

Cross-Calibration of Daily Growth Increments, Stable Isotope Variation, and Temperature in the Gulf of California Bivalve Mollusk *Chione cortezi*: Implications for Paleoenvironmental Analysis

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Annual-oxygen isotope profiles from two live-collected specimens of Chione cortezi Carpenter were analyzed in conjunction with daily growth-increment width profiles and high-resolution temperature records from the same site in the northern Gulf of California. The daily growth-increment profiles serve to date the deposition of the $\delta^{18}\text{O}$ samples. Then the $\delta^{18}\text{O}$ values were compared with high-resolution temperature records from the same site. Shell deposition began in late March or early April and ended in late November or early December. $\delta^{18}\text{O}$ -derived estimates of the maximum and minimum temperature thresholds of growth agree well with those obtained from the dated increment width profile. Shell deposition in these two specimens of C. cortezi from the northern Gulf began when temperature warmed above $\sim 17^\circ\text{C}$ and slowed or halted when temperature rose above $\sim 31^\circ\text{C}$. The temporal resolution of stable isotope samples varies throughout the year. Samples with the coarsest resolution (>3 weeks) were taken from parts of the shell deposited near the minimum and maximum temperature thresholds of growth. Higher resolution samples have intermediate $\delta^{18}\text{O}$ values and most represent less than five days of growth. Calculated temperatures from the dated oxygen-isotope samples are similar to observed temperatures. Differences reflect the effects of daily temperature variation, tidal emergence, and enrichment in $\delta^{18}\text{O}$ of the water in which the clams grew. Stable oxygen-isotope samples used in conjunction with increment-width profiles can provide paleoenvironmental information at sub-weekly to sub-monthly resolution.

INTRODUCTION

The accretionary skeletons of intertidal marine bivalve mollusks contain a wealth of information about the environment in which they grew. The rate and timing of bivalve shell growth is controlled by temperature (Pannella and MacClintock, 1969; Jones et al., 1978; 1989), salinity (Koike, 1980), age and reproductive cycle (Sato, 1995), tidal cycle and intertidal position (Berry and Barker, 1975; Lutz and Rhoads, 1980; Ohno, 1989), and nutrient and food availability (Coe, 1948). These factors cause a wide variety of annual and sub-annual (seasonal, lunar, fortnightly, daily, and disturbance) growth patterns. This variation of growth patterns makes the shell a rich source of information on the environment in which it grew (Jones,

1996). It is clear that bivalve mollusk shells respond to a variety of environmental factors. Thus, calibration of environmental variation with aspects of their growth patterns is likely to yield important insight into the growth variations in fossil shells.

Although many environmental controls can affect growth, temperature is the dominant factor governing growth rates. Temperature's influence on bivalve-shell growth has been recognized for more than 60 years (see Davenport, 1938). In a later review, Gunter (1957) showed the importance of temperature to the ultimate size of marine mollusks. Berry and Barker (1975) correlated temperature with variation in seasonal growth rates, and also showed that specimens of the bivalve *Chione undatella* exhibit different growth patterns along a thermal gradient in the Gulf of California. Kennish and Olsson (1975) documented variation in daily growth-increment width as a function of seasonal temperature variation. The conclusions of these and many other observational studies have been confirmed from geochemical evidence. The development of isotope paleontology (Wefer and Berger, 1991) has given biologists and paleontologists a new tool to interpret bivalve-growth patterns. For example, Jones et al. (1983) used oxygen isotope ($\delta^{18}\text{O}$) variation to show that shell growth in the bivalve *Spisula solidissima* slows during cooler temperatures. Furthermore, they demonstrated the feasibility of reconstructing annual seasonal temperature fluctuations from stable isotopic profiles from clam shells. Annual $\delta^{18}\text{O}$ variation also has been used to reconstruct changes in seasonality in both time and space (e.g., Jones and Allmon, 1995; Khim et al., 2000).

Here climatic, isotopic, and sclerochronologic records from the northern Gulf of California are discussed (Fig. 1). The main goals in this study are: (1) to describe the annual pattern of shell growth in a bivalve species from the northern Gulf; (2) understand the relationship between temperature and shell growth; and (3) interpret annual oxygen-isotope profiles as potential sources of paleoclimatic information. Using daily growth increments from specimens of the intertidal bivalve *Chione cortezi* Carpenter, annual isotopic profiles have been calibrated with high-resolution temperature observations. This calibration has allowed the determination of the timing and rate of shell growth throughout the year. This high-resolution calibration should prove useful in interpreting isotopic and sclerochronologic variation in fossil shells of this and other species.

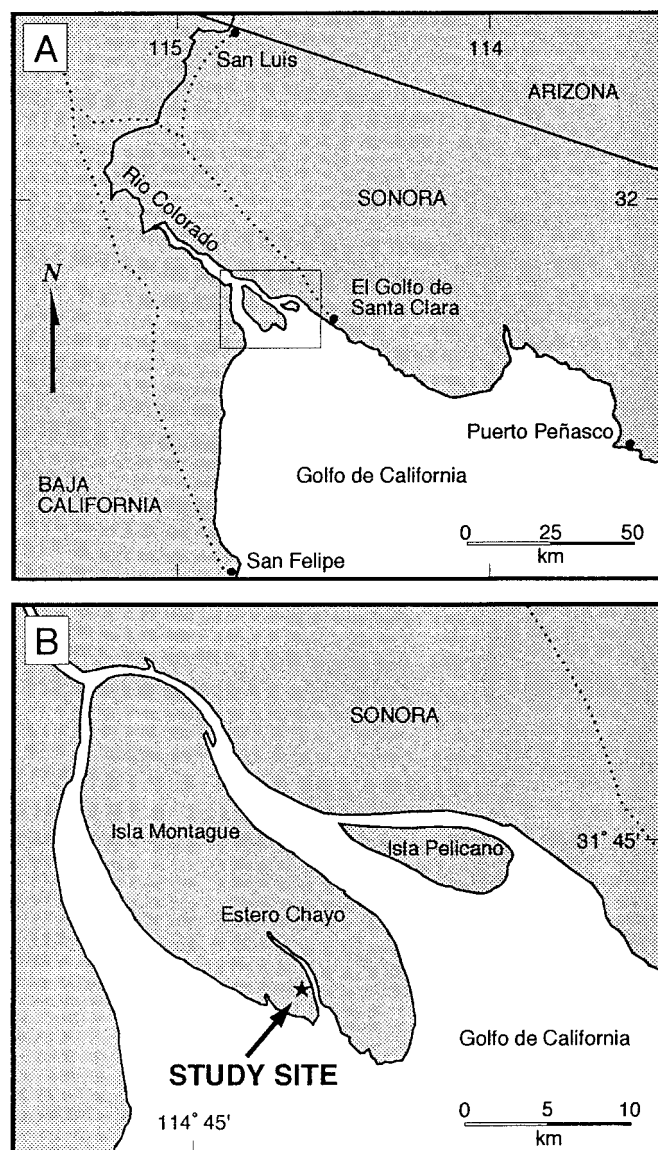


FIGURE 1—Study area. (A) Map showing political boundaries and towns in the study region. (B) Study site in Estero Chayo on Isla Montague. The outlines defining the areal extent of Isla Montague mark the approximate spring low-tide level. High tide fully submerges the study site.

MATERIALS AND METHODS

The study area is located on the southern margin of the Colorado River delta in the northern Gulf of California (Fig. 1). The Colorado River drains much of the southern Rocky Mountains and desert southwest. Prior to the 1930's, large quantities of fresh water were delivered to the northern Gulf by the Colorado River. However, since the construction of dams on the Colorado River very little fresh water reaches the Gulf, and normal marine conditions now persist in the delta year round (Lavin and Sánchez, 1999). The region experiences semi-diurnal tides with amplitudes up to 10 m (Thompson, 1968). The study area is extremely hot and arid: average summer monthly temperatures in San Felipe, located 70 km south of the

study area, exceed 32°C and the region receives approximately 60 mm of precipitation annually (Hastings, 1964).

In February 1999, three HOBO® Temp temperature loggers were deployed in waterproof containers chained to concrete anchors at Estero Chayo, Isla Montague (31° 40.22' N, 114° 41.41' W; Fig. 1). The loggers were placed 50 m apart in the intertidal zone approximately 3–4 m above the mean low-water level. Two of the three loggers were recovered in February, 2000. Each logger recorded temperature (resolution and accuracy ~0.5°C) every two hours for one complete year (10:00 AM, February 16, 1999, to 10:00 AM, February 16, 2000).

