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The oxygen isotopic record of seasonality in *Conus* shells and its application to understanding late middle Eocene (38 Ma) climate

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Abstract. **To better understand Eocene climate and the isotopic record of paleotemperature preserved in shells of the gastropod *Conus*, we serially sampled and analyzed four modern and two Eocene shells from the U.S. Gulf Coast and the Gulf of Mexico. The modern shells are from nearshore Mexico off Veracruz, offshore Texas (Stetson Bank), and nearshore Florida (Alligator Point). The fossil shells are of late middle Eocene (ca. 38 Ma) age from the Moodys Branch Formation in Mississippi (U.S.A.). The four modern shells yield three different oxygen-isotopic patterns of seasonality (asymmetrical saw-tooth, cuspate, and irregular) representing different seasonal growth patterns and environments. The asymmetrical sawtooth pattern occurs in the middle shelf specimen (Stetson Bank) and indicates rapid spring and declining autumn growth, presumably in response to increased nutrient supply and productivity associated with spring upwelling. The cuspate pattern indicates winter shutdown and occurs in the most northern specimen. The irregular pattern reflects seasonal freshwater input in a nearshore environment. The Eocene shells yield an asymmetrical sawtooth pattern suggestive of enhanced spring growth during upwelling.**

Assuming a constant seawater $\delta^{18}O$ of 0.24‰ (Lear et al., 2000), including correction for latitude (Zachos et al., 1994), oxygen isotope data yield a mean annual range of temperature (MART) for the late middle Eocene of 4–5°C, and a mean annual temperature (MAT) of 23°C. Taking the depth estimation (20–100 m) into consideration, sea surface temperatures are estimated to be >25°C for summer, ~21°C for winter, and MAT of >23°C. Compared with modern temperatures and isotopic paleotemperatures of modern shells, the late middle Eocene Gulf Coast experienced warmer winter temperatures. The difference between modern and late middle Eocene climate can partly be attributed to the development of a continental cold front during the modern winter, and to the increased marine influence during the middle Eocene caused by the warmer water mass of the ocean.

Key words: Eocene, *Conus*, Oxygen isotopes, Carbon isotopes, Watermass, Paleoclimate

Introduction

Seasonality or mean annual range of temperature (MART) is an important element of climate and ecology (Axelrod, 1984; Greenwood and Wing, 1995; Sloan and Barron, 1992; Sloan and Morill, 1998). For instance, MART has a significant effect on the distribution of taxa (Axelrod, 1984). One of the best methods for measuring MART in ancient environments is through oxygen isotopes.

Previous studies show that oxygen isotopes can reveal the temperatures at which calcium carbonate-secreting organisms such as bivalves, gastropods, and foraminifera lived (e.g., Epstein *et al.*, 1953; Horibe and Oba, 1972; Grossman and Ku, 1986; Kobashi *et al.*, 2001). Mollusks are known to secrete their shell in oxygen isotopic equilibrium with ambient water, that is, without significant vital effect (Epstein *et al.*, 1953; Grossman and Ku, 1986). For that reason, mollusk shells have frequently been used to reveal past environments over a wide temporal and spatial range (e.g., Late Cretaceous and Paleogene Laramide Rocky Mountains: Dettman and Lohmann, 2000; late Paleocene Arctic: Bice and Arthur, 1996; early middle Eocene North Atlantic region: Andreasson and Schmitz, 2000; Holocene North Atlantic Ocean: Weidman *et al.*,

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1994). Recent isotopic studies of modern bivalves have modeled the relationship between shell growth and isotopic record to enhance the interpretation of the isotopic record (Goodwin *et al.*, 2001, 2003; Wilkerson and Ivany, 2002; Schöne *et al.*, 2003).

In this study, we utilized two *Conus tortilis* Conrad (1854) specimens from the Moodys Branch Formation (ca. 38 Ma; P 14: Dockery, 1996, Berggren *et al.*, 1995) to reconstruct the late middle Eocene climate of the Mississippi embayment region. To better understand the environment of the northern Gulf of Mexico coast during Eocene time, we also studied the isotopic systematics of four modern *Conus* specimens from three different Gulf of Mexico settings.

During the late Eocene, global climate was in a transition period from warm greenhouse to cold icehouse (Prothero, 1994). Several lines of evidence, such as ice-drifted debris (Wise *et al.*, 1991) and oxygen isotope values coupled with magnesium contents of foraminiferal tests (Lear *et al.*, 2000), show that the Antarctic icesheet started to develop or temporarily existed at this time. Several paleobotanical studies of the northern Gulf region (e.g., Frederiksen, 1988; Yancey *et. al.*, 2003) show a cooling and drying trend from tropical-dwelling species to cool- and dry-dwelling species during the late Eocene. In addition, the great variety of molluscan species and the diversity of such groups as cypraeids in the Moodys Branch Formation indicate a tropical to subtropical climate (Dockery, 1977).

Samples and Methods

The gastropod genus *Conus* is known to live only in full marine conditions and mostly in tropical regions within reefs in shallow or moderately shallow water (Walls, 1978), and thus is well suited for oxygen isotope study of ocean paleotemperatures. We have sampled four modern *Conus* shells from three sites from the Gulf Coast of the U.S. and Mexico: Stetson Bank, Alligator Point, and Enmedio Reef. Two *Conus ermineus* specimens were collected live in August, 1971 from 20 to 30 m depth at Stetson Bank (28° 09′N, 94°18′W). Stetson Bank is a small, offshore coral bank within the Flower Garden Banks National Marine Sanctuary. It is located on the outer continental shelf 170 km south of the U.S. coast at the Texas-Louisiana border. Sea-surface temperatures at Stetson Bank vary from 18°C in winter to 30°C in summer and average 24°C (GDEM, 2000). Being so distant from the coast, Stetson Bank experiences only minor salinity fluctuations (2–3 psu at 13 m; LATEX, 1993) as a result of spring rains in the central and southern U.S. An additional large *Conus* shell was collected from Alligator Point, a sand beach southwest of Tallahassee, Florida (29°54′N, 84°31′W). This *Conus spurious atlanticus* specimen was found in beach drift and presumably lived nearshore. Temperatures in the region vary from 15° to 29°C, with a MAT of 22°C (NDBC station 42005; NDBC, 2003). Lastly, one shell of *Conus spurious* was collected from tropical Enmedio Reef (19°06′N, 95°56′W) off Veracruz, Mexico. The reef is part of the Veracruz Reef complex and is about 4 m deep at its shallowest point. Average monthly temperatures in Veracruz harbor about 20 km to the northwest vary from 22° to 29 °C and average 26.0°C (Secretaria de Marina, Dirección General de Oceanografía, 1978). Salinities in Veracruz harbor average 35–35.5 psu from November through May and 31–32 psu in July and August (Secretaria de Marina, Dirección General de Oceanografía, 1978). Salinities at Enmedio Reef can vary considerably. In June 1987 salinity was 26 psu at the surface and 32 psu at the bottom (Tunnell and Nelson, 1989).

