Coral Sclerochronology: Similarities and Differences in the Coral Isotopic Signatures Between Mesophotic and Shallow-Water Reefs

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Abstract

Coral sclerochronology is a powerful tool for understanding environmental and ecological changes on coral reefs. Geochemical, isotopic, and skeletal density banding analyses along the major growth axis of massive coral skeletons from tropical shallow-water reefs have been used successfully to reconstruct decadal- to centennial-scale histories of climate and coral growth with annual to seasonal resolution. However, little is known about how coral sclerochronological approaches could capture environmental and/or physiological changes in mesophotic coral ecosystems (MCEs), which occur at depths ranging from 30 to 150 m. We compared the oxygen and carbon isotopes and growth records of coral from upper MCEs with those from adjacent shallow reefs by examining *Porites* corals

collected at 4 and 40 m from Okinawa, Japan, and from 5 and 50 m water depths from the Gulf of Eilat, Red Sea, Israel. *Porites* corals in MCEs exhibited low calcification rates, but still recorded distinct seasonal to interannual variability in oxygen and carbon isotope signals consistent with coral isotopic records on shallow reefs. The amplitudes of the seasonality in the isotopic records in corals from MCEs were larger than those expected from seasonal environmental variations and those recorded in shallow reefs, indicating that coral growth rate and/or physiological changes affected skeletal isotopic composition. Our results suggest that sclerochronological records have great potential for reconstructing environmental and ecological characteristics of MCEs. The isotopic records of MCE corals are also more influenced by physiological processes such as symbiotic photosynthesis, calcification rates, and trophic levels than their shallow-water counterparts.

Keywords

Coral sclerochronology · Oxygen isotope · Carbon isotope · Mesophotic coral ecosystems · *Porites* corals

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36.1 Introduction

Symbiotic scleractinian reef-building corals (“corals” hereafter) occur in a range of environments from shallow-water coral reefs to depths >150 m (Kahng et al. 2010). Mesophotic coral ecosystems (MCEs) occur at depths ranging from 30–40 to 150 m, where photosynthetically active radiation (PAR; 400–700 nm) is limited (Loya et al. 2016). Corals continuously accumulate calcium carbonate skeletons as they grow, providing a record of environmental conditions throughout the life span of the colony. Coral sclerochronology, a combined approach using physical and chemical

analyses along the major growth axis, can provide a wealth of information about the environmental and physiological changes experienced by corals hundreds of years old (e.g., Gagan et al. 2000; Grottoli and Eakin 2007; Abram et al. 2016). Isotopic, geochemical, and skeletal growth analyses of certain massive corals (e.g., *Porites* and *Orbicella*) in tropical shallow reefs have been successfully used to reconstruct seasonal- to century-scale variation in environmental parameters (e.g., temperature, salinity, light intensity, nutrient dynamics, marine pollution, and ocean pH) and coral growth (e.g., skeletal density, linear extension rate, and calcification rates) (see Table 36.1 and associated references).

The stable oxygen isotope ratio ($\delta^{18}\text{O}$) in shallow-water corals is widely used to reconstruct sea surface temperature (SST) and sea surface salinity (SSS) (Table 36.1). The $\delta^{18}\text{O}$ in the carbonate minerals that comprise the coral skeleton reflects both the water temperature and the chemical composition of the surrounding seawater (Epstein et al. 1953). Coral $\delta^{18}\text{O}$ is biologically mediated and precipitated under isotopic disequilibrium from seawater $\delta^{18}\text{O}$ (Weber and Woodhead 1970); however, the offset from equilibrium is assumed to be relatively constant within the same coral species. Carbon isotope ratios ($\delta^{13}\text{C}$) preserved in coral skeletons have also been used as an indicator for environmental parameters such as sunlight and dissolved inorganic carbon (DIC) (Table 36.1), although the factors controlling coral $\delta^{13}\text{C}$ are more complicated due to the complex pathways and sources of carbon from the ambient seawater to the coral skeletons (Table 36.1).

Reef-building (symbiotic algae bearing) corals are typically associated with shallow-water habitats, but many species also occur in MCEs at water depths >30–40 m. MCEs have received increasing attention in recent years because of their potential to act as refuges for shallow-water coral reef taxa (Glynn 1996; Bongaerts et al. 2010; Loya et al. 2016) especially as shallow reefs become increasingly impacted by the changing global climate system, such as mass bleaching events (Hughes et al. 2017, 2018) and more intense tropical cyclones (Cheal et al. 2017). Sclerochronological approaches combined with geochemical analyses and growth characteristics in massive corals with depth provide an opportunity to identify historical environmental conditions and potentially environmental stress by analyzing key demographic indicators (e.g., extension rates, skeletal densities, calcification rates, and isotopic records in coral skeletons) in mesophotic corals. Numerous studies have examined the influence of depth on growth characteristics of massive corals (reviewed by Lough and Cooper 2011), but only a small number of studies from a single location (Gulf of Eilat, Red Sea) have examined the geochemical characteristics of mesophotic corals (Huston 1985; Klein et al. 1993; Al-Rousan et al. 2003; Rosenfeld et al. 2003). MCEs worldwide are poorly studied, and their long-term ecological dynamics remain virtually unknown (Loya et al. 2016).