On February 16, 2000, two live specimens of *C. cortezi* (IM11-A1L and IM11-A2L; CEAM Research Collection) were collected from the same Isla Montague locality. *Chione cortezi* is a shallow infaunal bivalve found most often in muddy substrates. Shells of *C. cortezi* are exclusively aragonite.

The *C. cortezi* specimens were sacrificed immediately after collection and the flesh removed. In the lab, the left valve from each specimen was sectioned along the dorso-ventral axis of maximum shell height, and thick sections were mounted on microscope slides. Samples weighing ~50–100 µg were drilled from the prismatic layer using 0.5- and 0.3-mm drill bits. Samples were heated in vacuo at 70°C for 30 minutes to remove volatile material. Carbonate isotopic analyses were performed on a Micromass Optima IRMS with an Isocarb common acid-bath autocarbonate device. Samples were reacted with 105% orthophosphoric acid at 90°C. Results are presented in permil notation with respect to the V-PDB carbonate standard. The standard deviation of replicate carbonate standards was 0.08‰.

Paleotemperature estimates are based on Grossman and Ku's (1986) empirically determined temperature relationship for biogenic aragonitic carbonates. However, a small modification of their equation was required because they report water values as SMOW minus 0.2‰. Their paleothermometry equation has been rewritten such that all water values derived from this equation are corrected to the SMOW scale:

$$T(^{\circ}\text{C}) = 20.6 - 4.34 (\delta^{18}\text{O}_{\text{aragonite}} - (\delta^{18}\text{O}_{\text{water}} - 0.2))$$

This equation suggests that each 4.34°C change in temperature results in a one permil shift in shell carbonate.

Daily growth-increment widths from the shells were measured from the same plane as the $\delta^{18}\text{O}$ samples. Cut valves were polished smooth with 0.3 micron grit. They then were placed in 0.25 M EDTA solution for 1 hour. This procedure results in differential dissolution of the daily increments (Fig. 2) and heightens the contrast between growth bands and growth intervals (*sensu* Richardson et al., 1981). Daily increments were photographed under reflected light magnification and increment widths were measured from digital images.

Each of these records—observed temperature, isotopes, and daily growth increments—contains environmental information, but they differ in temporal resolution. The temperature loggers recorded temperature variation at the study site every two hours, and provide the highest resolution data. A single isotopic sample can represent from days to weeks of environmental conditions because *C. cortezi* grows at different rates through the year. During the

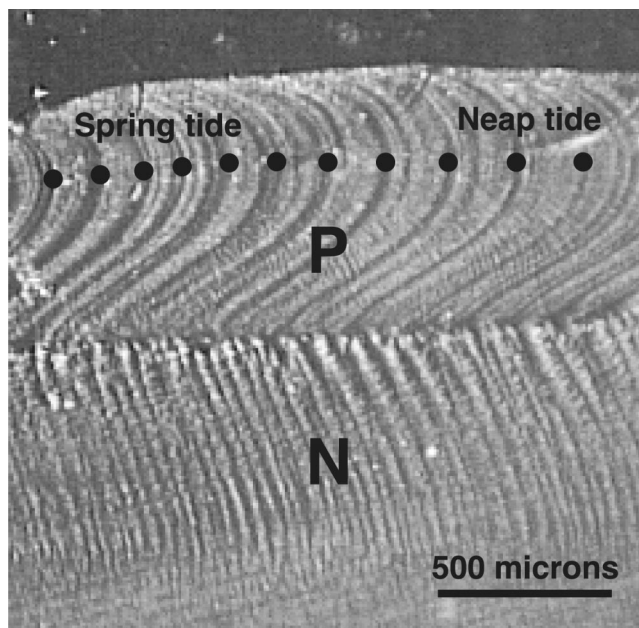


FIGURE 2—Daily growth increments from shell IM11-A1L. Etching results in differential dissolution of portions of daily growth increments. Individual circadian increments are marked with filled circles. Note variation in daily increment widths associated with fortnightly tidal cycle. Narrower increments were deposited during spring tides. Wider increments were deposited during neap tides. For a detailed discussion of daily growth increments in *C. cortezi* see Schöne et al. (in press). P, prismatic layer; N, nacreous layer.

spring and early summer, when growth rates are highest and new shell material is added quickly, a single isotopic sample may represent conditions over approximately two to five days. In contrast, when growth rates are low during the hot summer and cold winter months, a sample of the same size can represent nearly a month of growth. Specimens marked in the field deposit a single growth-increment each day; thus, individual growth increments represent circadian resolution (Schöne et al., in press).

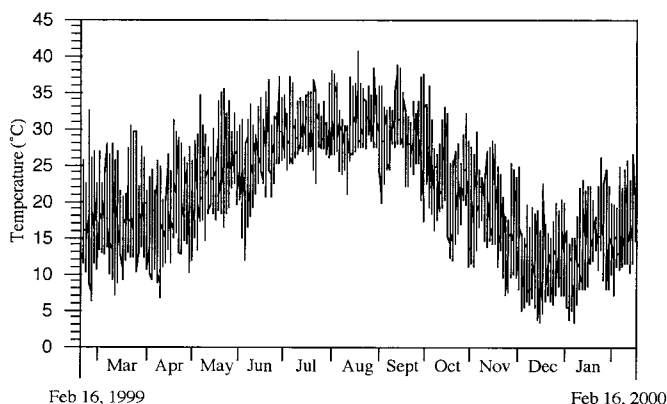


FIGURE 3—Observed temperatures at the study site. Temperatures were recorded every two hours from 10:00 AM, February 16, 1999 to 10:00 AM, February 16, 2000. Note the large amount of variation about the overall annual temperature cycle. This variation represents diurnal temperature cycles as well as fortnightly cycles associated with the large tidal amplitude in the northern Gulf of California.

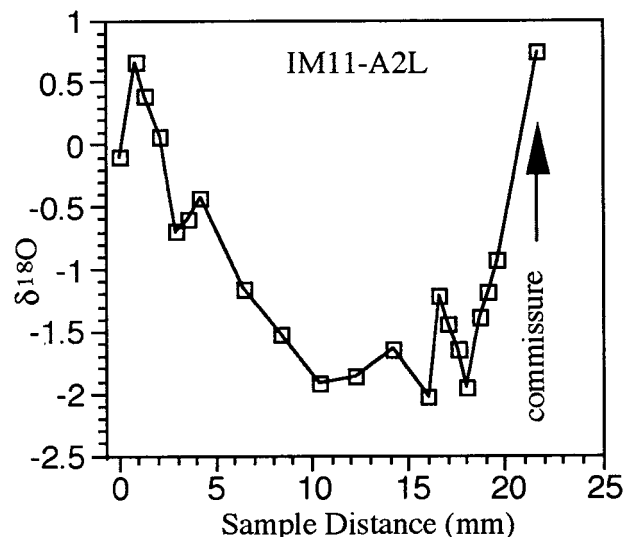
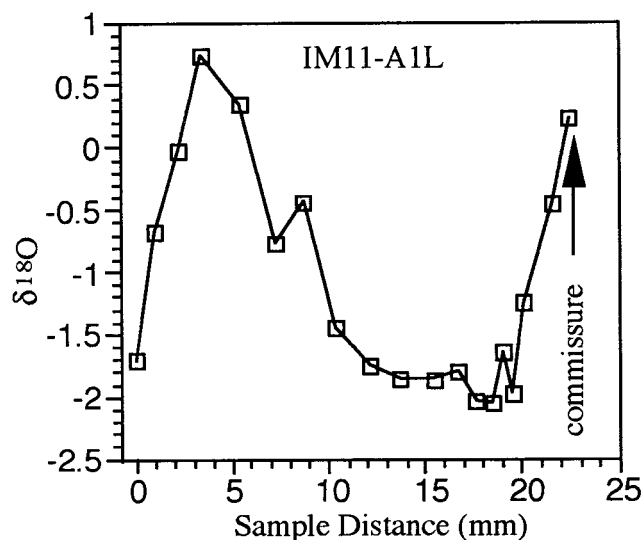


FIGURE 4—Stable isotope profiles from the specimens used in this study, (A) IM11-A1L, (B) IM11-A2L. In both graphs, the $\delta^{18}\text{O}$ values are plotted versus sample position (Zero marks the position of the most dorsal sample).