Two *Conus tortilis* shells were collected from the Late Middle Eocene Moodys Branch Formation at Town Creek along a north-southeast stretch in the SE/4, SW/4, Section 10, T.5 N, R.1 E., Jackson, Hinds County, Mississippi (Dockery, 1980). The Moodys Branch Formation is the lower unit of the Jackson Group in Mississippi (Dockery, 1977). Mollusks from this formation lived in shallow marine waters near a retrograde shoreline (Dockery, 1977). The depositional environment at this specific locality is classified into "E" of Elder and Hansen (1981), which represents "inner middle shelf" (D. Dockery, pers. comm.). In addition, Elder and Hansen (1981) observed a dramatic increase of bryozoans at this locality, probably indicating a paleobathymetry of 20–100 m based on present bryozoan distributions.

Before sampling, *Conus* shells are cleaned by ultrasonification in distilled water, and polished with sandpaper to remove possible surface contamination. Before isotopic analyses, we conducted x-ray diffraction analysis to confirm the preservation of original aragonite. The results showed <1% of calcite in aragonite. We used a 0.5 mm Brasseler carbide bit to collect samples at 1.5 or 3.0 mm intervals along the whorls from shell apex to aperture. Each sample pit is approximately 0.5 mm deep (Figure 1).

We use a Finnigan Kiel II automated reaction system to react powdered samples with "100" phosphoric acid at 70 °C. The CO_2 produced is introduced into a Finnigan MAT 251 isotope ratio mass spectrometer for isotopic analysis. For calibration to the Peedee belemnite (PDB) standard, the carbonate standard NBS-19 ($\delta^{13}C$ = 1.95‰, $\delta^{18}O$ = −2.20‰) is used (i.e., VPDB). As an in-house standard, we use B2 (belemnite calcite from the Peedee formation ($\delta^{13}C$ = −0.44 ‰, $\delta^{18}O$ = −0.04‰) at the beginning and end of each sample set of eight. Analytical precision is ±0.04‰ for $\delta^{13}C$ and ±0.05‰ for $\delta^{18}O$.

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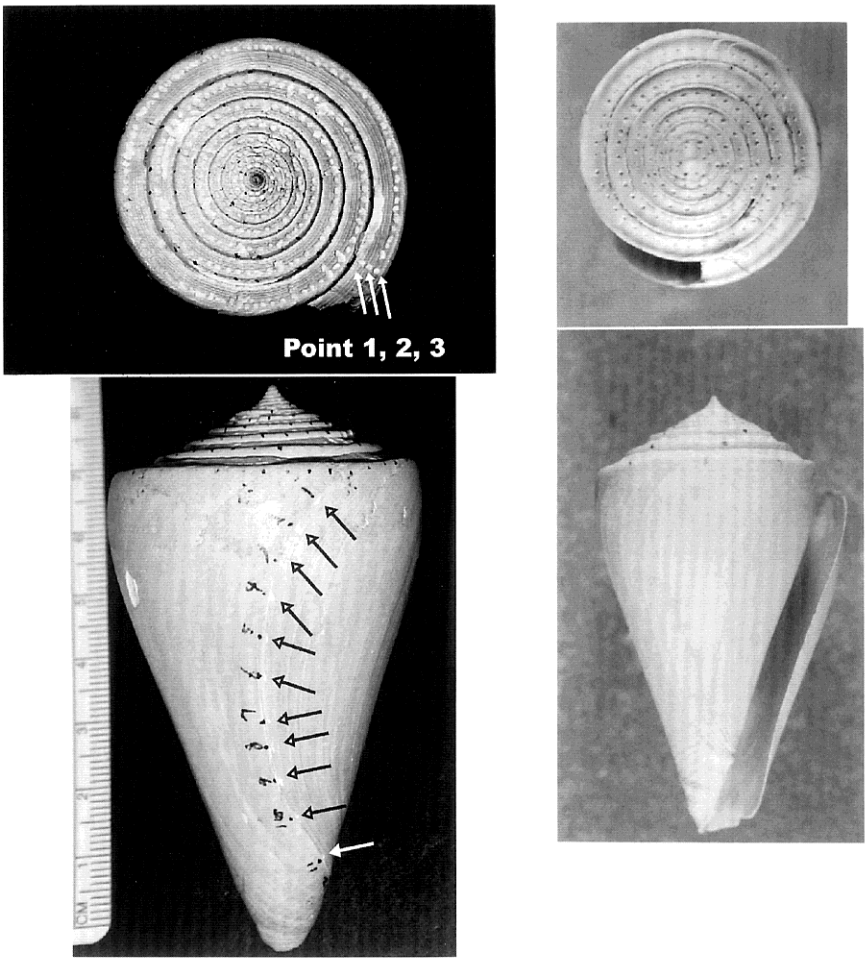


Figure 1. Moodys Branch *Conus* shells, MBC-2 (left), and MBC-1 (right). Arrows point to the sampling points along the growth band.

Results

Tests of isotopic variability within growth bands

To evaluate isotopic variability along a growth band and as a function of sample depth, we conducted isotope analyses along a growth band of MBC-2, and at four different depths (deepest depth, 1 mm) on the spire of the *Conus* (Figure 1). The variation of the carbon and oxygen isotope values along the growth band (0.06‰) approximates the analytical error (Table 1). The isotope values for different sampling depths are also within analytical error (Table 2). These results demonstrate that carbon and oxygen isotope values of *Conus tortilis* along the growth bands are homogeneous and that slight differences in sampling depth, which could potentially mix different shell layers, do not cause differences in isotopic values.