Table 36.1 Summary of published coral geochemical and isotopic parameters and their environmental interpretation and coral growth histories

Proxy	Controlling factor	References
Isotopes		
$\delta^{18}\text{O}$	Sea surface temperature	Dunbar and Wellington (1981), Klein et al. (1992), Cole et al. (1993), Dunbar et al. (1994), Gagan et al. (2000), Tudhope et al. (2001), Felis et al. (2000), Watanabe et al. (2003), and Correge et al. (2004)
	Seawater	
	$\delta^{18}\text{O}$ (precipitation, evaporation, sea surface salinity)	
	Kinetic fractionation	McConnaughey (1989b)
$\delta^{13}\text{C}$	Physiological factors (e.g. symbiont photosynthesis and host respiration, spawning, internal pH, feeding, trophic level)	Swart (1983), Muscatine et al. (1989), McConnaughey (1989a, b), McConnaughey et al. (1997), Grottoli and Wellington (1999), and Gagan et al. (1998)
	Environmental factors (e.g., solar irradiance, dissolved inorganic carbon, upwelling)	Nozaki et al. (1978), Cole and Fairbanks (1990), Grottoli and Wellington (1999), Reynaud-Vaganay et al. (2001), Grottoli (2002), and Watanabe et al. (2017)
	Kinetic fractionation	McConnaughey (1989b)
$\delta^{11}\text{B}$	pH	Hönisch et al. (2004), Reynaud et al. (2004), and Trotter et al. (2011)
$\delta^{15}\text{N}$	Inorganic nitrogen sources	Marion et al. (2005), Yamazaki et al. (2011), and Wang et al. (2015)
Trace and minor elements		
Sr/Ca	Sea surface temperature	Smith et al. (1979), Beck et al. (1992), Alibert and McCulloch (1997), Gagan et al. (1998), Correge et al. (2000), Tudhope et al. (2001), Watanabe et al. (2001), Marshall and McCulloch (2002), Stephans et al. (2004), Felis et al. (2004), and Zinke et al. (2004)
Mg/Ca	Sea surface temperature	Mitsuguchi et al. (1996) and Watanabe et al. (2001)
Ba/Ca	Upwelling	Lea et al. (1989) and Montaggioni et al. (2006)
	River outflow	McCulloch et al. (2003)
P/Ca	Phosphorus concentrations, upwelling	LaVigne et al. (2008, 2010)

(continued)

Table 36.1 (continued)

Proxy	Controlling factor	References
Skeleton		
Skeletal growth bands	Density, extension (growth) rates, calcification rates,	Knutson et al. (1972), Dodge and Thomson (1974), Dodge and Brass (1984), Huston (1985), Lough and Barnes (2000), and Tortolero-Langarica et al. (2016)
Luminescence bands	Freshwater input, ocean productivity	Scoffin et al. (1989), Klein et al. (1990), Barnes and Taylor (2001); Nyberg (2002), Lough (2007, 2011), and Grove et al. (2010)

Here, we present $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records reconstructed from the skeletons of the massive *Porites* corals collected from upper mesophotic depths (40–50 m) at Sesoko and Ie islands, Okinawa, Japan, and from Gulf of Eilat, Red Sea, Israel, and compare their geochemistry to *Porites* corals collected from adjacent shallow (~5 m) reefs. We examine the similarities and differences in coral isotopic signatures between MCEs and shallow reefs and assess the potential for using coral sclerochronological records as environmental/ecological recorders in MCEs.

36.2 Methods

Porites lutea from water depths of 4 m and *P. lobata* from 40 m off Sesoko Island were collected in 20 August 2014, and *P. lutea* at 40 m depth off Ie Island, Okinawa, Japan, was collected on 26 January 2013. Two *P. lutea* colonies were also collected at water depths of 5 and 50 m from the Gulf of Eilat, Red Sea, Israel, on 29 October 2013 and 1 May 2015, respectively (Fig. 36.1).

36.2.1 Study Sites

Sesoko Island is located to the northwest of Okinawa (26°38' N, 127°51' E; Fig. 36.1). Seasonal characteristics of seawater temperatures and light intensity both at the surface and upper mesophotic depths (40 m) were collected from April 2014 to April 2017 (Prasetia et al. 2017). Mean annual water temperature at the surface (1–2 m) around Sesoko Island was 24.9 °C, ranging from 20.6 °C (February) to 29.2 °C

(August). The seawater temperature at 40 m depth averaged 24.3 °C, ranging from 21.2 °C (February) to 27.7 °C (August; Fig. 36.1). The seasonal amplitudes of seawater temperatures were 8.6 °C and 6.4 °C at the surface and 40 m depth, respectively (Fig. 36.1). Mean annual light intensity at 40 m depth was 7.7% of the light intensity at the surface in cloudy conditions and 9.7% in sunny conditions (Prasetia et al. 2017, see also Sinniger et al. 2019).