RESULTS

Temperature loggers recorded temperatures every two hours for one year (Fig. 3). Because the loggers were placed in the intertidal zone, some of the measurements represent ambient air temperatures. Temperatures from the two recovered loggers are correlated highly ($r^2 = 0.995$, $n = 4381$). The average annual temperature (Feb. 16, 1999 to Feb. 16, 2000) was 21.3°C . The annual range was 37.3°C , with a maximum value of 40.6°C (2:45 PM, August 17, 1999) and minimum value of 3.3°C (6:45 AM, December 16, 1999).

The oxygen-isotope profiles from the specimens show a strong annual cycle (Fig. 4; Table 1). This is expected, given the large annual temperature cycle of the water. The annual oxygen isotope amplitude from IM11-A1L and IM11-A2L are 2.78 per mil and 2.76 per mil, respectively.

TABLE 1—Sample information from shells IM11-A1L and IM11-A2L. ¹ Sample numbers are assigned from umbo end (low numbers) to the commissure (high numbers); ² Sample hole diameter in mm; ³ Number of increments represented in the stable isotope sample; ⁴ Approximate deposition date of the first increment in the stable isotope sample; ⁵ Approximate deposition date of the last increment in the stable isotope sample.

Sample # ¹	$\delta^{18}\text{O}$	Diameter ²	# of incr. ³	Beginning date ⁴	Ending date ⁵
IM11-A1L					
1	-1.71	0.5	5	NA	NA
2	-0.69	0.3	5	NA	NA
3	-0.03	0.3	8	NA	NA
4	0.73	0.5	8	NA	NA
5	0.34	0.5	10	NA	NA
6	-0.77	0.5	6	April 19, 1999	April 24, 1999
7	-0.43	0.5	4	May 5, 1999	May 8, 1999
8	-1.45	0.5	4	May 18, 1999	May 21, 1999
9	-1.75	0.5	4	May 31, 1999	June 3, 1999
10	-1.86	0.5	5	June 12, 1999	June 17, 1999
11	-1.86	0.5	4	June 25, 1999	June 28, 1999
12	-1.80	0.5	5	July 8, 1999	July 12, 1999
13	-2.04	0.3	4	July 19, 1999	July 22, 1999
14	-2.05	0.5	7	July 26, 1999	August 1, 1999
15	-1.65	0.3	3	August 4, 1999	August 6, 1999
16	-1.97	0.3	4	August 8, 1999	August 11, 1999
17	-1.26	0.5	19	August 14, 1999	September 2, 1999
18	-0.47	0.5	8	September 23, 1999	September 30, 1999
19	0.24	0.3	26	October 13, 1999	November 8, 1999
IM11-A2L					
1	-0.11	0.5	13	NA	NA
2	0.66	0.3	24	NA	NA
3	0.38	0.3	27	NA	NA
4	0.06	0.5	9	April 6, 1999	April 14, 1999
5	-0.70	0.3	4	April 19, 1999	April 22, 1999
6	-0.61	0.3	2	April 26, 1999	April 27, 1999
7	-0.43	0.5	3	April 10, 1999	May 2, 1999
8	-1.16	0.5	3	May 14, 1999	May 17, 1999
9	-1.53	0.5	3	May 27, 1999	May 29, 1999
10	-1.92	0.5	3	June 9, 1999	June 11, 1999
11	-1.88	0.5	4	June 22, 1999	June 25, 1999
12	-1.65	0.5	4	July 8, 1999	July 11, 1999
13	-2.03	0.5	4	July 25, 1999	July 28, 1999
14	-1.23	0.3	4	July 31, 1999	August 3, 1999
15	-1.45	0.3	2	August 4, 1999	August 5, 1999
16	-1.64	0.3	4	August 7, 1999	August 10, 1999
17	-1.95	0.5	17	August 11, 1999	August 28, 1999
18	-1.40	0.3	9	September 3, 1999	September 11, 1999
19	-1.19	0.3	4	September 14, 1999	September 18, 1999
20	-0.93	0.5	5	September 20, 1999	September 24, 1999
21	0.73	0.5	NA	NA	NA

The most positive values in both shells occur in dark bands expressed on both the shell surface and in cross section. Because these dark bands were forming at the time of collection, they have termed "winter bands" and the positive isotopic values, "winter peaks." Between winter peaks, the oxygen-isotope curve follows a gradual trend toward more negative values. This decline is then followed by an increase into the following winter.

Like the oxygen profiles, the daily increment-width profiles show an annual cycle (Figs. 5C and 6C). Increments were counted from the umbo end to the commissure. Counting of increments began at the approximate position of the first isotope sample in each specimen. In both specimens, the first bands counted were deposited in the fall of the clam's second year of life. Increment-width profiles from both specimens are similar, reflecting their deposition in response to similar environmental conditions. There were 351 increments identified in IM11-A1L, while

341 increments were counted in IM11-A2L. In both specimens, increment widths decreased from the first increments counted to very narrow increments at approximately increment 100. These narrow increments are coincident with the penultimate winter band on the surface of the shell. From this position to the commissure, 241 increments in IM11-A1L and 214 from IM11-A2L were counted. In both specimens, the number of increments counted from the penultimate winter band to the commissure was less than the number of lunar days in one year (353). Thus, more than three months of growth are missing from both specimens, indicating that growth halts during some part of the year.

To better understand the pattern of daily growth increment deposition, specimens at other times throughout the year were also collected. Regardless of the date of collection, increment width shows a strong fortnightly periodicity, which presumably reflects the tidal cycle. However,

because of local environmental variations and differences in growth rates, it is difficult to assign a calendar date to particular increments with an accuracy better than $\pm$ two weeks. Thus, individual growth increments are dated with an uncertainty of $\pm$ two weeks. Similar uncertainties have been reported elsewhere (e.g., Koike, 1980).

Shell IM11-A1L (Fig. 5C) shows a strong initial decrease in increment width, while early increments from IM11-A2L (Fig. 6C) have variable widths, showing an increase between increments 70 and 100. Following this initial interval, increment widths increase rapidly in both specimens (IM11-A1L, #110–150; IM11-A2L, #125–170). The remainder of the interval is characterized by erratically decreasing widths to increment 250 in both specimens. This minimum is followed by a gradual increase, followed by a decline in both specimens. The latest increments counted in both specimens are very narrow and were the most recently formed bands prior to collection in February, 2000.

DATING THE DAILY INCREMENT PROFILE

The variation in thickness of daily increments is mainly controlled by temperature variation (Pannella and MacClintock, 1968; Koike, 1980; Schöne et al., in press). Thus, features of the increment-width profiles can be calibrated with temperatures observed during the interval of deposition. This method can be used to fit real time to the increment-width profile and, thus, relate observed temperatures with increment widths. This calibration, in turn, can be used to relate stable isotope values to temperatures experienced during deposition (see below).

That bivalve-shell growth varies as a function of temperature has been documented numerous times (Pannella and MacClintock, 1968; Berry and Barker, 1975; Jones et al., 1978; Koike, 1980; Killingly, 1981; Jones and Quitmyer, 1996). However, many of these studies do not discuss the influence of temperature on daily increment widths. Schöne et al. (in press) recently correlated daily increment widths with temperature. Using specimens collected at different times of year, they identified an annual cycle of shell formation and showed the influence of temperature on daily increments. They identified two growth breaks within the annual cycle. The first "biocheck" (sensu Hall et al., 1974) occurred during winter months. This growth break is characterized by continuously decreasing increment widths in the fall, followed by a shutdown of growth during the coldest winter months. The second growth break identified by Schöne et al. (in press) is characterized by a rapid decrease in increment widths followed by a gradual recovery to widths slightly smaller than those deposited prior to the decrease. This zone often is expressed as a purple band in cross-section. Counting daily increments from the commissure to this purple band from specimens collected in late October and November indicates that this biocheck was deposited in early August (Schöne et al., in press). This growth break is not present in specimens collected in May, while specimens collected in early August have a narrow purple band, further indicating that the purple band forms in early August.

Both of these biochecks were identified in IM11-A1L and IM11-A2L. Increments at the commissure are very narrow. These increments were deposited just prior to col-

lection and correspond to the final annual winter bands on the surface of the clams' shells. These narrow increments were deposited at or near the cold temperature threshold of growth. The purple band also was identified in both specimens. Increments in the purple band show an abrupt decrease in width followed by an increase to widths slightly less than those deposited just prior to the purple band (IM11-A1L, #245–290; IM11-A2L, #250–290). Because the purple band is deposited in August, the warmest month of the year (Fig. 3), the formation of these narrow increments were interpreted as a result of hot conditions. Assuming that this summer biocheck was formed as a result of heat stress, we can use these narrow increments to assign a calendar date to particular increments in the shell.