Table 1. Isotopic values (in per mil) for different samples along a growth band in MBC-2 (Fig. 1 [left])

Sample	$\delta^{13}C$	$\delta^{18}O$
1	1.29	−0.54
2	1.25	−0.59
3	1.17	−0.51
4	1.23	−0.54
5	1.23	−0.54
6	1.24	−0.53
7	1.18	−0.58
8	1.31	−0.50
9	1.39	−0.52
10	1.34	−0.49
11	1.30	−0.49
12	1.26	−0.67
Average	1.27	−0.54
Standard Deviation	0.06	0.05

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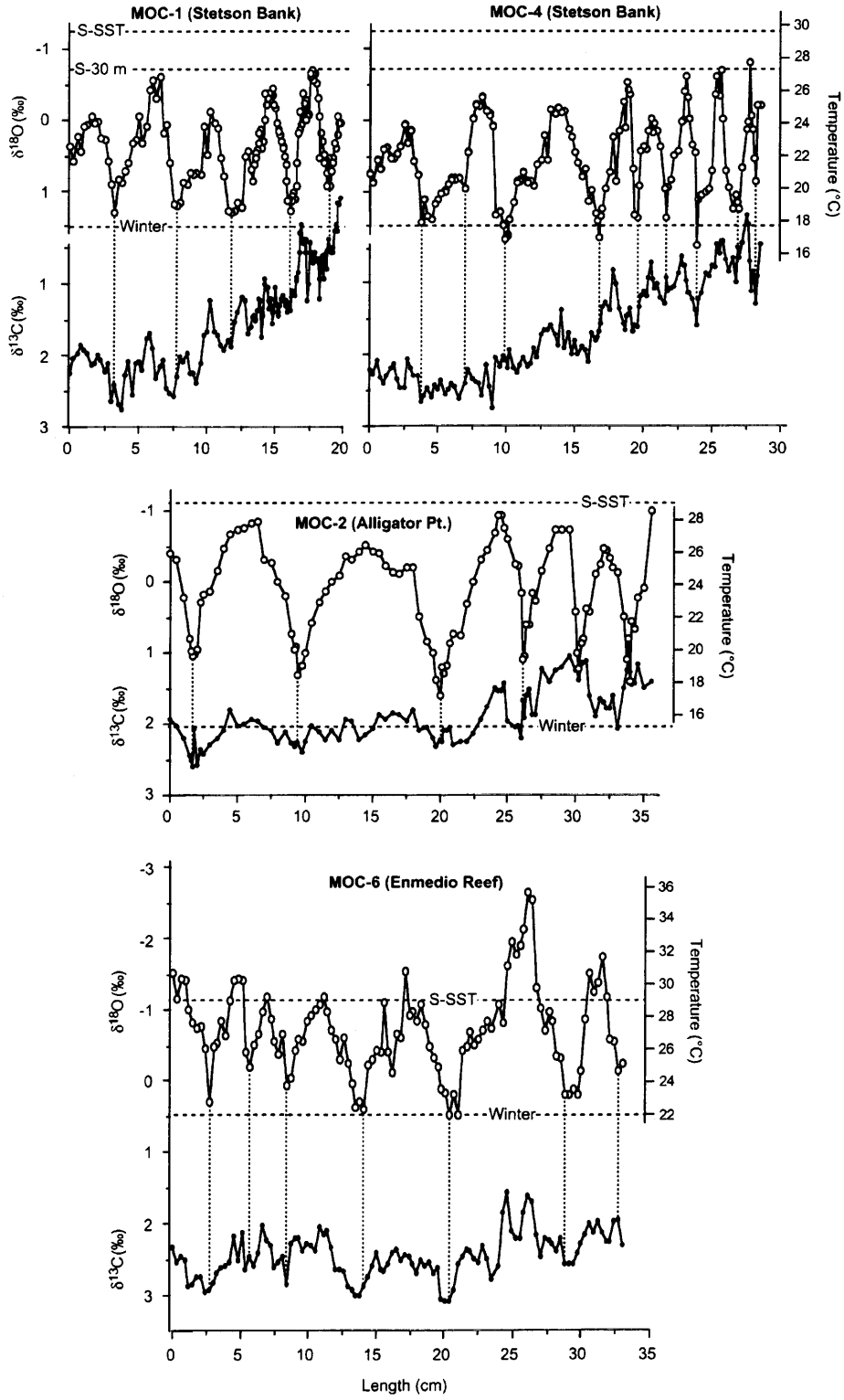


Figure 2. Oxygen and carbon isotope profiles of modern *Conus* shells. Temperature calibration from Grossman and Ku (1986) using seawater $\delta^{18}O$ values in Table 3. Environmental temperatures from National Data Buoy Center (NDBC, 2003) and Secretaria de Marina, Dirección General de Oceanografía (1978). Isotopic values decrease upward.

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Table 2. Isotopic values (in per mil) for different sampling depths in MBC-2. Level 1, 2, 3, and 4 represents the first, second, third, and fourth sampling from the same hole. The depth of Level 4 is approximately 1 mm.

Depth	Point 1		Point 2		Point 3		Average ± σ	
	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$
Level 1	1.19	−1.14	1.35	−1.15	1.31	−1.20	1.28 ± 0.08	−1.16 ± 0.03
Level 2	1.28	−1.04	–	–	1.22	−1.28	1.25	−1.16
Level 3	1.28	−1.15	1.41	−1.22	1.27	−1.31	1.32 ± 0.08	−1.23 ± 0.08
Level 4	1.30	−1.11	1.41	−1.22	1.35	−1.14	1.36 ± 0.05	−1.16 ± 0.06
Average	1.26	−1.11	1.39	−1.19	1.29	−1.23		
±σ	±0.05	±0.05	±0.03	±0.04	±0.06	±0.08		

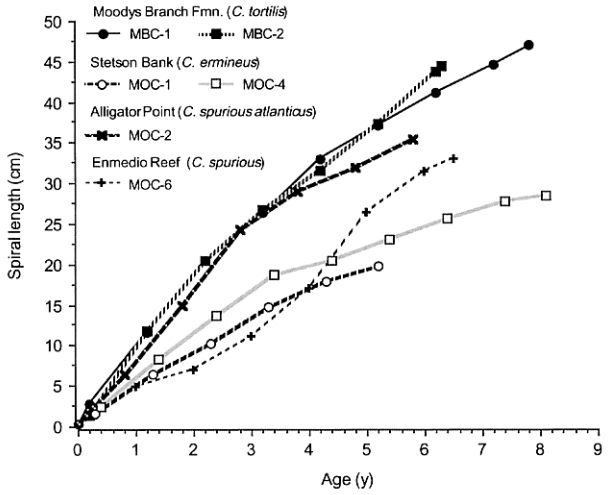


Figure 3. Growth rate as a function of length along whorl for modern and Eocene specimens.

