

ISOTOPIC ECOLOGY OF THE MODERN LAND SNAIL *CERION*, SAN SALVADOR, BAHAMAS: PRELIMINARY ADVANCES TOWARD ESTABLISHING A LOW-LATITUDE ISLAND PALEOENVIRONMENTAL PROXY

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ABSTRACT

The isotopic ecology of terrestrial snails from tropical island settings is not known despite the importance of such data sets for paleoenvironmental reconstructions. In this study, variations in carbon (¹³C/¹²C) and oxygen (¹⁸O/¹⁶O) isotope ratios obtained during whole-shell and sequential-rib analyses of the modern land snail, *Cerion*, reveal a record of diet and local environment on San Salvador, Bahamas. The mean $\delta^{13}\text{C}$ value of adult *Cerion* shells collected from C₄ vegetation is higher by 1.0‰ relative to snails collected from C₃ plants, suggesting that carbon isotopes in shell carbonate reflect the dominant plant type in the diet, though the broad range of shell carbonate $\delta^{13}\text{C}$ confirms a varied diet for this genus. The mean $\delta^{18}\text{O}$ values of adult *Cerion* shells collected from the west coast of San Salvador are 0.8‰ higher than those collected from the east coast of the island. This difference may reflect the incorporation of water vapor derived from ¹⁸O-rich hypersaline lakes located in the island's western interior. Sequential-rib analysis of one adult *Cerion* shell reveals variations in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values through ontogeny that may reflect changes in food source and rainfall seasonality, respectively. This study lays the groundwork for future studies to establish fossil *Cerion* as a valuable paleoenvironmental proxy for San Salvador and the Bahamas.

INTRODUCTION

Data in this paper demonstrate that shell carbonate of the land snail genus *Cerion* is capable of recording such environmental conditions as predominant vegetation type and the isotopic composition of local environmental moisture. This research is an important first step toward establishing *Cerion* as a viable paleoclimate proxy in the low-latitude island setting of the Bahamas and for understanding paleoenvironmental change in the Bahamian archipelago.

Paleoclimate research relies on the availability of reliable climate proxies if the research is to extend beyond the instrumental record. Proxies such as ice cores have characterized high-latitude terrestrial paleoclimatic variations, but paleoclimate in tropical settings is less well constrained due to fewer terrestrial climate proxies.

Terrestrial snails are abundant in many continental and coastal regions globally, and they are an excellent source potentially for paleoenvironmental information because local environmental and climatic conditions influence the isotopic composition of their shell carbonate. Their restricted movement facilitates preservation of a local environmental record, and the shells of fossil snails have a high-preservation potential. Amino acid racemization, accelerator mass spectrometry radiocarbon, and U-Series techniques can be used to date independently the shells of fossil snails, and the latter can extend paleoclimate and paleoenvironmental studies of land snails beyond 50,000 yr B.P. (the oldest radiocarbon date attainable;

see Hillaire-Marcel et al., 1995). Additionally, because many land snail species present in the Quaternary fossil record are extant, comparative studies of modern and fossil populations are possible, thus facilitating paleoenvironmental reconstructions (Goodfriend, 1992).

The majority of paleoenvironmental reconstructions based on isotope ratios in fossil land snails have been conducted in continental regions, specifically Europe (Lécolle, 1985; Kaiser and Eicher, 1987; Bonadonna and Leone, 1995; Zanchetta et al., 1999; Leone et al., 2000), Israel (Margaritz and Heller, 1980; Goodfriend, 1991, 1999), South Africa (Abell and Plug, 2000), South America (Bonadonna et al., 1995, 1999), and North America (Yapp, 1979; Sharpe et al., 1994; Goodfriend and Ellis, 2000; Balakrishnan et al., 2005a). In contrast, few studies of this nature have been conducted in tropical island settings.