It is assumed that the first narrow increment from the purple band was deposited on the hottest day of the year: August 17, 1999 (average temperature 32.7°C). Thus, increment #249 from IM11-A1L is assigned to August 17, 1999 $\pm$ two weeks. Similarly, the same date is assigned to increment #263 from IM11-A2L. All increments are assigned dates with uncertainty of $\pm$ two weeks.

Using this date, dates can be assigned to other portions of the growth-increment profile. However, lunar days first must be converted to solar days. Because the daily growth increments are deposited in response to the tidal cycle (Evans, 1972; Lutz and Rhodes, 1980), they correspond to lunar rather than solar days. In one year there are 353 lunar days as compared to 365 solar days. To correct for this discrepancy, one solar day has been subtracted from each month. Thus, accounting for the difference of 12 days. Because of the uncertainty in assigning dates to individual increments ($\pm$ two weeks), this correction does not affect the results. Thus, an interval of 30 growth increments (30 lunar days) corresponds to one month of 31 solar days. The 15th solar day arbitrarily was omitted from each month when assigning dates to individual increments. For example, the first 14 increments from a month are assigned the dates 1–14, while increments 15 through 30 are assigned 16–31. There are 102 increments between #249 (August 17, 1999) and the last increment counted at the commissure in IM11-A1L. Using the method outlined above, the date November 30, 1999 was assigned to the final increment. Unfortunately, the growth increments deposited at the commissure in the other shell (IM11-A2L) were obscure and a date cannot be assigned to its final increment. However, the last obvious increment counted from this specimen (#341) is dated as November 5, 1999, and there is 0.82 mm between this increment and the commissure. Thus, active shell deposition continued for a short time after November 5, 1999. Based on the similarity of the increment profiles from the two specimens and the isotopic values at the commissures (see below) it is assumed that active shell deposition in IM11-A2L halted in late November or early December, 1999.

In addition to dating the final increments at the commissure, it is possible date the initiation of growth in the preceding spring. In both increment profiles, there is a dramatic increase in increment widths (IM11-A1L: #110; IM11-A2L: #127) that coincides with the ventral margin of the penultimate winter band deposited in winter 1998/1999. These increments mark the initiation of growth following the deposition of the 1998/1999 winter band. The number of increments between those at the ventral mar-

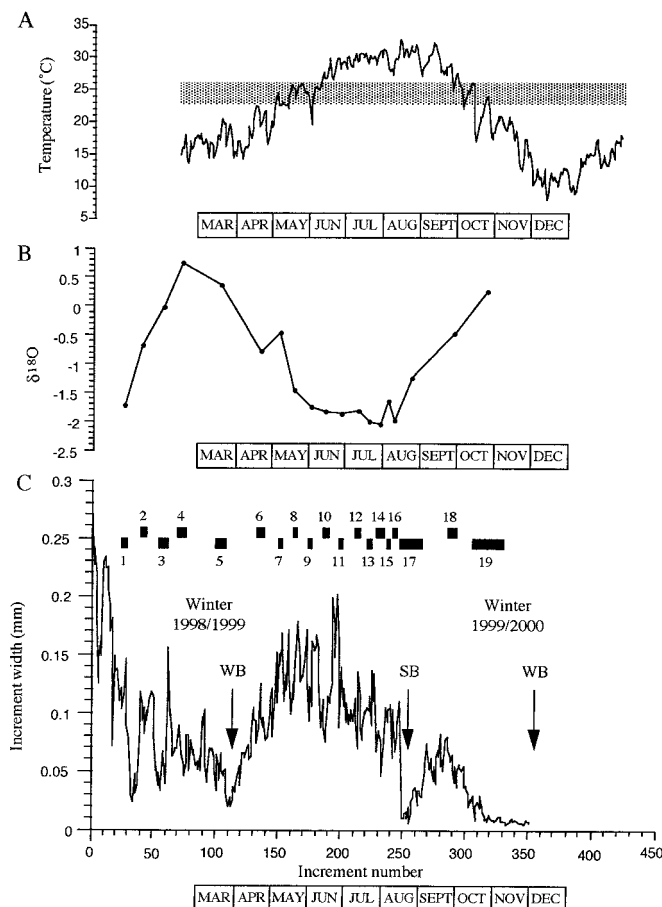


FIGURE 5—Relationship among temperature, $\delta^{18}\text{O}$, and increment width from IM11-A1L. (A) Average daily temperature at the study site from February 16, 1999 to February 16, 2000. The shaded area marks the optimal growth temperatures of *C. cortezi*. (B) Oxygen isotope profile from IM11-A1L. Sample positions mark the center of the interval sampled. (C) Daily increment-width profile. Increments 0–109 were deposited prior to winter 1998/1999. The remainder were deposited during 1999 and 2000. Increment 110 marks the initiation of growth in the spring of 1999. The small widths around increment 250 mark the position of the summer biocheck. This interval is marked by a slowing and/or shutdown of growth. The final increment marks the position of the commissure. The position of annual growth bands are marked by the word “winter.” WB marks the position of winter growth breaks, SB marks the position of the summer break. The resolution of each isotopic sample also is shown by rectangular blocks. The numbers refer to the stable isotope sample number.

gin of the winter band and the narrow increments in the purple band is similar in both specimens (IM11-A1L: 139; IM11-A2L: 136). By counting back from the purple band, the date March 26, 1999 is assigned to the increment marking the initiation of growth following the deposition of the winter band in the winter 1998/1999 in IM11-A1L. Similarly, initiation of growth in IM11-A2L is dated as March 29, 1999.

Increments deposited prior to the initiation of growth in the spring of 1999 cannot be dated precisely. Because growth halts between December and late March, the increments deposited prior to the spring 1999 initiation of growth represent growth in the fall of 1998. Based on the timing of shutdown in the fall of 1999, it is assumed that these early increments were deposited prior to December

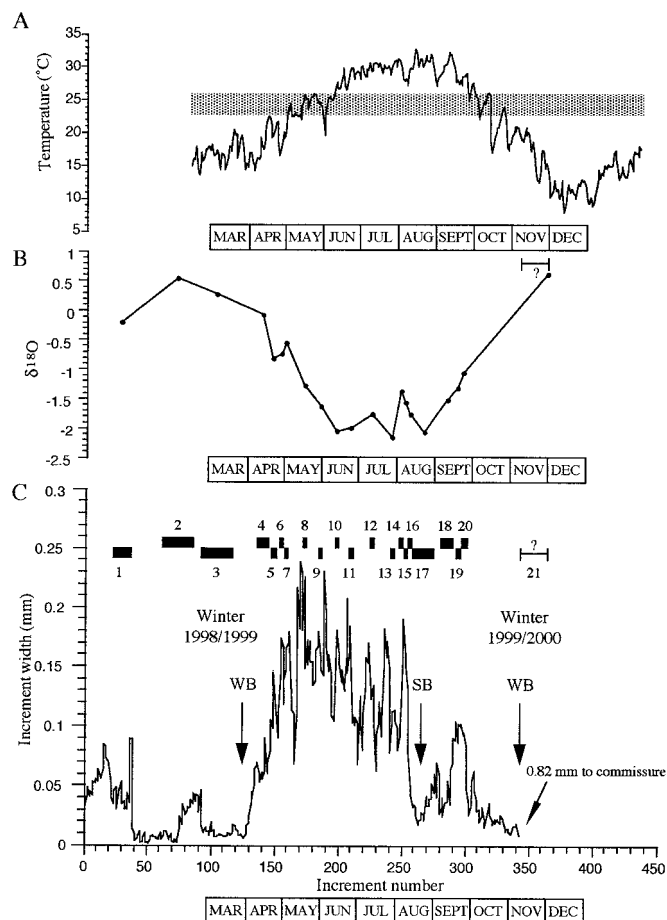


FIGURE 6—Relationship among temperature, $\delta^{18}\text{O}$, and increment width from IM11-A2L. (A) Average daily temperature at the study site from February 16, 1999 to February 16, 2000. The shaded area marks the optimal growth temperatures of *C. cortezi*. (B) Oxygen isotope profile from IM11-A2L. (C) Daily increment-width profile. Increments 0–126 were deposited prior to winter 1998/1999. The remainder were deposited during 1999 and 2000. Increment 127 marks the initiation of growth in the spring of 1999. The small widths around increment 265 mark the position of the summer biocheck. This interval is marked by a slowing and/or shutdown of growth. The last increment counted was deposited in early November. 0.82 mm of shell was deposited between the last counted increment and the commissure. The positions of annual growth bands are marked by the word “winter.” WB marks the position of winter growth breaks, SB marks the position of the summer break. The resolution of each isotopic sample also is shown by rectangular blocks. The numbers refer to the stable isotope sample number. Dating sample #21 was not possible because increments from the final 0.82 mm of growth could not be resolved.