Modern *Conus*

The oxygen isotopic records of the four modern *Conus* specimens show distinct records of seasonality. MOC-1 and MOC-4, the Stetson Bank shells, show oxygen isotopic records of 5 and 8 cycles of growth (Figure 2; Kobashi *et al.*, 2001). Growth rate slows with ontogeny (Fig. 3). The juvenile portions of the records provide the best resolution and show a distinct cuspate pattern, with rapid growth in spring (high to low $\delta^{18}O$) and slow growth in fall (low to high $\delta^{18}O$). For MOC-1, the average $\delta^{18}O$ minimum and maximum for the 5 cycles are −0.4 ± 0.3‰ and 1.2 ± 0.2 ‰, respectively. For MOC-4 the values are −0.4 ± 0.3 ‰ and 1.4 ± 0.3‰. Both MOC-1 and MOC-4 show the same pattern in $\delta^{13}C$, with values increasing to approximately 2.3‰ during the first year, then decreasing with ontogeny to as low as −0.7‰ in the more long-lived specimen (MOC-4).

Oxygen isotope data for MOC-2 from Alligator Point show a distinctly cuspate pattern indicative of diminished growth or shutdown during winter (Kobashi *et al.*, 2001; Wilkinson and Ivany, 2002; Goodwin *et al.*, 2003). The specimen lived for about 6 years and grew at a constant rate during the first three years, then slowed (Figures 2 and 3). The average minimum and maximum $\delta^{18}O$ values for MOC-2 are −0.7 ± 0.2 and 1.3 ± 0.2‰. The carbon isotope values decrease with ontogeny, but at a slower rate than do Stetson Bank specimens.

Compared with Stetson Bank and Alligator Point specimens, Enmedio Reef *Conus* shows much more irregular isotopic trends and values. The specimen appears to have lived for about 6 years, though the irregularity of the $\delta^{18}O$ record introduces some subjectivity to age assignments. Despite this, it is clear that growth rates are variable and somewhat inverted, with slower growth during the juvenile portion than during parts of the adult portion. The average minimum and maximum $\delta^{18}O$ for MOC-6 are −1.7 ± 0.5 and 0.2 ± 0.3‰. The irregular growth pattern and unusually low $\delta^{18}O$ values may have been caused by growth in low-salinity waters. Salinity at Enmedio Reef is at a minimum during July and August, enhancing ^{18}O depletion during summer. This might explain the extreme $\delta^{18}O$ minima at 26–27 cm (−2.6‰). Excluding this value yields an average $\delta^{18}O$ minimum of −1.5 ± 0.2‰. Unlike the other modern specimens, MOC-6 does not show an ontogenetic effect in $\delta^{13}C$ and shows a strong $\delta^{13}C$–$\delta^{18}O$ correlation ($R^2 = 0.422$, $p < 0.0001$, N = 110; Table 3).

Eocene *Conus*

The isotopic data for the *Conus tortilis* specimens from the Moodys Branch Formation show distinct cyclicity in both $\delta^{18}O$ and $\delta^{13}C$. The oxygen isotopic records typically have an asymmetrical sawtooth pattern, especially in the juvenile portions of the shells (Figure 4). The cyclicity of the carbon isotope record is so systematic that in two cases (5w and 7w) this record was used to help define $\delta^{18}O$ cycles. MBC-1 shows eight cycles. The average $\delta^{18}O$ minimum and maximum for the eight cycles are −1.1 ± 0.3 ‰, and 0.0 ± 0.2‰, respectively (Table 4). The average minimum $\delta^{13}C$ for the cycles 1.7 0.1‰, and the average maximum is 2.8 ± 0.2‰ (Table 5). The growth rate

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Table 3. Data for size, growth rates, isotopic compositions, isotopic temperatures, and paleotemperatures for *Conus* specimens and their collection sites. Sources of ambient temperature data and $\delta^{18}O$ of seawater discussed in text.

Specimen	MOC-1	MOC-4	MOC-2	MOC-6	MBC-1	MBC-2
Location	Stetson Bank	Stetson Bank	Alligator Point	Enmedio Reef	Moodys Branch Fmn.	Moodys Branch Fmn.
Species	*Conus ermineus*	*Conus ermineus*	*Conus spurious atlanticus*	*Conus spurious*	*Conus tortilis*	*Conus tortilis*
Shell height (cm)	60	78	64	60	78	87
Shell width (cm)	29	38	32	39	45	50
Whorl length (cm)	19.8	28.5	35.5	33	46.2	44.5
Estimated life-span (y)	5.2	8.1	5.8	6.5	7.8	6.3
Mean whorl length (cm) per year	3.8	3.5	6.1	5.1	5.9	7.1
Maximum monthly ambient T (°C)	27 (30 m)	27 (30 m)	29	29	-	-
Minimum monthly ambient T (°C)	18	18	15	22	-	-
$\delta^{18}O$ Minimum	−0.39	−0.24	−0.69	−1.47*	−1.05	−1.09
$\delta^{18}O$ Mid-point	0.41	0.63	0.29	−0.64	−0.52	−0.61
$\delta^{18}O$ Maximum	1.2	1.5	1.27	0.20	0.00	−0.11
$\delta^{18}O$ Range	1.59	1.74	1.96	−1.67	1.06	1.02
Estimated δ_w (‰)	1.04	1.04	1.04	0.95	0.24	0.24
Temperature maximum	25.9	25.3	27.2	30.2	25.3	25.5
Temperature midpoint	22.5	21.5	23	26.6	23.0	23.4
Temperature minimum	19.0	17.7	18.7	23.0	20.7	21.2
Temperature range	6.9	7.6	8.5	7.2	4.5	4.5
Mean$\delta^{13}C \pm 1\sigma$ (‰)	1.4 ± 0.7	1.6 ± 0.7	1.9 ± 0.4	2.5 ± 0.3	2.2 ± 0.4	1.8 ± 0.4
Mean $\delta^{18}O \pm 1\sigma$ (‰)	0.3 ± 0.5	0.6 ± 0.6	0.2 ± 0.7	−0.7 ± 0.6	−0.6 ± 0.4	−0.5 ± 0.3
R^2 ($\delta^{13}C$ vs. $\delta^{18}O$)	0.10	0.10	0.04	0.42	0.33	0.43
Level of significance *p*	0.0003	0.0003	0.039	<0.0001	<0.0001	<0.0001
R^2 ($\delta^{13}C$ vs. $\delta^{18}O$, years 1 and 2)	0.14	*0.01*	0.45	0.34	0.48	0.46
Level of significance *p*	0.0005	*0.56*	<0.0001	<0.0001	<0.0001	<0.0001
R^2 ($\delta^{13}C$ vs. $\delta^{18}O$, detrended $\delta^{13}C$)	0.17	0.05	0.12	-	-	-
Level of significance *p*	<0.0001	0.007	0.001	-	-	-
Slope ± standard error ($\delta^{13}C$ vs. $\delta^{18}O$, 1: normal, 2: detrended $\delta^{13}C$)^	0.206 ±0.039 (2)	0.091 ± 0.033 (2)	0.124 ± 0.035 (2)	0.330 ± 0.037 (1)	0.525 ± 0.062 (1)	0.898 ± 0.061 (1)
Number of analyses	132	136	101	110	152	297

*Excludes −2.63‰ value

^In these regressions, $\delta^{18}O$ is the independent variable, $\delta^{13}C$ is the dependent variable

Table 4. Oxygen isotope values (in per mil) of each peak and mean annual temperature (MAT) and mean annual range of temperature (MART). Each peak is labeled in Figure 4. The number in parentheses is temperature in °C.