Paleoenvironmental reconstructions based on carbon and oxygen isotope compositions of fossil land snails require assumptions regarding snail feeding behaviour, activity cycle, and physiology (e.g., lifespan and growth rate; Stott, 2002; Metref et al., 2003; Balakrishnan et al., 2005a). Studying live-collected snail specimens allows for determination of factors influencing isotope ratios in shell carbonate and for understanding subtle isotopic variations. The latter is particularly important in the Bahamas, where low-lying topography, small island size, and reduced seasonality may dampen climate signals in shell carbonate.

BACKGROUND

Cerion Ecology

Two of the over 600 species of *Cerion* in the Bahamas, identified on the basis of shell morphological variations, live on San Salvador: *Cerion watlingense* and *C. rodrigo* (Gould, 1997). In this paper, San Salvador *Cerion* are referred to by their genus only because (1) extensive hybridization across the island has led to a spectrum of shell morphologies between the two end-member species; (2) the two morphological end members have not yet been proven to represent true biological species; and (3) no geographic pattern in *Cerion* shell carbonate $\delta^{13}\text{C}$ values is observed on San Salvador despite the east-west distribution in snail species, and no conclusive evidence exists to suggest that a $\delta^{18}\text{O}$ offset should occur between different species of the same snail genus (Lécolle, 1985; Goodfriend and Ellis, 2002).

While several studies have addressed the ecology of modern *Cerion* (Bartsch, 1920; Mayr and Rosen, 1956; Woodruff, 1978; Quensen, 1981; Rose, 1989), snails of this genus have not been raised under controlled laboratory conditions or observed in nature through an entire life cycle. Thus, the snail's lifespan and diet remains largely enigmatic. *Cerion* transplanted to a natural laboratory were reported to reach reproductive and possibly developmental maturity at an age of <2–3 years (Bartsch, 1920). Although no estimate of the maximum lifespan of the snail was provided, *Cerion* were observed to be healthy at an age of 8 years (Bartsch, 1920). In the same study, *Cerion* were found in leaf litter, on bare carbonate rocks, on the leaves and bark of trees and shrubs, and on blades of grass (Bartsch, 1912, 1913, 1920). In response to dry and hot conditions, *Cerion* accrete a thin calcareous epiphragm and attach them-

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selves to plants to await a return to more favorable humidity and temperature conditions. Depending on the microhabitat, *Cerion* may remain on the same plant for 2–3 years (Woodruff, 1978) or migrate as much as 30 m in a year (Bartsch, 1920). During the present study, daytime field observations of *Cerion* revealed a relatively high level of activity during and following rain events, suggesting that movement between several different plants during their lifetime is likely.

Several studies have speculated about the *Cerion* diet, though no definitive accounts exist (Bartsch, 1920; Mayr and Rosen, 1956; Quensen, 1981; Rose, 1989). The consensus is that *Cerion* may consume vascular plants on which they are attached (Mayr and Rosen, 1956) or eat such epiphytes as mold, lichen, and fungi (Bartsch, 1920; Quensen, 1981; Rose, 1989). In captivity, *Cerion* are known to consume paper (Bartsch, 1920; Mayr and Rosen, 1956), cornmeal, and other vegetable products (Bartsch, 1920).