1, 1998. However, because the temperature records do not go back this far, it is not possible to date the 1998 increments.

CROSS-CALIBRATION

Increment Width and Temperature

Annual variation in the daily growth-increment widths from both specimens (Figs. 5C and 6C) is similar to the annual variation in average daily temperature (Figs. 5A and 6A) except that very high temperatures also result in very narrow bands. In March 1999, when temperatures are rel-

atively cool ($\sim 17^{\circ}\text{C}$), growth increments in both specimens are narrow. During April and May, when temperatures begin to rise, daily increment widths increase dramatically, from 0.01 mm to more than 0.2 mm (Figs. 5C and 6C). In June, increment widths stabilize and then decrease as conditions warm to near their mid-summer maximum temperatures. The hottest temperatures of the year, in August, are accompanied by a dramatic decrease in increment widths. When temperatures decrease in September, increment widths rebound to widths slightly less than those deposited just prior to the hottest time of the year. The final increments from both specimens were deposited in October and November. November is characterized by some of the narrowest growth increments deposited during the study interval. No increments were deposited after November, but temperatures continue to fall through the end of 1999.

Isotopic Variation and Temperature

The oxygen isotope values (Figs. 5B and 6B), like the daily increment widths, show a strong annual cycle that can be correlated with temperature (Figs. 5A and 6A). Because the fractionation of oxygen isotopes largely is controlled by temperature (Grossman and Ku, 1986), this annual cycle is expected given the strong annual temperature cycle in the northern Gulf of California. The most positive isotopic values correspond to cold temperatures, while negative isotopic values occur in portions of the shells deposited during warmer conditions. In late March and early April 1999, when temperatures begin to rise, the $\delta^{18}\text{O}$ values become more negative; as temperatures continue to rise through May and June, $\delta^{18}\text{O}$ values continue to fall. This trend is interrupted in late April by a slightly positive shift in $\delta^{18}\text{O}$ ratios. By July and August, $\delta^{18}\text{O}$ values are at their most negative. During these months, temperatures are in excess of 30°C . The hottest month of the year, August, includes a brief positive shift in the isotope values in both specimens. Following this hot interval, temperatures begin to fall and $\delta^{18}\text{O}$ values increase. Finally, as temperatures continue to cool in October and November, isotopic values rise to their most positive values; nearly identical to those deposited the previous spring.

A more precise calibration of individual $\delta^{18}\text{O}$ samples with temperature was attempted by comparing each sample's isotopically derived temperature estimate with the observed temperature that occurred during that sample interval. This comparison only was carried out for those samples that could be dated accurately from the increment-width profile (IM11-A1L, 6–19; IM11-A2L, 4–20; Table 1). Because increments cannot be dated more precisely than $\pm$ two weeks, it is not possible confidently to place each $\delta^{18}\text{O}$ sample in a time interval shorter than four weeks. Accordingly, comparison of isotopic estimates with temperature records was accomplished by relating the average observed temperature over a period that included two weeks before and two weeks after the estimated dates bracketing the $\delta^{18}\text{O}$ sample. Figure 7 shows the observed and calculated temperatures from both specimens. The curves are very similar in both plots. However, calculated temperatures from April and May are higher than the observed temperature, and after June, the observed temper-

atures are consistently higher than calculated temperatures.

Isotopic Variation and Increment Width

Because both increment widths and isotopic variation vary as a function of temperature, they can be calibrated with each other. In the late winter and early spring $\delta^{18}\text{O}$ values, are at their most positive values and increment widths are narrow. As temperatures rise and $\delta^{18}\text{O}$ values become more negative, increments become wider. In the late spring, increment widths stabilize as the $\delta^{18}\text{O}$ values continue to become more negative. In the mid-summer months, the isotopes have reached their most negative values, but increment widths decrease. In the late summer, the narrowest increments since the previous spring are deposited and the stable isotope values continue at their mid-summer negative values. For a short time following this interval of very narrow increments, the $\delta^{18}\text{O}$ values and increment widths both increase as temperatures fall from the highest values in the late summer. Finally, in the late fall, temperatures continue to cool, the stable isotope values rise to values equivalent to those deposited the previous year, and increments narrow to approximately the widths of those deposited in the early spring.

ESTIMATION OF SHUTDOWN TEMPERATURES

Because the deposition of geochemical and sclerochronological characters in bivalve shells occurs in response to an individual's surroundings, these characters are reliable indicators of environmental conditions. Both $\delta^{18}\text{O}$ values and daily growth-increment widths provide valuable information on the annual patterns of growth in marine bivalves. These characters can be used to determine if *C. cortezi* grows continually through the year. $\delta^{18}\text{O}$ values can be used to estimate the maximum and minimum temperatures of growth. Discrepancies between these estimates and observed temperature records indicate that the organism did not grow throughout the year. Because the full range of observed temperatures is not represented, then the maximum and minimum $\delta^{18}\text{O}$ derived temperatures estimate the maximum and minimum critical thresholds of growth. Furthermore, in addition to confirming maximum and minimum temperatures of growth, the dated increment-width profile can provide estimates of the timing of growth halts. Understanding growth patterns is critical because discrepancies between actual environmental conditions and those reconstructed from biological signals set the limits for paleoenvironmental reconstructions. That is, reconstructions from bivalve shells only reflect conditions that occurred during active shell growth. If the animal does not deposit shell material through the full range of conditions, then reconstructed environmental conditions merely reflect the environmental tolerances of that species, not the full range of temperatures in the bivalve's habitat.

The Grossman and Ku (1986) equation yields estimates of maximum temperatures that agree closely with measurements from the temperature loggers. Because water samples were not collected during the study interval, all temperature calculations initially assume that the isoto-

pic composition of the water is 0‰. The warmest isotopically derived temperature obtained from IM11-A1L is 28.6°C (sample #14; -2.05‰). The warmest seven day average (the number of increments in sample #14) temperature is 31.4°C. The difference between these estimates (2.8°C) likely results from seasonal changes in the isotopic composition of the water in which the clam grew. Using this temperature difference and solving the paleotemperature equation for the $\delta^{18}\text{O}$ of water yields a value of 0.64‰. This value agrees closely with measurements of the $\delta^{18}\text{O}$ of the water in the northern Gulf of California, which indicate that summer values range between approximately 0.6 and 1.0‰. Similarly, the warmest isotopically derived temperature from shell IM11-A2L is 28.5°C (sample #13; -2.03). The warmest 4 day average is 31.9°C. This temperature difference yields a water value of 0.77‰, again within the summer $\delta^{18}\text{O}$ range. Thus, allowing for variation in the $\delta^{18}\text{O}$ of the water, the maximum isotopically derived temperature suggests that little or no shell deposition occurs above temperatures of approximately 31°C.

Unlike calculated temperatures from the summer, temperatures calculated from the most positive isotopic values do not agree with the observed winter temperature record. The most positive winter sample is 0.73‰ (IM11-A1L, sample #4; IM11-A2L, sample #21). Again, for the moment, assuming that the isotopic composition of the water is 0‰, the calculated temperature is 16.6°C. Both samples come from slow growing parts of the year, representing several weeks of growth; thus, they are comparable to average monthly temperatures. The coldest average monthly temperature is 11.52°C. The difference between the minimum observed temperature and the calculated temperatures is 5.1°C. If this difference was solely the result of the isotopic composition, it would require that the water be -1.2‰. However, since the construction of dams on the Colorado River, very little isotopically light water reaches the Gulf and normal marine conditions prevail (Lavin and Sánchez, 1999). Furthermore, throughout observations associated with this study, the most negative isotopic value of the water was 0.21‰. Thus, the coldest isotopically derived temperature (~17°C) is an estimate of the lower temperature threshold of growth in *C. cortezi*, not the minimum temperature in its habitat.