MBC-1 Cycle	1	2	3	4	5	6	7	8	Average	σ
Summer	−1.19	−0.89	−1.14	−1.45	−0.80	−1.30	−0.60	−0.80	−1.05 (25.3)	0.29
Winter	−0.20	0.03	0.04	0.35	0.04	0.02	−0.29	0.04	0.00 (20.7)	0.19
MAT	−0.70	−0.55	−0.56	−0.71	−0.23	−0.63	−0.29	−0.55	−0.52 (23.0)	0.18
MART (w-s)		0.69	1.17	1.49	1.15	1.34	0.62	0.51	1.08 (4.7)	0.38
MART (s-w)	0.99	0.92	1.18	1.80	0.84	1.32	0.31	-	1.05 (4.6)	0.46
								Average MART =	1.06 (4.5)	0.42

MBC-2 Cycle	1	2	3	4	5	6	7	Average	σ
Summer	−0.94	−1.04	−1.16	−1.00	−1.06	−1.30	−1.13	−1.09 (25.5)	0.12
Winter	−0.32	−0.07	−0.10	−0.09	0.02	−0.12		−0.11 (21.2)	0.11
MAT	−0.63	−0.56	−0.63	−0.55	−0.52	−0.71	-	−0.61 (23.4)	0.05
MART (w-s)		0.72	1.09	0.90	0.97	1.32	-	1.00 (4.3)	0.22
MART (s-w)		0.97	1.06	0.91	1.08	1.18	-	1.04 (4.5)	0.10
							Average MART =	1.02 (4.5)	0.17

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Table 5. Carbon isotope values (in per mil) of each peak and range of variation between summer and winter. Each peak is labeled in Figure 4.

MBC-1 Cycle	1	2	3	4	5	6	7	8	Average	σ
Summer	1.70	1.83	1.74	1.70	1.56	1.64	1.62	1.75	1.68	0.08
Winter	3.03	3.06	2.43	2.81	2.71	2.83	2.61	2.39	2.78	0.22
Average	2.37	2.45	2.09	2.26	2.14	2.24	2.12	2.07	2.23	0.14
Range (w-s)		1.20	1.32	0.73	1.25	1.07	1.21	0.86	1.09	0.22
Range (s-w)	1.33	1.23	0.69	1.11	1.15	1.19	0.99	-	1.10	0.21
							Total mean range =		1.11	0.21

MBC-2 cycle	1	2	3	4	5	6	7	Average	σ
Summer	1.27	1.40	1.35	1.24	1.15	1.10	1.46	1.28	0.13
Winter	2.15	2.55	2.80	2.36	2.36	2.52		2.46	0.22
Average	1.71	1.98	2.08	1.80	1.76	1.81	-	1.85	0.14
Range (w-s)		0.75	1.20	1.56	1.21	1.26	-	1.20	0.29
Range (s-w)	0.88	1.15	1.45	1.12	1.21	1.42	-	1.21	0.21
							Total mean range =	1.20	0.25

(whorl length secreted per year) generally decreases through ontogeny (Figure 3). First year and average growth rates are 0.29 and 0.16 mm d^{-1}, respectively. Each 0.5-mm diameter sample averages ~3 days of growth, while the time interval between holes is roughly 19 days. The correlation between oxygen and carbon isotope data is 0.325 (R^2, p <0.0001, N = 152; Table 3).

MBC-2 data show six distinct cycles (Figure 4). The average cycle minimum and maximum values for $\delta^{18}O$, −1.1 ± 0.1‰ and −0.1 ± 0.1‰, respectively are similar to those for specimen MBC-1 (Table 4). The average minimum and maximum values for $\delta^{13}C$, 1.3 ± 0.1‰ and 2.5 ± 0.2‰, are lower than the values for MBC-1. Growth rate generally slows with ontogeny, but accelerates in the final year. First year and average growth rate of MBC-2 is 0.25 and 0.20 mm d^{-1}, respectively. Growth rate in terms of height is 14.5 mm y^{-1}, compared with 9.8 mm y^{-1} for MBC-1. Each isotopic analysis averages 2.5 days of growth, with sample spacing of about 7.5 days. The correlation between oxygen and carbon isotope data, 0.425 (R^2; p < 0.0001; N = 297), is better than for MBC-1.

The isotopic profiles of MBC-1 and MBC-2 are very similar, indicating that these shells experienced similar environmental conditions and/or had similar growth patterns. However, several differences are recognizable. First, the amplitude of $\delta^{18}O$ in MBC-1 fluctuates more than that of MBC-2 in spite of the similar average value (Figure 4, Table 4). Second, mean $\delta^{13}C$ value of MBC-1 is higher by 0.4‰ (p < 0.0005) compared with MBC-2. Possible reasons for the differences are discussed later. Both carbon and oxygen isotope records show abrupt changes during fall, and sometimes during spring (Figure 4).

Discussion

Oxygen isotopic temperatures in modern *Conus*

The isotopic data for the modern *Conus* can be used to evaluate whether it secretes its shell in oxygen isotopic equilibrium with ambient water. Grossman and Ku (1986) proposed the general temperature equation for aragonite precipitated in equilibrium with waters of known isotopic composition as follows:

$$T\ (°C) = 20.6 - 4.34\ (\delta^{18}O_{aragonite} - \delta_w) \quad (1)$$

Where $\delta^{18}O_{aragonite}$ is versus PDB and δ_w is the $\delta^{18}O$ of water versus "average marine water" ($\delta^{18}O$ vs. SMOW −0.2 ‰). This equation gives better agreement with biogenic aragonite in general than the first aragonite paleotemperature equation of Horibe and Oba (1972). When δ_w values are reported versus SMOW, the equation becomes:

$$T\ (°C) = 19.7 - 4.34\ (\delta^{18}O_{aragonite} - \delta_w) \quad (2)$$

We estimated the δ_w for the sites in which *Conus* were collected using the salinity-δ_w equation for Gulf of Mexico waters (Kirby *et al.*, 1998):

$$\delta_w\ (‰) = -3.28 + 0.12\ \text{Salinity (psu)} \quad (3)$$

Constant baseline salinity values were assumed with no effort to estimate the effect of low-salinity waters in spring or summer (Table 3).