The Gulf of Eilat is located in the northern part of the Red Sea (29°33' N, 34°57' E; Fig. 36.1). The Israel National Monitoring Program (INMP) at the Gulf of Eilat has measured in situ seawater temperature and salinity at different depths, ranging from 700 m to the surface, since 2004. From May 2004 to December 2016, annual seawater temperature in shallow water averaged 24.1 °C, ranging from 21.6 °C (February) to 27.2 °C (August). MCEs in the Gulf of Eilat occur from 35 to >150 m in depth (Loya and Slobodkin 1971; Eyal et al. 2019). The annual seawater temperature at 50 m depth averaged 23.6 °C, ranging from 21.4 °C (March) to 25.8 °C (August), during the same period (Eyal et al. 2019). The seasonal amplitudes of seawater temperatures in the Gulf of Eilat were 5.6 °C and 4.4 °C in shallow waters and MCEs, respectively (Fig. 36.1). Light intensity at 36 m depth was 5.5% of the light intensity measured at the surface at the Gulf of Eilat (Eyal et al. 2016). Salinity in the Gulf of Eilat is high (> 40.5 PSU) at shallow and mesophotic depths.

36.2.2 X-Radiography and Skeletal Parameters

Porites colonies were cut into 5-mm-thick slabs along the maximum growth axis of each colony for x-ray imaging. X-ray images were collected using a NAOMI (RF Co. Ltd., Japan) direct digital radiography CCD imaging sensor at Hokkaido University under exposure conditions of 50 kV, 1 mA, and an 8 s exposure time (Fig. 36.2). Extension rates along the maximum growth axis were estimated using the distance between pairs of high skeletal density maxima identified in the positive x-rays (Fig. 36.2). During the positive x-ray photography, density standardization samples prepared with *Tridacna* shells were photographed simultaneously to estimate skeletal densities from the grayscale value on the x-ray images. Skeletal density, linear extension, and annual calcification rates of each coral colony were calculated from the grayscale x-ray images following Sowa et al. (2014). Calcification rates were calculated following equation:

$$\text{Calcification rates (g cm}^{-2}\text{ year}^{-1}) = \text{Skeletal density (g cm}^{-3}) * \text{Extension rates (cm year}^{-1})$$

Fig. 36.1 Location of sampling sites in Gulf of Eilat, Red Sea, Israel (**a**, **b**), and Sesoko and Ie Islands, Okinawa, Japan (**a**, **c**). Also shown are the seasonal characteristics of water temperature at the depths where the *Porites* samples were collected for this study. The seasonal characteristics of the water temperature at each site were calculated from in situ water temperature observations during the periods from May 2004 to November 2013 for the Gulf of Eilat (**d**) and from April 2014 to 2017 for Sesoko Island (**e**)

Fig. 36.2 Positive prints of x-rays of *Porites* corals. Okinawa corals were collected from shallow (4 m) and mesophotic (40 m) depths at Sesoko and Ie Islands. Corals in the Gulf of Eilat were collected from 5 to 50 m depth. Red lines show the tracks for skeletal growth and isotope analysis. The blue arrows indicate the growth disturbance

following Lough and Barnes (2000). Height (H) and width (W) of coral slabs were measured along axes of maximum distances.

36.2.3 Subsampling for Isotopic Analysis

We determined the maximum growth axis of each coral slice from positive images of the x-rays to identify sampling tracks (Fig. 36.2). The sampling tracks were cut, and their edges formed into a ledge shape, 2.0 mm thick and 2.0 mm wide, using a micro drill. After creating the ledges, the coral slice was ultrasonically cleaned with tap water to remove the powder generated while creating the ledge. Ultrasonic washing with distilled water was carried out twice for 5 min each, after which the slab was dried in an oven at 40 °C for 24 h. Next, skeletal powder samples were obtained by a precise sampling method using a micro drill (1.8 mm diameter) and a precision control stage at Hokkaido University. Subsampling intervals

were determined depending on the extension rates of each coral colony to obtain >12 data points from each annual band, assumed as a couple of high skeletal density bands. Powder samples were collected at 0.4 mm (14 ± 4 samples/year) and 0.25 mm (36 ± 11 samples/year) intervals for shallow reef corals from Sesoko Island and the Gulf of Eilat, respectively, and 0.125 mm (22 ± 8 samples/year), 0.2 mm (15 ± 6 samples/year), and 0.25 mm (19 ± 4 samples/year) intervals for mesophotic corals from Sesoko Island, Ie Island, and the Gulf of Eilat, respectively.

36.2.4 Oxygen and Carbon Isotopic Analysis

Oxygen and carbon isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) in all *Porites* coral specimens were analyzed at Hokkaido University. Corals from 40 m depth in Ie Island and from 50 m in the Gulf of Eilat were analyzed by Finnigan MAT 251 isotope ratio mass spectrometry connected with Finnigan Kiel II car-

bonate devices, which required 100 μg (± 10 μg) of powder per sample. Corals from 4 to 40 m depth at Sesoko Island and at 5 m depth in the Gulf of Eilat were analyzed using a Thermo Scientific MAT 253 isotope ratio mass spectrometry connected with Thermo Scientific Kiel IV carbonate devices and required 30 μg (± 10 μg) of powder per sample. Coral carbonate powder was reacted with 100% H_3PO_4 at 70 $^\circ\text{C}$, and the CO_2 gas produced purified in the carbonate device before being introduced to the mass spectrometer. Measurement errors of the NBS-19 analysis were within 0.08‰ for $\delta^{18}\text{O}_{\text{VPDB}}$ and 0.05‰ for $\delta^{13}\text{C}_{\text{VPDB}}$ with both IRMS (MAT251 and MAT253).