The dated increment-width profile used in conjunction with average monthly temperatures also yields estimates of maximum and minimum thresholds of growth. In *C. cortezi* from the northern Gulf, rapid growth begins in early spring. Average monthly temperatures for March and April are slightly warmer than 17°C. Thus, the initiation of growth in the spring coincides with temperatures above ~17°C. The widest increments in both specimens were deposited in May and June when the average temperature was between 23 and 26°C. Increment widths decrease in late June and continue to gradually narrow through mid-August while average monthly temperatures during these months increase steadily. This suggests that warmer conditions adversely affect shell growth. In mid-August, increment widths decrease abruptly. This decrease coincides with both the warmest average monthly temperature (30.9°C) and the warmest average daily temperature (32.7°C) during the study interval, indicating that the maximum temperature threshold of growth has been

reached or exceeded. Thus, the upper temperature threshold of growth in *C. cortezi*, estimated from daily increment widths, is approximately 31°C. When temperatures fall below this threshold in September, increment widths increase and active accretion of shell begins again and continues through November. During these months, the average monthly temperatures are between 31°C and 17°C. No shell material is deposited when temperatures fall below the minimum temperature threshold of 17°C.

The estimates of maximum and minimum temperature thresholds of growth from increment widths and oxygen isotopes agree closely. The increment-width profiles indicate that shell growth occurs between 17 and 31°C. Isotopically based estimates indicate temperatures of 16.6 and 31.9°C. These results agree closely with independent estimates provided by Schöne et al. (in press). Based on satellite sea-surface temperatures, they suggest that growth takes place between 16.7 and 29.3°C. These three independent estimates suggest active shell deposition in *C. cortezi* from the northern Gulf occurs between approximately 17 and 31°C.

COMPARISON OF $\delta^{18}\text{O}$ DERIVED TEMPERATURES WITH OBSERVED TEMPERATURES

Observed temperatures can be compared with those calculated from $\delta^{18}\text{O}$ values because of the assignment dates to individual oxygen-isotope samples. However, because growth stops below 17°C, increments deposited in 1998 prior to initiation of growth in spring 1999 cannot be dated by simple increment counting. Thus, temperatures cannot be assigned to the isotope samples that came from this interval (IM11-A1L, 1-5; IM11-A2L, 1-3; Table 1). Because each $\delta^{18}\text{O}$ sample represents several days of growth (see below), the average temperature from that interval has been calculated. Dates have been assigned to the first and last increment within each sample (Table 1) and the average observed temperature calculated from the sample interval. However, because each increment is assigned a date with an uncertainty of $\pm$ two weeks, this uncertainty also was incorporated into the average observed temperature. Therefore, the observed temperature is the average of conditions thought to have occurred during deposition of increments within an isotopic sample, plus the temperatures from the 14 days prior to the first increment and the 14 days following the last increment. Figure 7 shows the relationship between observed and calculated temperatures. The similarity certainly indicates that temperature is the main factor controlling the $\delta^{18}\text{O}$ profile. Furthermore, the overall correspondence of observed and calculated temperatures indicates that $\delta^{18}\text{O}$ derived temperature estimates may be reliable measures of paleotemperature variation within the period of growth. However, the observed and calculated temperature curves do not agree exactly. Calculated temperatures from both specimens are warmer than observed temperatures in April, May, and most of June. In late June through October, calculated temperatures are consistently cooler than observed temperatures.

The discrepancy between observed (logger) and calculated (isotopic) temperatures can be explained best by the preferential growth of the clams during optimal temperatures. Recall that the widest increments were deposited in

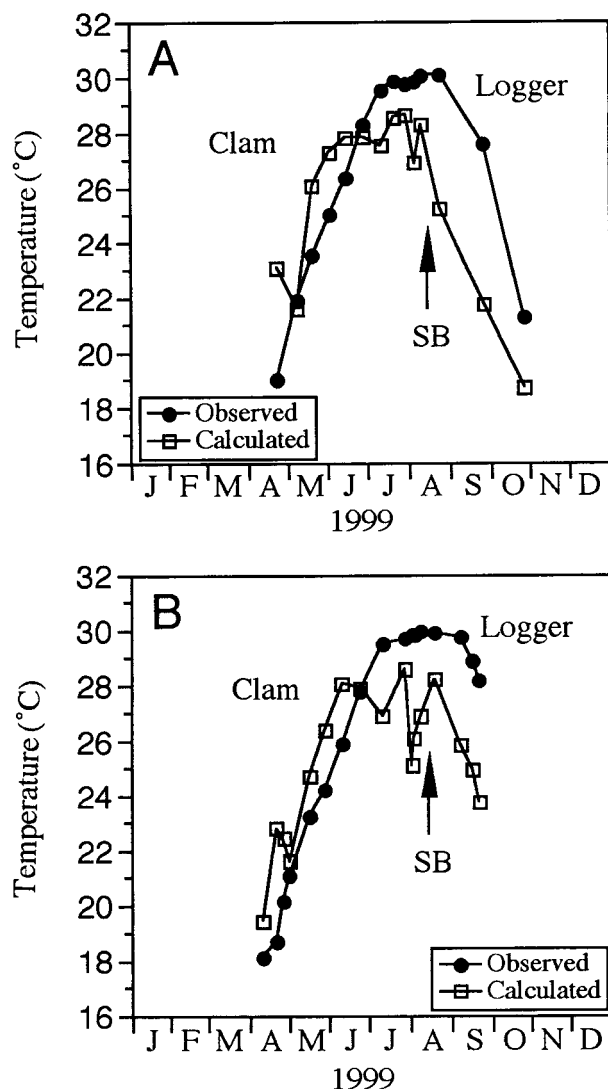


FIGURE 7—Comparison of observed (logger) and calculated (clam) temperature from IM11-A1L (A) and IM11-A2L (B). In both graphs, the solid circles represent observed temperatures from the loggers and the open squares are calculated temperatures from $\delta^{18}\text{O}$ samples. SB marks the position of the summer break.

May and June when the average temperature was between 23 and 26°C (Figs. 5A and 6A). This estimate of the optimal growth temperatures agrees well with that of Schöne et al. (in press), who suggested that maximum growth occurs between 21 and 24°C.

In the spring, temperatures fluctuate about the lower end of the optimal range (Figs. 5A and 6A). During the day, temperatures warm into the optimal range, while temperatures cool below 23°C at night. Slow growth during overall cool intervals results in isotope samples that contain a greater volume of shell material deposited during warmer daytime conditions. In other words, while the temperature loggers continue to record low temperatures, the clam "recorders" have temporarily slowed or shut down. Thus, temperatures calculated from spring $\delta^{18}\text{O}$ samples will over-estimate observed temperatures (Fig. 7). Similarly, during the warmest months of the year (June through September), temperature fluctuates about

the upper limit of the optimal range. Daytime temperatures climb well above 26°C, while nighttime conditions cool into the optimal range. Thus, most growth occurs at night and little shell material is deposited during the hottest part of the day (especially during low tides; see Richardson et al., 1981). Isotope samples taken from this part of the shell reflect the greater influence of cool nighttime-shell deposition, and temperatures reconstructed from these $\delta^{18}\text{O}$ samples underestimate average observed temperatures (Fig. 7).

An additional factor resulting in discrepancies between the observed and calculated temperatures may be variation in the isotopic composition of the water in which the clams grew. Although oxygen isotope ratios are mostly controlled by temperature, changes in the isotopic composition of the water also have a significant effect (Grossman and Ku, 1986). The Gulf of California is an evaporative basin (Bray, 1988) and evaporation rates are highest in the summer (Roden, 1958); thus, the isotopic composition of the water in the northern Gulf of California becomes progressively more positive throughout the summer and early fall. Because the most positive isotopic values of the water coincide with the warmest temperatures, the $\delta^{18}\text{O}$ derived temperatures from shell material deposited during the summer will tend to underestimate the actual temperatures. Hence, the low calculated temperatures from mid-June through October (Fig. 7) probably reflect the increasingly more positive $\delta^{18}\text{O}$ values of the water. During August, the hottest month of the year, the $\delta^{18}\text{O}$ from the shells are expected to be at their most negative values. However, the calculated temperatures may underestimate the observed temperature record because enhanced evaporation increases water $\delta^{18}\text{O}$ to more positive values.