Previous Land Snail Isotopic Studies

Carbon Isotopes.—Previous studies have demonstrated that $^{13}\text{C}/^{12}\text{C}$ ratios in snail shell carbonate are influenced primarily by diet and can provide valuable paleoenvironmental information regarding the relative distribution of C_3 and C_4 plants consumed by the organism (Goodfriend and Hood, 1983; Goodfriend and Magaritz, 1987; Goodfriend, 1999; Goodfriend and Ellis, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan et al., 2005a, 2005b). Studies of raised land snails reveal a clear diet effect on shell carbonate $\delta^{13}\text{C}$ with little to no influence from ingested CaCO_3 (Stott, 2002; Metref et al., 2003). Contrary to the findings of Goodfriend and Hood (1983), the relative contribution of atmospheric CO_2 to shell $\delta^{13}\text{C}$ does not appear to increase significantly with decreasing shell volume (Stott, 2002; Metref et al., 2003). Consequently, shell carbonate of land snails feeding exclusively on C_4 plants (e.g., tropical grasses; mean $\delta^{13}\text{C} = -13.5 \pm 1.5\text{‰}$) will be enriched in ^{13}C relative to snails with a diet of exclusively C_3 plants (e.g., trees and shrubs; mean $\delta^{13}\text{C} = -28.1 \pm 2.5\text{‰}$; see O'Leary, 1981; Goodfriend and Magaritz, 1987; Goodfriend and Ellis, 2002; Stott, 2002; Metref et al., 2003; Balakrishnan and Yapp, 2004). *Cerion* shell isotope composition has the potential to resolve the diet of modern *Cerion* while concomitantly establishing a foundation for the study of fossil *Cerion* to reconstruct paleovegetation distribution on San Salvador.

Oxygen Isotopes.—Several studies have explored the link between local climate and the oxygen isotope composition of land shell carbonate (Yapp, 1979; Magaritz and Heller, 1980; Magaritz et al., 1981; Lécolle, 1985; Goodfriend et al., 1989; Leng et al., 1998; Goodfriend and Ellis, 2002; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a, 2005b; Zanchetta et al., 2005). The primary influence on shell carbonate $\delta^{18}\text{O}$ is the $\delta^{18}\text{O}$ of local environmental water, including atmospheric water vapor (Magaritz et al., 1981; Magaritz and Heller, 1983; Goodfriend et al., 1989; Goodfriend, 1991; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005b), local relative humidity (Balakrishnan and Yapp, 2004), local temperature (Balakrishnan et al., 2005b), and the $\delta^{18}\text{O}$ of local meteoric precipitation (Yapp, 1979; Lécolle, 1985; Goodfriend and Magaritz, 1987; Goodfriend, 1991; Leng et al., 1998; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005b; Zanchetta et al., 2005).

Simple flux balance models combining the effects of temperature, relative humidity, water vapor, and the $\delta^{18}\text{O}$ of liquid water ingested by the snail have predicted shell $\delta^{18}\text{O}$ values (Balakrishnan and Yapp, 2004). Lécolle (1985) demonstrated that shell carbonate $\delta^{18}\text{O}$ and the annual mean $\delta^{18}\text{O}$ value of meteoric precipitation in French maritime and alpine regions covary (Lécolle, 1985). Comparison of coastal to inland snail populations in the Levant region of Israel revealed a geographic correlation between the $\delta^{18}\text{O}$ of rainwater and shell carbonate $\delta^{18}\text{O}$ (Goodfriend and Magaritz, 1987). In nearly all studies, shell carbonate is heavier than local rainwater by $<2\text{‰}$ – 8‰ (Lécolle, 1985; Goodfriend and Magaritz, 1987; Sharpe et al., 1994).

Though seasonality in temperature is muted in tropical regions, such

islands as San Salvador can experience pronounced seasonality in rainfall. Therefore, this study also examines the extent that *Cerion* shell carbonate reflects variability in rainfall and other moisture-driven systems related to San Salvador's numerous inland lakes.

Geologic Setting

San Salvador is an isolated carbonate platform island, 11 km wide (east to west) and 19 km long (north to south), located on the northeastern edge of the Bahamian archipelago ($24^\circ 01' 44'' \text{N}$; $74^\circ 29' 36'' \text{W}$; Fig. 1A). San Salvador's topography is dominated by lithified Pleistocene and Holocene eolian ridges reaching elevations up to 40 m (above sea level) and low interdune areas occupied by inland hypersaline lakes (Erdman et al., 1997; Fig. 1B). Freshwater lenses supplied by rainwater underlie San Salvador's eolian ridges. Water from these lenses drains into hypersaline inland lakes where it later evaporates (Davis and Johnson, 1990). These inland lakes are either seep fed by adjacent freshwater lenses or conduit fed by a direct connection to ocean water via dissolution conduits (Davis and Johnson, 1990). Inland lakes that are seep fed exhibit typically twice the salinity of ocean water owing to evaporation effects, while conduit-fed lakes exhibit salinities similar but slightly higher than ocean water (Davis and Johnson, 1990). Examples of seep-fed inland lakes are the northern portion of Little Lake, Great Lake, and Stouts Lake (Fig. 1B). The lower portion of Little Lake is also conduit fed (Davis and Johnson, 1990).