An age model for the isotopic records was established by identifying areas of high density corresponding with annual low $\delta^{18}\text{O}$ in mesophotic corals from Sesoko Island and high density with high $\delta^{18}\text{O}$ in other specimens. Seasonal minimal and maximal $\delta^{18}\text{O}_{\text{VPDB}}$ were selected as time control points and tied to seasonal maximal and minimal seawater temperature records, respectively. Daily resolution AVHRR SST data at 26.375° N, 127.625° E (NCDC 2018) were used to establish the age model of coral isotopic records on shallow reefs in Sesoko Island. In situ seawater temperature at 5 and 40 m depth in Sesoko Island revealed congruence of seasonal maximum and minimum seawater temperatures (August and February) on both shallow and mesophotic reefs (Fig. 36.1). The age model of isotopic records in mesophotic corals from Okinawa was determined in the same way. To establish age model for coral specimens from the Gulf of Eilat, we used in situ monthly seawater temperature at 5 and 40 m depth from the Gulf of Eilat (INMP 2004–2016). The time series of coral isotopic records were interpolated to monthly resolution with 12 samples per year using AnalySeries software 2.0.8 (Paillard et al. 1996). Annual extension rates for each colony were estimated based on the age model established from seasonal cycle of $\delta^{18}\text{O}$.

36.3 Results

36.3.1 Shallow Corals

We found significantly higher annual extension rates (0.60–0.86 cm year^{-1}) and calcification rates (0.86–0.93 $\text{g cm}^{-2} \text{ year}^{-1}$) in shallow corals than those in mesophotic corals from Sesoko Island and Gulf of Eilat (annual extension rate, 0.26–0.47 cm year^{-1} ; calcification rates, 0.36–0.53 $\text{g cm}^{-2} \text{ year}^{-1}$). However, we found no difference in skeletal density (Table 36.2). $\delta^{18}\text{O}$ in the shallow-water corals from Sesoko Island showed a distinct seasonal cycle, and averaged -4.56 ± 0.60 ‰, ranging from -5.60 ‰ to -3.43 ‰. $\delta^{18}\text{O}$ on the shallow-water reef in the Gulf of Eilat averaged -3.05 ± 0.35 ‰, ranging from -3.05 ‰ to -2.15 ‰. The average seasonal amplitude of coral $\delta^{18}\text{O}$ was 1.55‰ and 0.75‰ for the

shallow reefs at Sesoko Island and the Gulf of Eilat, respectively (Fig. 36.3; Table 36.3). In the x-ray of corals from the Gulf of Eilat (Fig. 36.2), we observed growth disturbance that may have influenced the anomalously high $\delta^{18}\text{O}$ value relative to SST in winter of 2011 (Fig. 36.3). According to INMP records during 2005–2014, the seasonal variation of salinity in the Gulf of Eilat was between ± 0.13 at the surface (0 m) and ± 0.12 at 40 m depth, corresponding to seawater $\delta^{18}\text{O}$ values of ± 0.036 and ± 0.033 , respectively ($\delta^{18}\text{O}_{\text{sw}} = 0.281 \times \text{Salinity} - 9.14$; Al-Rousan et al. 2003). Consequently, seasonal variation of seawater $\delta^{18}\text{O}$ could be disregarded as a source in the seasonal variation in $\delta^{18}\text{O}$ in the corals, at least in the Gulf of Eilat. Therefore, assuming that temperature was the primary control of coral $\delta^{18}\text{O}$, the relationship between coral $\delta^{18}\text{O}$ in the shallow depths and SST in monthly resolution at each site were:

Sesoko Island :

$$\delta^{18}\text{O}_{\text{coral}} = -0.20 \pm 0.01 \times \text{SST} - 0.64 \pm 0.37 (R = -0.95, n = 26) \quad (36.1)$$

Gulf of Eilat :

$$\delta^{18}\text{O}_{\text{coral}} = -0.16 \pm 0.01 \times \text{SST} + 0.82 \pm 0.25 (R = -0.98, n = 13) \quad (36.2)$$

The temperature dependence in the seasonality of $\delta^{18}\text{O}$ on shallow reefs in both Sesoko Island and Gulf of Eilat is consistent with observations of corals in other tropical and subtropical regions and also with estimates based on abiotic aragonite (-0.16 to -0.23 ; see Fig. 36.4). To evaluate control of $\delta^{18}\text{O}_{\text{coral}}$ in mesophotic corals, we compared $\delta^{18}\text{O}_{\text{coral}}$ with expected $\delta^{18}\text{O}$ from water temperature. Expected $\delta^{18}\text{O}$ from water temperature in Sesoko Island and Gulf of Eilat were estimated to convert from water temperature on shallow and mesophotic depths in each site of Sesoko Island and Gulf of Eilat to $\delta^{18}\text{O}$ using regression equation of $\delta^{18}\text{O}_{\text{coral}}$ vs. water temperature on shallow depths in each site (36.1 and 36.2). $\delta^{13}\text{C}$ in the shallow reef averaged 2.91 ± 0.91 ‰ (range -4.78 ‰ to -1.02 ‰) at Sesoko Island and -2.90 ± 0.54 ‰ (range -4.36 ‰ to -1.69 ‰) in the Gulf of Eilat. The average seasonal amplitudes of the $\delta^{13}\text{C}$ were 1.72‰ and 0.75‰ for the shallow reefs at Sesoko Island and the Gulf of Eilat, respectively (Fig. 36.3; Table 36.3).