The effects of subaerial exposure also may cause some of the discrepancy between the observed and calculated temperatures. Because the temperature loggers were placed in the intertidal zone, some of the observed temperatures represent air temperatures. However, because shell deposition occurs when the clam is submerged, the calculated temperatures mostly will reflect water temperatures. The greatest discrepancy between air and water temperatures in the northern Gulf of California occurs in the winter months of December, January, and February when water temperatures are warmer than air temperatures (Fig. 8). However, this difference is not reflected in the comparison of observed and calculated temperatures (Fig. 7) for the simple reason that the clams did not grow during this interval. Nevertheless, some of the discrepancy between the observed and calculated temperatures could be due to the effects of subaerial exposure on the temperature loggers and the growth of the bivalves. Exposure to the air in the hot summer probably causes the loggers to overestimate the water temperatures experienced by the clams.

The close agreement between observed temperatures and $\delta^{18}\text{O}$ derived temperature estimates shows that sub-annual temperature variation can be reconstructed from *C. cortezi* shells. Because shells of *C. cortezi* are common constituents of fossil deposits in the northern Gulf, they are a rich source of information with which to reconstruct seasonal temperature variation in the northern Gulf of California.

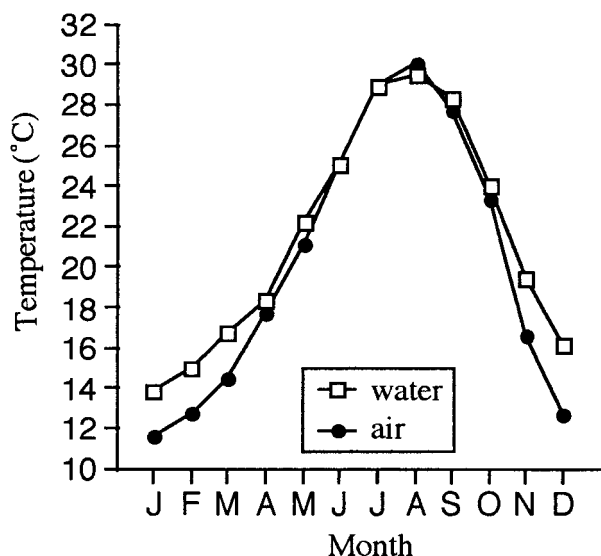


FIGURE 8—Average monthly air (solid circles) and water (open squares) temperatures in the northern Gulf of California. Note that air temperatures are lower than water temperatures through most of the year. Data from Thomson (2000).

VARIABILITY IN $\delta^{18}\text{O}$ SAMPLE RESOLUTION

Comparing daily increment widths within isotope samples has allowed an estimation of the resolution of individual $\delta^{18}\text{O}$ values. Because daily increment widths vary within the year (see above), samples taken from different parts of the year will have different temporal resolutions. When daily increment widths are narrow, a sample will contain more increments than a sample taken from wide increments. Because daily increment-width variation and $\delta^{18}\text{O}$ resolution set the limits for high-resolution isotopic analysis, information on sample resolution is particularly important when reconstructing sub-annual temperatures. Figures 5C and 6C show how temporal resolution varies throughout the year. During cooler conditions, daily increment widths are narrow and isotope samples can represent more than three weeks of growth. This is seen clearly in the first three samples from IM11-A2L (Fig. 6C; Table 1). $\delta^{18}\text{O}$ resolution is also coarse (>2 weeks of growth per sample) during the hottest part of the summer when growth rates are also slow (Fig. 5C, IM11-A1L, sample #17; Fig. 6C, IM11-A2L, samples #17–18; Table 1). These examples illustrate that in *C. cortezi*, sample resolution is coarsest when taken from slow growing parts of the shell deposited close to the maximum and minimum critical thresholds of growth. However, the vast majority of samples have much better resolution. Most samples (33 of 39; $\sim 85\%$; Fig. 9) represent less than 10 days of growth, 27 samples ($\sim 70\%$) represent less than a week and 25 samples ($\sim 65\%$) were taken from less than 5 days of growth. These data indicate that the majority of samples can be used to reconstruct conditions with approximate sub-weekly resolution.

In specimens that demonstrate temperature-controlled shutdowns, samples taken from shell material deposited prior to the shutdown will have coarse resolutions. *Chione cortezi* from the northern Gulf slows and/or stops growing in both the winter and summer. Because narrow daily in-

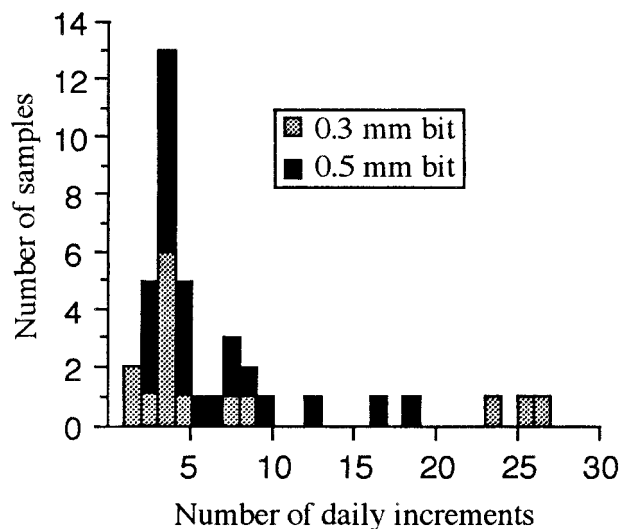


FIGURE 9—Frequency distribution of sample resolutions. Samples were taken with drill bits of two different sizes, 0.3 mm (stippled area) and 0.5 mm (solid area). The majority of stable isotope samples include fewer than five increments. Two samples, taken from rapidly growing parts of the shell, sampled just two days of growth. Three samples represent more than three weeks of growth. Data are from both specimens.

crements generally are associated with growth halts, samples taken from these slow-growing parts of the shell contain the largest number of daily growth increments. Furthermore, winter and summer shutdowns are associated with the most positive and negative $\delta^{18}\text{O}$ values. Thus, the most positive (winter) and most negative (summer) $\delta^{18}\text{O}$ values have the coarsest resolutions. The occurrence of coarse-resolution samples with the most positive and/or negative $\delta^{18}\text{O}$ values from the annual profile may be a useful criteria for identifying thermally controlled growth halts in fossil shells.

INTEGRATING ISOTOPIC AND SCLEROCHRONOLOGICAL ANALYSES

Both isotopic and sclerochronologic analyses have proven their value in paleontological studies (e.g., Rhoads and Lutz, 1980; Wefer and Berger, 1991). While each tool provides powerful insight in paleontological study, used together they can provide information otherwise unavailable. Perhaps the most significant insight is the dating of individual stable isotope samples. When stable isotope samples are taken from a shell with a dated daily increment profile, samples can be assigned a particular date within the year. This allows seasonal and even sub-seasonal environmental analysis. Furthermore, if particular characters of the increment-width profile can be recognized in different specimens (e.g., summer shutdown, etc.), then isotopic samples can be approximately dated without investing the time and energy for detailed counts of increments. This approximate dating technique is attractive because many features of the increment-width profile can be observed on polished sections with a hand lens, thus eliminating the need for elaborate sample preparation.

Dated increment profiles and $\delta^{18}\text{O}$ values used together

also can be a useful tool in evolutionary studies. For example, as shown here, it is possible to identify thermally controlled growth checks and growth-limiting temperatures. Thus, the limiting temperatures of growth can be compared within and across evolutionary lineages. This information then can be used to trace changes in environmental tolerances within a group or to document how environmental conditions affect different species.

Dated increment profiles used in conjunction with stable isotopes also can be useful in paleoclimatological studies. Understanding the timing of thermally controlled growth patterns permits the recognition of regional climatological changes. For example, Berry and Barker (1975) showed that *C. undatella* from the northern Gulf of California deposited approximately eight months of daily growth increments between winter breaks. However, farther south in the Gulf, where winters are shorter and milder, daily increments between winter bands from *C. undatella* represent approximately ten months. The temperature of shutdowns in each region then could be determined by isotopic analysis of the first and last increments deposited during the year. This technique could be used to determine regional differences in the duration of intervals when temperatures are above or below growth thresholds. While this example illustrates how a geographic climatic gradient could be reconstructed, this approach also could be applied to noncontemporaneous specimens from a single region to reconstruct climate changes through time. Furthermore, rates of temperature change could be estimated by counting increments between the most positive and negative isotopic values. This approach could be used to reconstruct patterns such as the rate of warming in the spring or the how fast temperatures cool in the fall. Reconstructing such detailed patterns of seasonality will be a valuable new tool in paleoclimate analysis.

