
| Mean annual $\delta^{13}C$ (‰) | 5 | −1.58 | 0.12 | 8 | −1.92 | 0.14 | < 0.05 |
| Mean seasonal $\delta^{18}O$ amplitude (‰) | 5 | 1.14 | 0.15 | 8 | 1.49 | 0.20 | < 0.05 |
| Mean seasonal $\delta^{13}C$ amplitude (‰) | 5 | 1.13 | 0.21 | 8 | 0.80 | 0.19 | < 0.05 |

In the current study, the environmental changes experienced by the coral were extreme and did not allow for any acclimatization period. The uninterrupted skeleton accretion observed in the x-ray image of the coral (Fig. 2) rules out the possibility that a new *Porites* spp. planula settled upon the shallow-water coral following transplantation. The two missing density band pairs (Fig. 2), as confirmed by the number of $\delta^{18}O$ cycles (Fig. 3), and observations made after the transplantation procedure suggest that the colony did not produce skeleton for 2 years following transplantation. It seems that although the downward transplantation was stressful, the light reduction and spectrum change were not lethal and the colonies were able to adapt to the new environment.

## Morphology and growth rate

Acclimatization of the coral to a deep-water environment involved changes in colony growth form, which are consistent with the overall morphological change from a massive growth form in shallow water to columnar growth form in deep water (Riegl and Piller 1990). In addition, a decrease in mean annual extension rates was also observed. Mean annual extension rates for *Porites* spp. colonies sampled from different water depths at the same General area (Klein et al. 1992, 1993; Heiss et al. 1993, 1996, 1999; Felis et al. 1998) are in good agreement with the values we recorded in the two growth phases of this colony. It appears therefore that the transplanted coral had shifted from a massive, fast-growing, shallow-water, and high-light ecotype to columnar, slow-growing, deep-water, and low-light ecotype.

## Stable isotopes

The measured differences in mean monthly temperature between deep and shallow habitats are large enough to induce variations in skeletal $\delta^{18}O$ between corals living at these habitats. The seasonal temperature amplitude in surface water in Eilat is 5.5 °C (Fig. 1). This translates to an annual $\delta^{18}O$ variability of 1.15‰, assuming a negligible $\delta^{18}O_{sw}$ variation throughout the year (Felis et al. 1998) and using $\delta^{18}O = 0.594–0.21$ SST as the relationship between *Porites* spp. skeletal $\delta^{18}O$ to SST (McConnaughey 1989a). The measured average annual range in $\delta^{18}O$ in the "shallow skeleton" is 1.14‰,

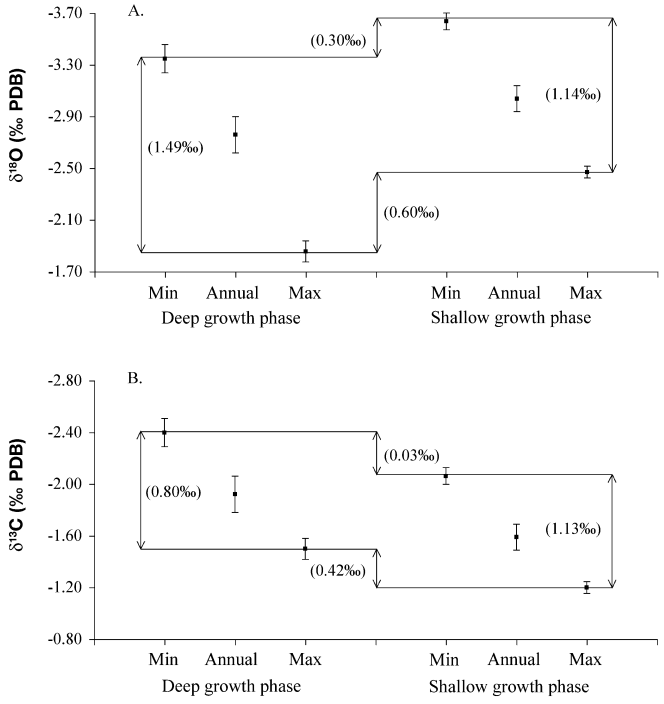


**Fig. 4** **A** Average minimum (summer), maximum (winter), and annual coral skeletal $\delta^{18}O$ composition ($\pm$SD) in the shallow and deep growth phases of the coral. Each mean comprises five and eight samples for shallow and deep growth phases, respectively. *Values in brackets* are the difference between the corresponding points. **B** Average minimum, maximum, and annual $\delta^{13}C$ composition ($\pm$SD) in the shallow and deep growth phases of the coral. Each mean comprises five and eight samples for shallow and deep growth phases, respectively. *Values in brackets* are the difference between the corresponding points