36.3.2 Mesophotic Corals

The morphological characteristics of the *Porites* colonies varied between shallow and mesophotic sites, with mesophotic coral colonies exhibiting more flattened forms (H, 7.6 cm, and W, 32.4 cm, at Sesoko Island and H, 6.4 cm, and W, 17.9 cm, at Ie Island) and massive forms on shallow reefs at Sesoko Island (H, 9.6 cm; W, 14.5 cm) (Fig. 36.2; Table 36.2). Average annual linear extension rates in MCEs were 0.26 ± 0.11 cm year^{-1} (1988–2014) at Sesoko Island, 0.28 ± 0.11 cm year^{-1} (1991–2013) at Ie Island, and 0.47 ± 0.12 cm year^{-1}

Table 36.2 Colony size (height, width, and tissue thickness) and growth parameters (annual linear extension rate, skeletal density, and calcification rate) for *Porites* colonies from shallow and mesophotic reefs at Sesoko and Ie Islands, Japan, and the Gulf of Eilat, Israel

	Depth (m)	Period	Colony size (cm)				Annual extension rates (cm year ⁻¹)				density (g cm ⁻³)			Calcification rates (g cm ⁻² year ⁻¹)		
			Height	Width	F-ratio	Tissue	Min	Max	Average (SD)	Min	Max	Average (SD)	Min	Max	Average (SD)	
Site	4	2004–2014	9.6	14.5	−0.32	0.45	0.40	0.80	0.60 (±0.13)	1.31	1.62	1.44 (±0.12)	0.65	1.11	0.86 (±0.17)	
Sesoko Island,	40	1988–2014	7.6	32.4	0.53	0.40	0.08	0.64	0.26** (±0.11)	1.09	1.57	1.37* (±0.11)	0.09	0.84**	0.36 (±0.16)	
Okinawa	40	1991–2013	6.4	17.9	0.28	0.35	0.12	0.52	0.28** (±0.11)	1.35	1.36	1.35** (±0.00)	0.16	0.71**	0.39 (±0.15)	
Ie Island, Okinawa	5	2008–2014	9.1	11	−0.65	0.30	0.49	1.07	0.86 (±0.22)	1.05	1.07	1.07 (±0.01)	0.54	1.16	0.93 (±0.24)	
Gulf of Eilat, Israel	50	2006–2012	4.9	12	0.18	0.35	0.28	0.60	0.47** (±0.12)	0.92	1.19	1.12** (±0.03)	0.32	0.67**	0.53 (±0.13)	

* and ** show $t < 0.05$ and $t < 0.01$ between growth parameters on shallow reef and MCEs

Fig. 36.3 Monthly time series of the coral isotope records from shallow (4 m, light blue line) and mesophotic (50 m, red line) at Sesoko Island (blue line) and Ie Islands (dark blue line), and from shallow (5 m, orange line) and mesophotic (50 m, red line) in the Gulf of Eilat. Black lines indicate SST variation of each site. Data source of SST for Sesoko Island was AVHRR SST dataset (daily resolution; NCDC 2018); and the Gulf of Eilat is in situ SST from INMP dataset (monthly resolution SST at the Gulf of Eilat; INMP 2004–2016). The axis of $\delta^{18}\text{O}$ is inverted to show seawater temperature variation as smaller $\delta^{18}\text{O}$ means higher temperature. Gray-hatched area shows the seasonal range of coral $\delta^{18}\text{O}$ estimated from monthly SST variation in Fig. 36.1

Table 36.3 Oxygen and carbon isotopes in *Porites* colonies from shallow and mesophotic reefs from Okinawa (Sesoko and Ie Islands), Japan, and the Gulf of Eilat, Israel

Site	Depth (m)	Period	$\delta^{18}\text{O}$ (‰VPDB)				$\delta^{13}\text{C}$ (‰VPDB)			
			Average (SD)	Max	Min	Seasonal amplitude	Average (SD)	Max	Min	Seasonal amplitude
Sesoko Island, Okinawa	4	2002–2014	-4.56 ± 0.60	-3.43	-5.60	1.55	-2.91 ± 0.91	-1.02	-4.78	1.72
	40	1987–2014	$-4.10^{**} \pm 0.52$	-2.73	-5.44	1.39	$-3.05^{**} \pm 0.78$	-1.19	-4.85	1.74
Ie Island, Okinawa	40	1991–2012	$-4.11^* \pm 0.54$	-3.00	-5.48	1.20^{**}	-2.75 ± 0.61	-1.01	-4.30	1.40^*
Gulf of Eilat, Israel	5	2008–2015	-3.05 ± 0.35	-2.15	-3.05	0.87	-2.90 ± 0.54	-1.69	-4.36	1.38
	50	2005–2013	$-2.67^{**} \pm 0.53$	-1.35	-3.54	1.36^{**}	$-3.41^{**} \pm 0.92$	-0.91	-5.12	2.35

* and ** show $t < 0.05$ and $t < 0.01$ between isotopic values in *Porites* on shallow reef and MCEs