Climatic Setting

Temperature.—The length of the Bahamian Archipelago and its geographic position induces regional variations in weather and climate for individual islands (Shaklee, 1996). Latitude, ocean temperatures, ocean currents, prevailing winds, hurricane activity, and seasonally migrating high- and low-pressure systems affect the climate on San Salvador Island. San Salvador experiences only minimal annual temperature variations (6°C) between the coolest mean monthly temperature (22°C) in January/February and the warmest mean monthly temperature (28°C) in July/August based on climate data collected from 1921 to 1981 (Shaklee, 1996).

Precipitation.—The dry season occurs between January and March with most days receiving only trace precipitation in the form of isolated storms and evening rains, based on San Salvador island rainfall records from 1921 to 1999 (compiled from the Bahamas Department of Meteorology, Headquarters, Nassau Bahamas; Bahamian Field Station, San Salvador, Bahamas; and Shaklee, 1996). The wet season begins in April and reaches an annual maximum in October, interrupted only by a brief mid-summer dry period (Fig. 2A). The rainfall variation commonly observed during the peak of the rainy season is primarily due to hurricanes and tropical storms (Shaklee, 1996).

San Salvador mean monthly rainwater $\delta^{18}\text{O}$ values (Fig. 2A) range from -4.4‰ to -1.2‰ VSMOW (Vienna Standard Mean Ocean Water; $\sigma = 1.1\text{‰}$ amount-weighted annual mean = -3.4‰) and were calculated using the Online Isotopes in Precipitation Calculator (Bowen and Wilkinson, 2002; Bowen and Revenaugh, 2003). The model is based on an algorithm that uses data from the Global Network for Isotopes in Precipitation database (IAEA/WMO, 2006) and incorporates the primary factors controlling isotopes in precipitation (e.g., Rayleigh distillation, latitude, altitude, and vapor-transport pathways; see Rozanski et al., 1993). Comparison of model-generated San Salvador rainwater $\delta^{18}\text{O}$ data to measured mean monthly rainfall amount data reveals the relatively strong control ($r^2 = 0.68$) of the amount effect—an inverse relationship between rainwater $\delta^{18}\text{O}$ and rainfall amount (Dansgaard, 1964; Yapp, 1982; Rozanski et al., 1993) on San Salvador precipitation $\delta^{18}\text{O}$. From 1994 to May 1999, when the snails were collected live for this study, total annual rainfall decreased from 1333 mm in 1994 to 669 mm in 1998 (Fig. 2B), precipitation varied seasonally as well as interannually (Fig.