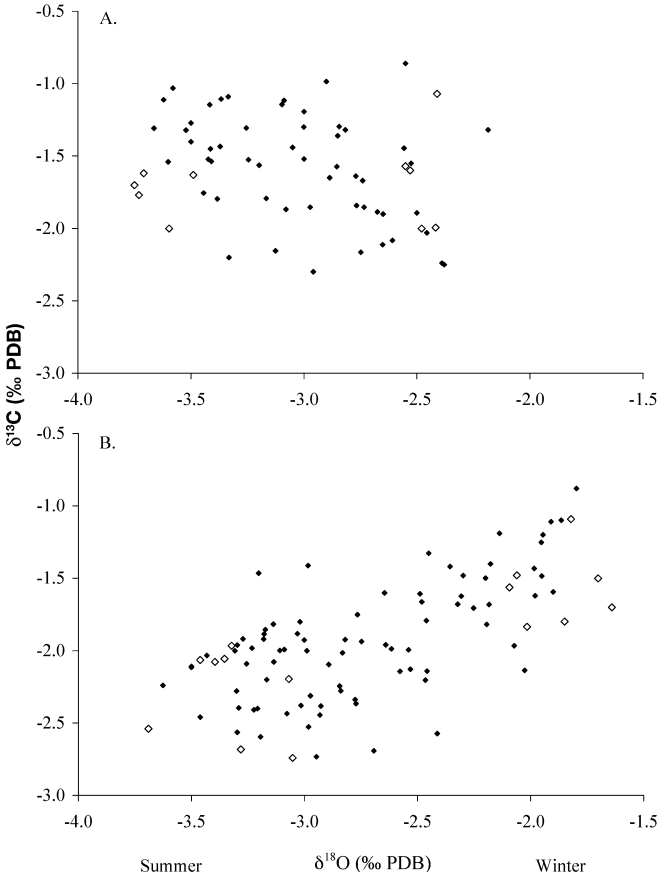


**Fig. 5** $\delta^{13}C$ vs. $\delta^{18}O$ plot of the shallow (**A**) and deep (**B**) growth phases of the transplanted colony. *Open symbols* represent maximal summer and winter values

suggesting that in shallow water the annual temperature change accounts for all the skeletal $\delta^{18}O$ variance. On the other hand, the annual temperature amplitude in deep water is only 4.5 °C (Fig. 1). Thus, we expected that the $\delta^{18}O$ amplitude of the deep skeletal phase would be smaller than that of the shallow skeletal phase. Surprisingly, we measured annual range in $\delta^{18}O$ of 1.49‰, significantly higher than in the "shallow skeleton" (Fig. 4A; Table 1). It appears that $\delta^{18}O$ of the "deep skeleton" is 0.30 and 0.60‰ enriched relative to the "shallow skeleton" $\delta^{18}O$ in summer and winter, respectively (Fig. 4A).

During the summer months when the water column is stratified, the temperature at 40 m is 1.5 °C cooler than at 6 m (Fig. 1). This difference corresponds to the 0.3‰ enrichment measured in the skeleton deposited in summer during the deep growth phase of the colony versus that deposited in summer during the shallow growth phase (Fig. 4A). During winter months, on the other hand, the water column is well mixed (Genin et al. 1995) and we did not detect any water temperature difference between the two depths (Fig. 1). Hence, temperature does not account for the 0.6‰ enrichment observed in the corresponding skeletal portion. The contribution of salinity to the vertical variations in water density at the study site is negligible (Wolf-Vecht 1992; Berman 2000) and rules out the possibility that difference in $\delta^{18}O_{sw}$ compositions at the two depths caused the measured difference in skeletal $\delta^{18}O$. Therefore, an alternative explanation must be invoked to account for the unusual winter enrichment in $\delta^{18}O$ of the skeleton during the deep growth phase of the colony.

During winter in Eilat, the water column is well mixed and mixing can reach down to 800 m. This seasonal deep-water mixing results in an increased supply of nutrients to the surface waters, leading to massive algal blooms (Genin et al. 1995). As a result, during winter only 5% of the surface light is available for photosynthesis at 40 m water depth as opposed to 30% that is available during summer at the same depth (Titlyanov et al. 2000). Generally, photosynthesis stimulates calcification in scleractinian corals and calcification rates in the light were calculated to be three-fold higher than in the dark (Gattuso et al. 1999). The extreme light attenuation along the murky water column during winter may decrease photosynthesis activity and calcification rate in corals inhabiting deep-water environments. Variations in calcification rates were found to generate a considerable impact on carbon and oxygen fractionation processes and were associated directly to rates of photosynthesis by the zooxanthellae and

calcification by the coral host (Land et al. 1975; McConnaughey 1989a, 1989b; de Villiers et al. 1995; Allison et al. 1996). This kinetic effect causes a significant isotopic enrichment when accretion rates are low. Therefore, it is reasonable to assume that a decline in growth rate during the winter months in the deep growth phase of the coral explains the observed enrichment in skeletal $\delta^{18}O$ due to kinetic effects.

The change in phase relation between $\delta^{18}O$ and $\delta^{13}C$, from a negative correlation with a 3-month time lag in the shallow growth phase to an in-phase positive correlation in the deep growth phase, reflects the change in the environment in which the colony grew. In Eilat, light intensity is maximal during May while water temperature is maximal only 3 months later, during August (Klein et al. 1992; Israel meteorological service, Eilat station). This phase shift is detected in the shallow growth phase of the coral. The skeletal $\delta^{13}C$, governed mainly by light intensity through the photosynthetic activity of the zooxanthellae, reaches a maximum in May, while $\delta^{18}O$ that is mainly temperature dependent, reaches its minimal value 3 months later, during August, when water temperature is maximal.