Fig. 36.4 Temperature dependencies of oxygen isotopes in carbonates from shallow corals at Sesoko Island and the Gulf of Eilat, compared with previous studies (Japanese high latitude corals from Kochi: Yamazaki et al. (2009), Koshiki: Watanabe et al. (2014), and Amakusa: Omata et al. (2006); tropical corals from Galapagos: McConnaughey (1989a) and New Caledonia: Quinn et al. (1996); inorganic synthesis of aragonite: Kim et al. (2007) and calcite: Kim and O’Neil (1997); and average of biogenic carbonates: Grossman and Ku (1986))

(2006–2012) at the Gulf of Eilat. Average annual skeletal density in MCEs was $1.37 \pm 0.12 \text{ g cm}^{-3}$ (1988–2014) at Sesoko Island, $1.35 \pm 0.00 \text{ g cm}^{-3}$ (1991–2013) at Ie Island, and $1.12 \pm 0.03 \text{ g cm}^{-3}$ (2006–2012) at the Gulf of Eilat. Average coral annual calcification rates in MCEs were $0.36 \pm 0.15 \text{ g cm}^{-2} \text{ year}^{-1}$ (1988–2014) at Sesoko Island, $0.39 \pm 0.15 \text{ g cm}^{-2} \text{ year}^{-1}$ (1991–2013) at Ie Island, and $0.53 \pm 0.13 \text{ g cm}^{-2} \text{ year}^{-1}$ (2006–2012) at the Gulf of Eilat (Table 36.2). Although both linear extension and calcification rates were much lower at mesophotic depths than in adjacent shallows ($t < 0.01$), skeletal densities in mesophotic corals were similar to shallow-water corals at each site ($t > 0.01$).

$\delta^{18}\text{O}$ in the mesophotic corals at Sesoko Island averaged $-4.10 \pm 0.52\text{‰}$ (range -5.44 to -2.73‰), while the amplitude of seasonal cycles tended to decrease through time from 1988 to 2014 (Fig. 36.3). $\delta^{18}\text{O}$ in mesophotic corals averaged $-4.11 \pm 0.54\text{‰}$ (range -5.48 to -3.00‰) at Ie Island and $-2.67 \pm 0.53\text{‰}$ (range -3.54 to -1.35‰) in the Gulf of Eilat. The average seasonal range of $\delta^{18}\text{O}$ was 1.33‰ , 0.68‰ , and 1.20‰ for the mesophotic corals at Sesoko Island, Ie Island, and the Gulf of Eilat, respectively (Table 36.3).

$\delta^{13}\text{C}$ in the mesophotic corals at Sesoko Island averaged $-3.05 \pm 0.78\text{‰}$ (range -4.85 to -1.19‰), $-2.75 \pm 0.61\text{‰}$ (range -4.30 to -1.01‰) at Ie Island, and $-3.41 \pm 0.92\text{‰}$ (range -5.12‰ and -0.91‰) in the Gulf of Eilat. The average seasonal range of $\delta^{13}\text{C}$ was 1.69‰ , 1.15‰ , and 1.65‰ for the mesophotic corals at Sesoko Island, Ie Island, and the Gulf of Eilat, respectively (Table 36.3).

36.4 Discussion

36.4.1 Coral Growth and Morphological Characteristics in MCEs

Flattening colony morphology to increase surface area for light capture is a widespread response to increasing depth across a wide range of coral taxa (Fricke and Schuhmacher 1983; Einbinder et al. 2009; Nir et al. 2011), including for *Porites* colonies transplanted from shallow to deep water in the Gulf of Eilat (Rosenfeld et al. 2003). Lough (2008) demonstrated that the averages of annual linear extension rates, calcification rates, and skeletal densities in corals on shallow reefs were mostly governed by average water temperature. Therefore, corals at mesophotic depths exposed to lower temperatures would be expected to grow more slowly than shallower counterparts. However, coral growth rates may also be influenced by other factors such as light irradiance—the key energetic resource for reef corals. Figure 36.5 shows the comparison between the values of coral growth parameters and annual averages of water temperature in each site of this study, compared to relationships for other shallow reefs

in the Indo-Pacific (Lough 2008). In Okinawa, extension rates and calcification rates were much lower at mesophotic depths than expected based on seawater temperature, although there was no effect on skeletal density (Fig. 36.5). In the Gulf of Eilat, skeletal densities in both shallow and mesophotic corals were much smaller than expected from seawater temperature, even though linear extension and calcification rates were consistent with predictions based on seawater temperature (Fig. 36.5).

The variability in coral growth characteristics among habitats and geographic regions suggests that massive *Porites* may employ different strategies for building their carbonate skeletons based on their environment. While skeletal density was similar for both shallow and mesophotic corals, annual calcification rates were much lower at mesophotic depths ($t < 0.01$ at both Okinawa and the Gulf of Eilat: Table 36.2), suggesting a limited ability to produce carbonate. The morphological characteristics and small calcification rates of mesophotic corals reported in this study could be influenced by low-light levels, since the temperature differences between shallow and mesophotic reefs are relatively small (Fig. 36.1), but light irradiance at mesophotic depths is only 10% of that in the shallows (Eyal et al. 2016; Prasertia et al. 2017). In addition, corals in Okinawa are exposed to typhoon disturbances, which sometimes overturn large ($>1 \text{ m}$ diameter) massive *Porites* (Hongo et al. 2012), but such events would never occur in an arid climate such as Gulf of Eilat. This variability in hydrodynamics between locations could also influence coral growth and morphology.