The oxygen isotopic compositions of the modern *Conus* specimens support the contention that they secrete their shell in oxygen isotopic equilibrium with seawater. We

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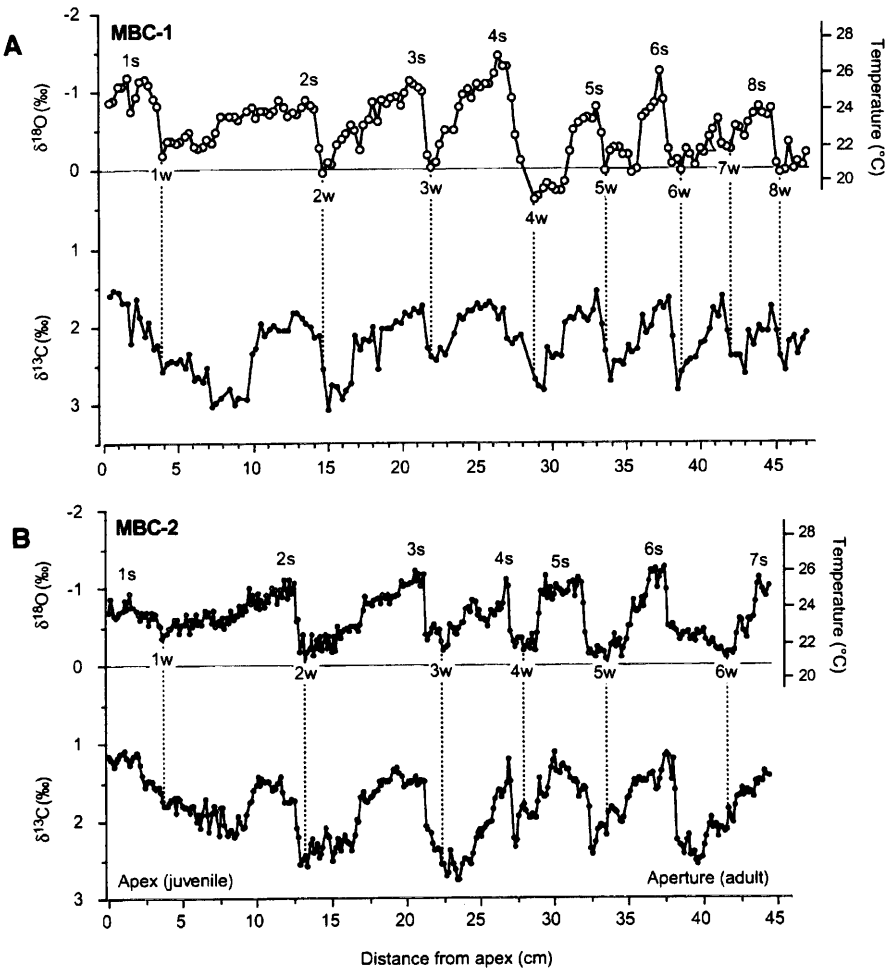


Figure 4. Oxygen and carbon isotope profiles of Moodys Branch *Conus* shells and temperature calibration. **A.** MBC-1, **B.** MBC-2. Summer (s) and winter (w) values are labeled. Temperature calibration from Grossman and Ku (1986) using seawater $\delta^{18}O$ values discussed in text. Isotopic values decrease upward.

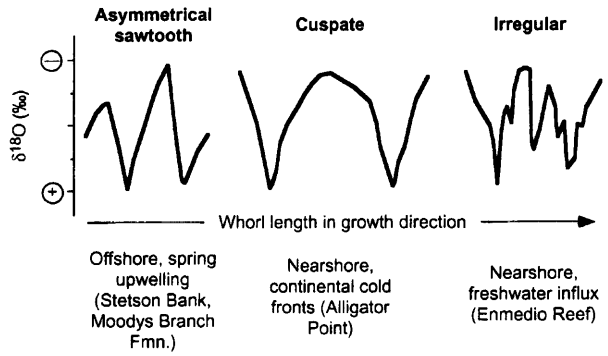


Figure 5. Summary diagram showing the three different patterns observed in the *Conus* shell $\delta^{18}O$ values, the environmental interpretation, and the examples.

are limited by a lack of temperature data for the exact time and location of shell growth, and in the case of the Alligator Point specimen, a lack of knowledge of the depth at which the specimen lived. Nevertheless, the data permit several important observations regarding isotopic composition and paleoclimate. Figure 5 summarizes the observed patterns, their interpretations, and examples.

The Alligator Point $\delta^{18}O$ data exhibit a cuspate pattern suggestive of significant winter shutdown (Kobashi *et al.*, 2001; Ivany and Wilkinson, 2002; Goodwin *et al.*, 2003). Summer temperatures of up to 29°C are well represented, but winter temperatures of less than 17°C are not (Figure 2). Coming from the most northern site, the Alligator Point specimen is the one most likely to be influenced by continental cold fronts. Thus, the cuspate isotopic pattern is expected and combined with paleogeographic information may be used to identify the importance of cold fronts

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in Tertiary climate.

The Stetson Bank specimens provide an asymmetrical sawtooth $\delta^{18}O$ record indicating rapid spring growth and slow autumn growth. The specimens were collected from 20–30 m and thus yield summer temperatures that are colder than those measured at the surface (Figure 2). However, the summer isotopic temperatures slightly underrepresent those predicted for 20–30 m depth (25–26° vs. 27°C). MOC-4 reproduces estimated winter temperatures well, whereas MOC-1 slightly overestimates these temperatures by 1°C. This may be caused by a longer winter shutdown in MOC-1 compared with MOC-4, consistent with the slower growth rate of MOC-1 (Figure 3). This reinforces the observation that faster shell growth often results in more accurate seasonal range (e.g., Goodwin *et al.*, 2003). Considering only the 5-year period in which the records overlap, MOC-1 and MOC-4 show similar average winter and summer temperatures (19.0° versus 18.5°C, and 25.9° and 26.5°C). Thus, the isotopic record of temperature extremes reproduces well.

The $\delta^{18}O$ pattern in the Enmedio Reef specimen is irregular and not easily characterized. Nevertheless, the temperature extremes show reasonable agreement with expected temperatures with one exception. The $\delta^{18}O$ minimum at ~26 cm is −1.5‰ more negative than the −1.1‰ value expected for 29°C temperature maximum. Using equation 3 yields a salinity of 22 psu, though this is likely a lower limit because water entering the ocean likely has a δ_w of less than the figure of −3.28‰ used in equation 3. The Enmedio Reef specimen is the only modern specimen influenced by a large summer salinity minimum, accounting for the irregular $\delta^{18}O$ record.