During the time period that the colony grew in deep water, this phase shift was absent. The measured depletion of mean annual $\delta^{13}C$, as well as the lower seasonal $\delta^{13}C$ amplitude in the deep growth phase of the colony are in agreement with findings that skeletal $\delta^{13}C$ values gradually decrease with depth (Weber et al. 1976; Fairbanks and Dodge 1979; Swart and Coleman 1980; McConnaughey 1989a; Muscatine et al. 1989; Aharon 1991; Leder et al. 1991; Juillet-Leclerc et al. 1997; Grottoli and Wellington 1999) and may suggest that photosynthesis by the zooxanthellae was reduced because of the poor light conditions in deep water. This conclusion is in accordance with indications that deep-water corals may not have the potential to be autotrophic with respect to carbon, and must therefore obtain some carbon heterotrophically (Davies 1977; Muscatine et al. 1984, 1989; Grottoli 1999; Grottoli and Wellington 1999). In addition to the change in the absolute $\delta^{13}C$ values, a positive correlation between $\delta^{18}O$ and $\delta^{13}C$ without a phase shift was observed (Fig. 5). Such positive correlations are common to carbonates showing mainly kinetic patterns (McConnaughey 1989a). The relationship between $\delta^{18}O$ and $\delta^{13}C$ in the shallow and deep growth phases of the colony, as demonstrated in Fig. 5, is strikingly comparable to that in the Galapagos corals discussed by McConnaughey et al. (1997) (see Fig. 6 therein). The shallow growth phase is analogous to the Galapagos hermatypic corals, while the deep growth phase is analogous to the ahermatypic Galapagos corals. It appears that the importance of light intensities in the forcing of skeletal $\delta^{13}C$ in deep-water corals is lower than in shallow water corals. Instead, the control of the kinetic effect over the skeletal $\delta^{13}C$ in deep-water corals is predominant.

Low photosynthetic rate due to light saturation (photoinhibition) may also explain the negative correlation observed between $\delta^{18}O$ and $\delta^{13}C$ in the shallow growth phase of the coral. The idea that photoinhibition may control the isotopic composition of shallow corals was suggested by Erez (1977, 1978). In contrast to previous models (Weber and Woodhead 1970; Goreau 1977a, 1977b), Erez (1977, 1978) concluded that the isotopic composition of the skeletal $\delta^{13}C$ becomes lighter as photosynthetic rate increases. More recent studies (Swart 1983; McConnaughey 1989a) confirmed and support the model of Weber and Woodhead (1970) and Goreau (1977a, 1977b) that skeletal $\delta^{13}C$ becomes heavier as photosynthesis rates increase.

### Density bands

Since skeletal density banding provides the foundation for most coral-based environmental reconstruction studies, it is of great importance to determine whether the timing of density-band formation is genetically and/or environmentally controlled. A cross-correlation analysis between skeletal optical density and $\delta^{18}O$ composition in the two growth phases of the coral revealed that the timing of density-band formation remained the same regardless of depth. In contrast, in previous work at the same study site with the same coral genus, the timing of density-band formation was found to be depth dependent, with opposite patterns in shallow (3 m) and deep (51 m) water (Klein et al. 1993). In the current study, the timing of density banding produced by the same colony (i.e., the same genotype) at the two depth environments (6 and 40 m) was similar, while in Klein et al. (1993), different colonies (i.e., different genotypes) produced opposite banding at the two depth environments (3 and 51 m). This disagreement between the results may imply that the timing of density band formation is intrinsically controlled rather than environmentally governed. Findings of other investigators who reported differences in timing of density band formation between closely situated colonies of the same species on the same reef support this hypothesis (Lough and Barns 1990).

## Summary

The present study investigated the effect of water depth on stable isotope composition and density band formation in a coral colony that experienced two distinct depth environments (6 and 40 m) for several years at each depth. The significant differences in isotopic composition, as well as the lack of difference in the timing of density-band formation between the shallow and deep growth phases of this colony, suggest that reconstruction of seasonal environmental variations must be achieved differently for shallow and deep water corals. While shallow corals at this site may faithfully record the full seasonal temperature variability, deep-water corals might be more influenced by kinetic effects. However, we

need to replicate this study in more colonies, in order to test this hypothesis. In the study site, the difference between periods of maximum temperature and light intensities enables the conclusion that a lack of phase shift between $\delta^{18}O$ and $\delta^{13}C$ was indicative of deep-water corals, while such a phase shift was consistent with our expectations for shallow-water corals. In view of the fact that diagenesis (e.g., recrystallization and secondary aragonite precipitation) may alter the original isotopic ratios in fossil corals, and since it is unlikely that these processes will mask the phase shift, this finding may serve as a novel indicator revealing the environmental setting in which such corals grew.

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