36.4.2 Comparison of Isotopic Signatures Between Shallow and Mesophotic Corals

Coral isotopic records from all three mesophotic sites (Sesoko Island, Ie Island, and the Gulf of Eilat) showed distinct seasonal cycles, despite lower extension rates than shallow corals (Fig. 36.5). In particular, seasonal variation in skeletal $\delta^{18}\text{O}$ was evident in mesophotic corals at all the three sites. High and low skeletal density couplets in positive x-ray images corresponded with seasonal cycles of $\delta^{18}\text{O}$, and the high skeletal density bands mostly corresponded to seasonally high $\delta^{18}\text{O}$ values in winter. The occurrence of high skeletal density bands in mesophotic corals during winter reported here is consistent with previous reports of *Porites* corals in high latitudes (the Gulf of Eilat: Klein et al. 1992; Northwest Pacific Ocean: Watanabe et al. 2014; Yamazaki et al. 2016). The similarity in coral $\delta^{18}\text{O}$ signals in both shallow and mesophotic corals, combined with confirmed temperature dependence of coral $\delta^{18}\text{O}$ on shallow reefs, suggests that the primary factor controlling coral $\delta^{18}\text{O}$ is seasonality in seawater temperature.

Fig. 36.5 Relationship between seawater temperature and average growth parameters (density, extension rates, and calcification rates) in *Porites* corals from shallow and mesophotic reefs at Sesoko and Ie Islands, Japan, and the Gulf of Eilat, Israel, compared with the linear relationship reported by Lough (2008)

Seasonal amplitudes in the isotopic signals of mesophotic corals from Sesoko Island were lower than those in shallows, while those in mesophotic from the Gulf of Eilat were higher (Fig. 36.3). Seasonal variability of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ was similar or smaller in MCEs than on shallow reefs in Okinawa. In the Gulf of Eilat, however, the seasonal variability of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ was larger in the MCEs than in the shallow reefs (Table 36.3; Fig. 36.3), even though the seasonal range of water temperature and irradiance in the MCEs were smaller. For example, the coral $\delta^{18}\text{O}$ in winter in the Gulf of Eilat was higher in mesophotic than shallow corals (Fig. 36.3). Additionally, the seasonal range of temperature estimated from coral $\delta^{18}\text{O}$ at 40 m depth at Sesoko Island was much higher than the observed in situ temperatures, although temperature records to compare with the isotopic records at mesophotic depths are not available at sufficient temporal scales. We also demonstrated that the range of $\delta^{18}\text{O}$ in mesophotic corals from Okinawa and the Gulf of Eilat was larger than the ranges of $\delta^{18}\text{O}$ estimated from seasonal amplitude of water temperature and temperature dependency of $\delta^{18}\text{O}$ in Eqs. (36.1) and (36.2) (Fig. 36.4). The larger seasonal range in the isotopic records of corals at mesophotic depths, where temperature seasonality and light irradiance are both lower, suggests a strong biological influence on coral isotope geochemistry in mesophotic corals.

36.4.3 Factors Controlling Coral Isotopic Signals in the MCEs and Their Potential as Environmental/Ecological Indicators

Environmental factors such as temperature, salinity, and water quality have long been demonstrated as important influences on isotopic variations in shallow corals (Table 36.1). Additional factors including calcification rate (McConnaughey 1989b), coral spawning (Gagan et al. 1996), respiration/photosynthesis in both the coral and symbiotic algae (Swart et al. 1996), the proportion of energy obtained by heterotrophy versus autotrophy (Swart et al. 1998), food sources (Grottoli 2002), and the carbonate ion species in calcified fluid (Adkins et al. 2003; Rollion-Bard et al. 2003) have also been suggested to influence isotopic signatures in corals. McConnaughey (1989b) proposed extension rate-related kinetic effects on coral isotopic records using carbon and oxygen isotopic values from different skeletal portions with different extension rates in a single *Pavona* coral colony. To examine the kinetic effects on coral isotopic records, we calculated the deviation of annual isotopic values in mesophotic corals from those in shallow corals and compared the deviations with corresponding annual extension rates in each year (Fig. 36.6). Our comparison between the $\delta^{18}\text{O}$ deviations and annual extension rates in all isotopic

Fig. 36.6 Comparison of coral linear extension rate with skeletal $\delta^{18}\text{O}$ (a) and $\delta^{13}\text{C}$ (b) anomalies. Fitting line for $\delta^{18}\text{O}$ (a) is $\delta^{18}\text{O}_{\text{anomaly}} = 1.24 \times (\text{Ext. rate})^2 - 2.24 \times (\text{Ext. rate}) + 1.00$ ($R^2 = 0.43$)

records in the *Porites* specimens showed a negative relationship (Fig. 36.6a). A similar trend in coral $\delta^{18}\text{O}$ was also reported by McConnaughey (1989b) and Felis et al. (2003), suggesting that extension rates can be a controlling factor for mesophotic coral $\delta^{18}\text{O}$. On the other hand, this extension rate-related influence was not evident for the coral $\delta^{13}\text{C}$ (Fig. 36.6b). The different responses of coral $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ to extension rate may imply that the controlling factors for extension rate in MCEs were similar for coral $\delta^{18}\text{O}$ (most likely temperature), but different for coral $\delta^{13}\text{C}$. If kinetic effects are one of the dominant controlling factors in coral isotopic signals, both carbon and oxygen isotopes should have been influenced in the same manner with varying extension rates (i.e., more negative at higher extension rates).