Oxygen isotopic temperatures in Eocene *Conus*

Calculation of isotopic paleotemperatures for the Eocene is hampered by the lack of direct knowledge of ambient water $\delta^{18}O$, thus some assumptions and estimations based on modern systems are required. Surface water δ_w can vary about 1.5‰ from low latitudes to high latitudes in the open ocean (Broecker, 1989). For this problem, Zachos *et al.* (1994) suggested an equation derived from the modern global δ_w distribution to predict δ_w as follows,

$$\Delta\delta\ (‰ \text{ vs. SMOW}) = 0.576 + 0.041x - 0.0017x^2 + 1.35 \cdot 10^{-5}x^3 \quad (4)$$

where δ is the latitudinal correction and x is absolute latitude in the range of 0° to 70°. The paleolatitude of Mississippi is estimated to be ~30° (Smith *et al.*, 1994). Thus, we use 0.64‰ as the latitudinal correction for δ_w. Lear *et al.* (2000) estimated Tertiary δ_w values by combining $\delta^{18}O$ with Mg/Ca data in benthic foraminiferal calcite. The latter is known to exhibit a temperature dependence in calcite (e.g., Nurnberg *et al.*, 1996). From their estimation, we use −0.4‰ for the global δ_w at this time (ca. 38 Ma). Combined with the latitudinal effect for the northern Gulf Coast (0.64‰), we obtain a local δ_w of 0.24‰.

Using equation 1 and a δ_w value of 0.24‰ yields a mean summer temperature (MST) for MBC-1 of 25.3°C, and a mean winter temperature (MWT) of 20.7°C (Figure 4). Average mean annual temperature (MAT) and mean annual range of temperature (MART) are 23.0°C and 4.5°C, respectively (Table 4). The largest seasonality, 8°C, occurs between cycle 4 summer (4s) and winter (4w) with a summer temperature of 27°C and a winter temperature of 19°C. Eocene winter temperatures are consistently above the minimum growth temperatures recorded in the modern *Conus* specimens, ~18°C, arguing against winter shutdown in the Eocene specimens. The oxygen isotope profile of MBC-2 yields a MST of 25.5°C and a MWT of 21.2 °C, very similar to the results for MBC-1. MAT and MART are 23.4°C and 4.5°C, respectively. The largest seasonality (MART) observed for one cycle within MBC-2 is 6°C, with MST and MWT of 26°C and 20°C, respectively (Table 4). Our best estimate of surface water MAT is about 23°C. This should be a minimum value based on the interpretation that the Moodys Branch Formation at this location was deposited in relatively deeper water (20–100 m). Thus, summer temperature may be underestimated because of the development of the seasonal thermocline during the summer. For MART of surface water, we use the >4°C seasonality recorded in *Conus tortilis* with a summer temperature of >25°C and a winter temperature of ~21°C. Winter isotopic temperatures should closely approximate surface water temperatures at that time despite the relatively deeper water environment because of vigorous mixing and the absence of a seasonal thermocline.

These isotopic temperatures are warmer than those obtained by Ivany *et al.* (2003) for an otolith from the Moodys Branch Formation. The otolith temperatures, about 14° to 22°C, are based on a wider range in $\delta^{18}O$ (−1.8 to 0.0‰) and an estimated δ_w (−0.8‰; Zachos *et al.*, 1994) not corrected for latitude. Our δ_w value (0.24‰) is based on the global estimates of Lear *et al.* (2000) and, importantly, is latitude-corrected. As the salinities of Gulf of Mexico waters (typically 36.0 psu) are higher than the global average (35 psu), we feel a latitude correction is warranted. Temperatures calculated from Ivany *et al.*'s data using 0.24‰ for δ_w are 19° to 27°C, similar to the values we obtain. Pearson *et al.* (2001) obtained temperatures of 25°C for mixed-layer and intermediate-habitat planktonic foraminifera from the Cocoa Sands Formation in Alabama (36.8 Ma). However, when our value for δ_w is applied, calculated temperatures (29°C) are higher than those obtained with mollusks and otoliths. Considering the older age of these sediments, they may have been de-

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posited during a warmer time.

Several independent lines of evidence support these warmer temperature estimates. Dockery (1977) suggests that the climatic conditions during the deposition of the Moodys Branch Formation were tropical or subtropical based on the great variety of mollusk species and by the presence and diversity of such groups as the cypraeids. Terrestrial climate proxy data such as pollen (Frederiksen, 1988; Yancey *et al.*, 2003) show a cooling and drying trend from the middle Eocene to Early Oligocene. At the age of the Moodys Branch Formation, these pollen data show subtropical climate in the northern region as indicated by the disappearance of such tropical species as *Bursera* spp. and *Friedrichipollis claibornensis* (Yancey *et al.*, 2003).

Modern Mississippi coastal waters (30°5′N, 88°46′W) show summer temperatures of 29°C, winter temperatures of 14°C, MAT of 22°C, and MART of 15°C (NOAA, 2000). Late middle Eocene temperatures were probably similar to the present temperature profile of this region, except for the fact that winter temperatures were about 6°C warmer than present. The present northern Gulf Coast region experiences several days with winter air temperatures below 0°C, but probably during the late middle Eocene winter air temperatures did not reach freezing temperatures (see below). Warmer winter temperatures are probably the reason why the Mississippi embayment at the late middle Eocene contains subtropical flora and fauna.

The reasons for warm winter temperatures can be explained by several factors. First, marine influence was likely fairly extensive during the early Paleogene owing to warm ocean water mass, especially in the deep sea and at high latitude (Miller *et al.*, 1987; Bice *et al.*, 2000). The less stratified and warm ocean was probably unstable with regard to density, causing vigorous mixing for a longer time of a year. The second explanation is the lesser impact of cold continental air compared with today largely because of warm high-latitude temperatures and the lack of a polar glacier (Andreasson and Schmitz, 2000). These factors combined to generate warmer winter temperatures.