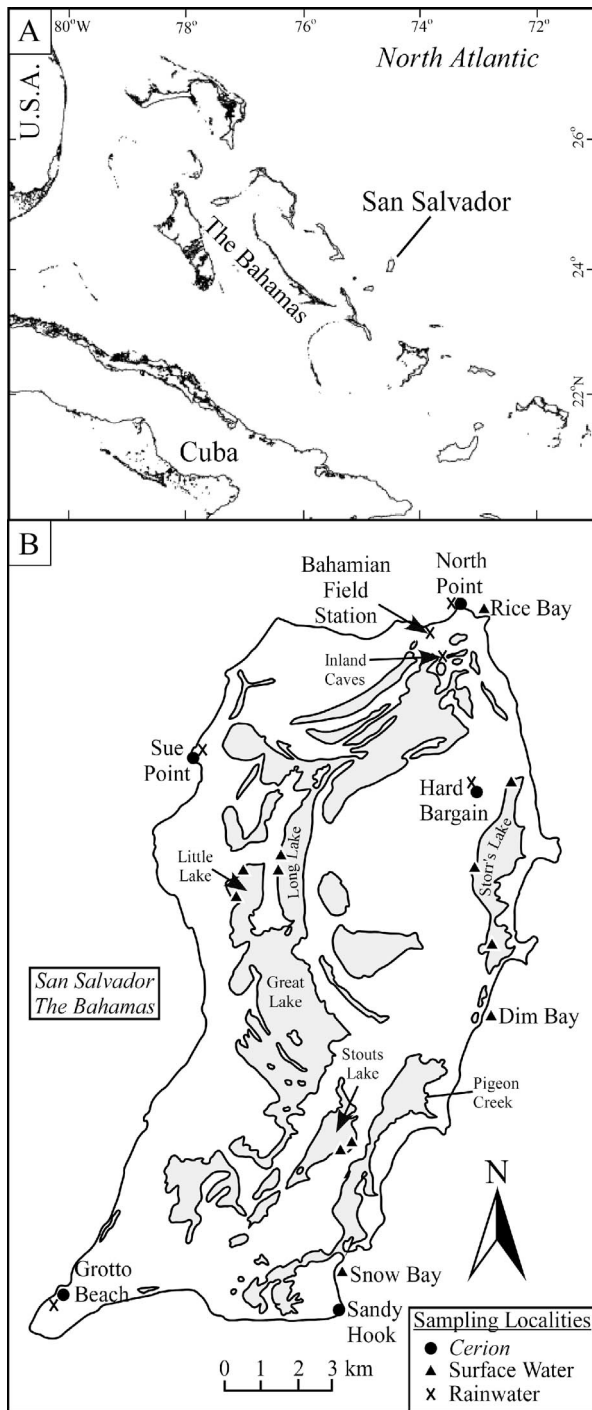


FIGURE 1—Schematic map of the study area. A) Map of the Bahamian Archipelago with San Salvador Island located on the northeastern edge. B) Map of San Salvador showing locations where *Cerion*, surface water, and rainwater samples were collected for this study (modified from Fronabarger et al., 1997).

2C), and mean annual potential evapotranspiration exceeded precipitation throughout the life cycle of the snails.

Wind Patterns.—San Salvador's wind patterns are primarily controlled by the Northeast Trade winds, with 81% of total winds originating from an easterly direction (Shaklee, 1996). The primary wind direction fluctuates north and south in response to seasonal variations in the location of the Bermuda High. Winds from the west are rare and are storm generated. During the dry season from late winter to spring, the Doldrums