Gagan et al. (2012) discussed how “bio-smoothing” within the living coral tissue layer can attenuate geochemical and isotopic signals in corals when the temperature dependency of $\delta^{18}\text{O}$ is less than $0.23\text{‰}/^\circ\text{C}$ (Eqs. 36.1 and 36.2). The tissue layer on the mesophotic corals from Okinawa was thicker than the average linear extension rates (Table 36.2), in contrast to shallow-water corals from Okinawa and the Gulf of Eilat. Bio-smoothing (Gagan et al. 2012) could potentially explain the isotopic variations in the mesophotic corals from Okinawa, but evaluating its effects would require analysis of Sr/Ca ratios. However, seasonal variations of coral isotopes in mesophotic corals are greater than those on shallow reefs even after accounting for bio-smoothing. Therefore, it is necessary to also consider other potentially important effects of the mesophotic environment on coral skeletons to fully interpret their isotopic signatures.

Adkins et al. (2003) explained the non-synchronized vital effects on carbon and oxygen isotope signals observed in

deep-sea corals using a conceptual model that proposed a mechanism in which the carbonate ion species shifts with changing pH in extracellular calcified fluid, thereby affecting coral $\delta^{18}\text{O}$ and growth. This hypothesis is consistent with the large heterogeneity of $\delta^{18}\text{O}$ and $\delta^{11}\text{B}$ (boron isotope as a proxy for pH) observed in the microstructures of *Porites* skeletons (Rollion-Bard et al. 2003) and might explain the isotopic patterns we observed in MCEs.

$\delta^{13}\text{C}$ in mesophotic corals must be influenced by other biological controls, although the mechanisms of coral $\delta^{13}\text{C}$ production are complicated (Table 36.1). Metabolic fractionation produces the skeletal $\delta^{13}\text{C}$ changes that reflect those in symbiont photosynthesis and host respiration (Swart 1983; Muscatine et al. 1989; McConnaughey 1989a, b; McConnaughey et al. 1997; Gattuso et al. 1999; Grottoli and Wellington 1999). Because a low rate of photosynthesis decreases the $\delta^{13}\text{C}$ values in the internal DIC pool, these values have been used as a proxy for solar irradiance (Cole and Fairbanks 1990; Grottoli and Wellington 1999; Reynaud-Vaganay et al. 2001; Grottoli 2002) and water depth (e.g., Weber et al. 1976; Grottoli and Wellington 1999; Heikoop et al. 2000; Rosenfeld et al. 2003; Dassié et al. 2013). Both annual mean and seasonal range of solar radiation are lower on mesophotic than shallow reefs at Sesoko Island and the Gulf of Eilat (Eyal et al. 2016; Prasetya et al. 2017), thus $\delta^{13}\text{C}$ in mesophotic corals should also show smaller seasonal amplitudes if amounts of CO_2 from photosynthesis of the symbiotic algae were the primary control factor of $\delta^{13}\text{C}$.

The similar or larger seasonal and interannual variability observed in $\delta^{13}\text{C}$ in mesophotic corals suggests that additional factors influence $\delta^{13}\text{C}$. Trophic changes between shal-

low and mesophotic corals offer one possible explanation. A high level of heterotrophic feeding in corals could decrease $\delta^{13}\text{C}$ in coral skeletons because zooplankton have the lower $\delta^{13}\text{C}$ values ($< -20\text{‰}$) than corals (Felis et al. 1998; Grottoli and Wellington 1999; Grottoli 2002; Palardy et al. 2008; Hughes et al. 2010). Heterotrophic pathways of organic carbon related to feeding may be more dominant and flexible on mesophotic than shallow reefs. Nevertheless, the coral isotopic time series of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in mesophotic corals from Okinawa showed a similar seasonal to interannual variability, which implies that isotopic signals in mesophotic corals captured environmental variability (Fig. 36.3). Environmental and physiological monitoring in MCEs (e.g., light intensity and particle flux on a seasonal cycle, photosynthetic rates, and respiration rates) and examination of additional geochemical proxies (Table 36.1) are required to understand the exact mechanisms for coral calcification and their physiological processes.

Future research to better understand the effects of depth on coral geochemistry could be aided by examining *Porites* corals across smaller intervals of depth and analyzing nitrogen isotopes in the plankton, polyp tissues, and the skeletal organic matter. In addition, aquaria experiments, which simulate light conditions in MCEs, to examine the responses in coral skeletal growth and geochemical composition, could provide greater insight into the response of corals to mesophotic environments. Although the isotopic signals in corals from MCEs recorded interannual variability and distinct seasonal cycles similar to shallow reefs, the isotopic values in MCEs showed large fluctuations and shifted to larger $\delta^{18}\text{O}$ and smaller $\delta^{13}\text{C}$ ratios. The differences in the isotopic signals between shallow and mesophotic corals suggest that coral geochemical records in MCEs are more sensitive to physiological processes such as symbiont photosynthesis, calcification rates, and trophic level than environmental variability. However, our results also show the strong potential of sclerochronological approaches to capture decadal changes in environmental conditions on mesophotic reefs, facilitating a greater understanding of the long-term environmental and ecological characteristics of these poorly known ecosystems.

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