SUMMARY AND CONCLUSIONS

Oxygen isotope samples from two live-collected specimens of *C. cortezi* from the northern Gulf of California were calibrated using dated daily increment-width profiles and compared with observed high-resolution temperature records from the same site. From this analysis the following conclusions are drawn:

(1) $\delta^{18}\text{O}$ profiles from both specimens range between 0.73‰ (winter) and -2.05‰ (summer). The $\delta^{18}\text{O}$ profile largely reflects the temperature cycle at the study site within the clams' eight months of growth.

(2) Increment-width profiles from the two specimens are similar, indicating their deposition in response to similar environmental conditions. Increment widths vary as a function of temperature: they are narrow near the maximum and minimum temperature threshold of growth and wide at intermediate temperatures.

(3) Daily increment counts from both specimens indicate that shell deposition begins in late March or early April. Vigorous shell deposition continues until the hottest part of the year (August) when growth slows and/or halts. Growth begins again when temperatures cool from their mid-summer highs. Growth halts in late November or early December. Little or no shell is deposited during the four coldest months of the year (December–March).

(4) The resolution of stable isotope samples varies

throughout the year. Samples with the coarsest resolution are from parts of the shell deposited near the minimum and maximum temperature thresholds of growth. Such samples represent more than three weeks of growth and generally have the most positive and negative values. Samples with intermediate $\delta^{18}\text{O}$ values have finer resolutions. The majority of samples represent five or fewer days of growth.

(5) Estimates of the maximum and minimum temperature threshold of growth from increment width counts and isotope profiles are similar. These estimates suggest that growth begins when temperature warms above $\sim 17^\circ\text{C}$ and halts when temperature rises above $\sim 31^\circ\text{C}$.

(6) Oxygen isotope samples used in conjunction with increment-width profiles can provide high-resolution paleoenvironmental information.

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REFERENCES

- BERRY, W.B.N., and BARKER, R.M., 1975, Growth increments in fossil and modern bivalves: in Rosenberg, G.D., and Runcorn, S.K., eds., *Growth Rhythms and the History of the Earth's Rotation*: John Wiley & Sons, New York, p. 9–25.
- BRAY, N.A., 1988, Water mass formation in the Gulf of California: *Journal of Geophysical Research*, v. 93, p. 9223–9240.
- COE, W.R., 1948, Nutrition, environmental conditions, and growth of marine bivalve mollusks: *Journal of Marine Research*, v. 7, p. 586–601.
- DAVENPORT, C.B., 1938, Growth lines in fossil pectens as indicators of past climates: *Journal of Paleontology*, v. 12, p. 514–515.
- EVANS, J.W., 1972, Tidal growth increments in the cockle *Clinocardium nuttalli*: *Science*, v. 176, p. 416–417.
- GROSSMAN, E.L., and KU, T.L., 1986, Oxygen and carbon fractionation in biogenic aragonite: Temperature effects: *Chemical Geology*, v. 59, p. 59–74.
- GUNTER, G., 1957, Temperature: in Hedgpeth, J.W., ed., *Treatise of Marine Ecology and Paleoecology*, Volume 1, Ecology: Memoir of the Geological Society of America, v. 67, p. 159–184.
- HALL, JR., C.A., DOLLASE, W.A., and CORBATÓ, C.W., 1974, Shell growth in *Tivela stultorum* (Mawe, 1823) and *Callista chione* (Linnaeus, 1758) (Bivalvia): Annual periodicity, latitudinal differences, and diminution with age: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 15, p. 33–61.
- HASTINGS, J.R., 1964, Climatological data for Baja California: Technical Reports on the Meteorology and Climatology of Arid Regions, no 14, p. 93.
- JONES, D.S., 1996, Playing back skeletal recordings: *PALAIOS*, v. 11, p. 293–294.
- JONES, D.S., and ALLMON, W.D., 1995, Records of upwelling, season-

- ality and growth in stable-isotope profiles of Pliocene mollusk shells from Florida: *Lethaia*, v. 28, p. 61–74.
- JONES, D.S., and QUITMYER, I.R., 1996, Marking time with bivalve shells: Oxygen isotopes and season of annual increment formation: *PALAIOS*, v. 11, p. 340–346.
- JONES, D.S., THOMPSON, I., and AMBROSE, W., 1978, Age and growth rate determinations for the Atlantic surf clam *Spisula solidissima* (Bivalvia: Mactracea), based on internal growth lines in shell cross-sections: *Marine Biology*, v. 47, p. 63–70.
- JONES, D.S., WILLIAMS, D.F., and ARTHUR, M.A., 1983, Growth history and ecology of the Atlantic surf clam, *Spisula solidissima* (Dillwyn), as revealed by stable isotopes and annual shell increments: *Journal of Experimental Marine Biology and Ecology*, v. 73, p. 225–242.
- JONES, D.S., ARTHUR, M.A., and ALLARD, D.J., 1989, Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island: *Marine Biology*, v. 102, p. 225–234.
- KENNISH, M.J., and OLSSON, R.K., 1975, Effects of thermal discharge on the microstructural growth of *Mercenaria mercenaria*: *Environmental Geology*, v. 1, p. 41–64.
- KHIM, B.-K., WOO, K.S., and JE, J.-G., 2000, Stable isotope profiles of bivalve shells: Seasonal temperature variations, latitudinal temperature gradients and biological carbon cycling along the east coast of Korea: *Continental Shelf Research*, v. 20, p. 843–861.
- KILLINGLY, J.S., 1981, Seasonality of mollusc collecting determined from ^{18}O profiles of midden shells: *American Antiquity*, v. 48, p. 152–158.
- KOIKE, H., 1980, Seasonal dating by growth-line counting of the clam, *Meretrix lusoria*: *University of Tokyo Bulletin*, v. 18, p. 1–120.
- LAVIN, M.F., and SÁNCHEZ, S., 1999, On how the Colorado River affected the hydrography of the upper Gulf of California: *Continental Shelf Research*, v. 19, p. 1545–1560.
- LUTZ, R.A., and RHOADS, D.C., 1980, Growth patterns within the molluscan shell: An overview: *in* Rhoads, D.C., and Lutz, R.A., eds., *Skeletal Growth of Aquatic Organisms*: Plenum Press, New York, p. 203–254.
- OHNO, T., 1989, Palaeotidal characteristics determined by micro-growth patterns in bivalves: *Palaeontology*, v. 32, p. 237–263.
- PANNELLA, G., and MACCLINTOCK, C., 1968, Biological and environmental rhythms reflected in molluscan shell growth: *in* Macurda, D.B., Jr., ed., *Paleobiological Aspects of Growth and Development*, A Symposium: *Paleontology Society Memoir*, v. 42, p. 64–81.
- RICHARDSON, C.A., CRISP, D.J., and RUNHAM, N.W., 1981, Factors influencing shell deposition during a tidal cycle in the intertidal bivalve *Cerastoderma edule*: *Journal of the Marine Biological Association*, v. 61, p. 465–467.
- RHOADS, D.C., and LUTZ, R.A., 1980, *Skeletal Growth of Aquatic Organisms*: Plenum Press, New York, 750 p.
- RODEN, G.I., 1958, Oceanographic and meteorological aspects of the Gulf of California: *Pacific Science*, v. 12, p. 21–45.
- SATO, S., 1995, Spawning periodicity and shell microgrowth patterns of the Venerid bivalve *Phacosoma japonicum* (Reeve, 1850): *Veliger*, v. 38, p. 61–72.
- SCHÖNE, B.R., GOODWIN, D.H., FLESSA, K.W., DETTMAN, D.L., and ROOPNARINE, P.D., in press, Sclerochronology and growth of the bivalve mollusks *Chione fluctifraga* and *Chione cortezi* in the northern Gulf of California, Mexico: *Veliger*.
- THOMPSON, R.W., 1968, Tidal flat sedimentation on the Colorado River delta, northwestern Gulf of California: *Geological Society of America Memoir*, v. 107, p. 1–133.
- THOMSON, D.A., 2000, *Tide calendar for the northern Gulf of California*. Printing and Graphic Services, University of Arizona: Tucson.
- WEFER, G., and BERGER, W.H., 1991, Isotope paleontology: Growth and composition of extant calcareous species: *Marine Geology*, v. 100, p. 207–248.

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