Carbon isotopes

The interpretation of carbon isotope data is complicated compared with oxygen isotopes owing to less systematic incorporation of ^{13}C into biogenic carbonate, and the short residence time of dissolved inorganic carbon (DIC) in the water column. Several factors such as the $\delta^{13}C$ of DIC, temperature, and metabolic activity (i.e., vital effects) directly or indirectly influence the $\delta^{13}C$ of biogenic aragonite. Numerous studies have shown that annual variations in DIC $\delta^{13}C$ are recorded in marine carbonates (e.g., Arthur *et al.*, 1983; McConnaughey *et al.*, 1997; Purton and Brasier, 1997). Local seawater $\delta^{13}C$ will vary in response to input of ^{13}C-depleted river water, seasonal upwelling, and local phytoplankton blooms. Input of fresh water generates depletion of the heavy isotopes and a positive $\delta^{13}C-\delta^{18}O$ correlation, whereas upwelling of cold, ^{13}C-depleted water induces low $\delta^{13}C$, high $\delta^{18}O$, and a negative $\delta^{13}C-\delta^{18}O$ correlation. Phytoplankton blooms will moderate ^{13}C depletion caused from upwelling, but increased productivity will enhance the flux of respired CO_2 from surface sediments.

Grossman and Ku (1986) observed a temperature dependence in the ^{13}C fractionation associated with precipitation of biogenic aragonite. Analyzing aragonitic taxa (foraminifera and mollusks) collected from depths of 74–1692 m, they found a negative correlation between ^{13}C fractionation and temperature. The temperature dependence, −0.13‰ per °C, was about half that observed for $\delta^{18}O$. In contrast, inorganically precipitated carbonate shows no significant correlation with temperature (Romanek *et al.*, 1992), indicating that the temperature dependence is biologically controlled (i.e., vital effect). Coincidentally, the 2 : 1 ratio of the $\delta^{18}O : \delta^{13}C$ temperature dependence follows that expected for kinetic fractionation, but in this case the oxygen isotopic variations are clearly thermodynamic.

All of the specimens show significant positive correlations between $\delta^{13}C$ and $\delta^{18}O$ values, with MOC-6, MBC-1, and MBC-2 showing especially strong positive correlations ($R^2 = 0.42$, 0.33, and 0.43, respectively; Table 3). Neither the strength of the $\delta^{13}C-\delta^{18}O$ correlation, the magnitude of the ontogenetic $\delta^{13}C$ change, nor the mean $\delta^{13}C$ values correlate with interspecimen differences in growth rate. The hypothesized freshwater spike in the MOC-6 record (~26 cm) coincides with extreme $\delta^{13}C$ values, consistent with that interpretation but also with a temperature dependence. The $\delta^{13}C-\delta^{18}O$ correlation is enhanced in MOC-1 and MOC-2 when the ontogenetic $\delta^{13}C$ trend is subtracted from the signal (Table 3). MOC-2 shows an especially strong $\delta^{13}C-\delta^{18}O$ correlation in the first two years. If the $\delta^{13}C-\delta^{18}O$ correlations are derived from the temperature-dependent metabolic effects discussed by Grossman and Ku (1986), then the amplitude of *Conus* $\delta^{13}C$ cycles should be half that of $\delta^{18}O$. For the modern specimens the $\delta^{13}C$ amplitude is 50% or less of the $\delta^{18}O$ amplitude, thus following the general relationship observed by Grossman and Ku. This implies a metabolic control on modern *Conus* $\delta^{13}C$. The $\delta^{18}O$ and $\delta^{13}C$ amplitudes of the Eocene shells are similar, suggesting that DIC $\delta^{13}C$ is changing seasonally.

In the shallow water environment (e.g., mixed surface layer), the $\delta^{13}C$ of the DIC varies seasonally according to light, temperature, and ventilation (see Arthur *et al.*, 1983; Purton and Brasier, 1997). During the summer, the water column stratifies due to surface water warming. This results in preferential withdrawal of ^{12}C from the surface euphotic layer mediated by decomposition of ^{12}C-enriched organic matter in the lower aphotic layer. Therefore, the

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lower layer would be depleted in ^{13}C, and the surface layer would be enriched in ^{13}C (Purton and Brasier, 1997). During the winter, strong mixing penetrates deeper in the water column and the DIC $\delta^{13}C$ becomes relatively constant. This seasonal change in the lower, aphotic layer results in positive correlation between $\delta^{13}C$ and $\delta^{18}O$ as observed in previous studies (e.g., Arthur *et al.*, 1983; Purton and Brasier, 1997). As we mentioned before, paleobathymetry of the Moodys Branch locality is estimated to be 20–100 m. Based on these observations, we conclude that the temperature effect in addition to the seasonal change of DIC $\delta^{13}C$ in the shallow aphotic environment controlled the distribution of $\delta^{13}C$ of MBC-1 and MBC-2.

Average $\delta^{13}C$ of MBC1 is enriched by 0.4‰ compared with MBC-2 (Figure 4). As mentioned above, $\delta^{13}C$ of DIC is strongly related to nutrient distribution. As a first approximation, $\delta^{13}C$ correlates negatively with nutrient concentration. Perhaps, the larger size and more rapid growth of MBC-2 compared with MBC-1 (Table 3) reflect a more nutrient-rich environment during the time in which MBC-2 lived.

Conclusion

Three patterns of oxygen isotopic variation occur in the modern *Conus* shells analyzed: asymmetric sawtooth, cuspate, and irregular (Figure 5). The asymmetric sawtooth pattern occurs in a middle to outer shelf environment and reflects rapid spring growth presumably in response to upwelling and increased productivity. The cuspate pattern occurs in the nearshore shell influenced by continental cold fronts, and the irregular pattern occurs in response to fresh-water influx in a tropical climate.

The late middle Eocene shells from the Moodys Branch Formation exhibit an asymmetric sawtooth $\delta^{18}O$ pattern consistent with rapid spring growth in a middle or outer shelf environment. These data reveal that during the late middle Eocene, the climate of the Mississippi region was equable compared with today owing to warmer winter temperatures. Mean annual temperature of water was 22°C and mean annual range of temperature of water was 4°C. Taking the depth estimation (20–100 m) into consideration, the surface water temperatures are estimated to be >25°C during summer and 21°C during winter, with a mean annual temperature of 23°C or probably slightly higher. In contrast, coastal waters off Mississippi today (30°5′N, 88° 46′W) have relatively severe seasonality (MART, 15°C) with a colder winter temperature of 14°C. The seasonality difference between the present and late middle Eocene Gulf Coast is mainly reflecting differences in winter temperature. This seasonality difference likely explains why the Mississippi embayment during the late middle Eocene contained subtropical flora and fauna.

There are several explanations for warm winter temperatures at the late middle Eocene. First, the marine influence was extensive during the early Paleogene owing to the warm ocean water mass. The less stratified ocean was probably unstable with regard to density, causing vigorous mixing for a longer duration throughout the year than present. The second explanation is the lesser impact of cold continental air compared with today largely owing to the lack of a polar glacier. These two factors likely worked together to generate warmer winter temperatures at this region.

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