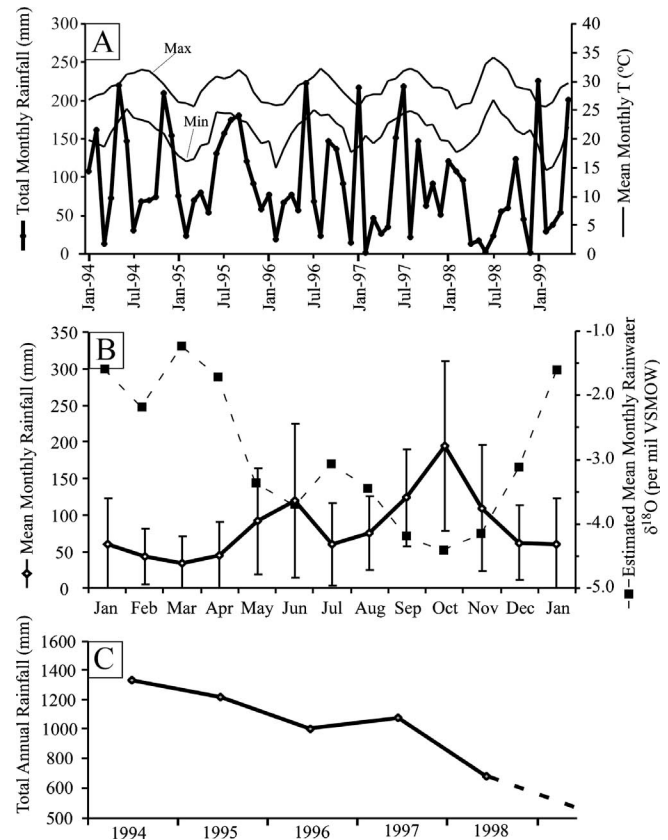


FIGURE 2—San Salvador Climate Data. A) Total monthly rainfall amounts (mm) and mean monthly maximum and minimum temperatures (°C) for the period from January 1994 to May 1999. B) Mean monthly rainfall amounts (mm) on San Salvador for the periods 1921–1981 and 1994–1999 plotted together with model-generated mean monthly rainwater $\delta^{18}\text{O}$ values for San Salvador Island (see text). C) Total annual rainfall amounts (mm) recorded from January 1994 to May 1999. VSMOW = Vienna Standard Mean Ocean Water.

are a common condition in which surface winds are minimal and concentrated along the coast (Shaklee, 1996).

Sample Localities

Living *Cerion* were collected from four coastal locations and one inland location on the island of San Salvador (Fig. 1B). These locations were chosen based on the abundance of *Cerion* and the diversity of plant species associated with them (see Supplementary Data 1¹). The North Point locality, located on the northeastern (windward) coast of the island (Fig. 1B), is a steep-sided eolianite peninsula with rocky, karstified substrate, scattered areas of sandy soil, and low-lying vegetation of the Coastal Rock Community (Smith, 1993). The Hard Bargain locality is about 2 km inland from the central eastern coast of the island (Fig. 1B). It is the only inland sample locality and is characterized by extensively karstified eolianite ridges and dense vegetation of the Blackland Community, resulting in higher humidity and reduced evaporation relative to coastal sites (Smith, 1993). The Sandy Hook locality, on the southeastern coast of the island (Fig. 1B), is characterized by open sandy areas with scattered vegetation of the *Coccothrinax*-shrub Subcommunity within the Coastal Coppice Community (Smith, 1993; see Supplementary Data 1–3¹). The Sue Point locality on the western (leeward) coast of San Salvador (Fig. 1B) is characterized by vegetation of the Coastal Thicket Subcommunity within the Coastal Coppice Community (e.g., shrubs and grasses) on the inland side of the locality and vegetation of the Sand Strand and

¹ www.sepm.org/archive/index.html

TABLE 1—Number of adult and juvenile *Cerion* collected from each plant species at each locality.

Plant type	Species	Common name	North Point	Hard Bargain	Sandy Hook	Sue point	Grotto Beach
C ₄	<i>Cenchrus incertus</i>	Coastal Sandspur	3A 1J ^a			3A	
	<i>Sporobolus domingensis</i>	Dominican drop-seed grass			5A 2J	5A 2J	
C ₃	<i>Reynosia septentrionalis</i>	Darling Plum		5A		5A 1J	5A
	<i>Sabal palmetto</i>	Sabel Palm		5A 1J			3A
	<i>Coccoloba wifera</i>	Sea Grape	4A		5A 2J	5A 2J	6A ^b
	<i>Lantana involucrata</i>	Wild Sage		1A		4A 4J	
		TOTAL		8	12	13	31

^a A = Adult; J = Juvenile.

^b One adult *Cerion* collected from *Coccoloba wifera* at the Grotto Beach locality was analyzed sequentially.

Uniola Plant Community (e.g., creeping vines and *Uniola paniculata*, or sea oats) on the seaward side (Smith, 1993). Finally, the sandy substrate of the Grotto Beach locality on the southeastern (leeward) coast of the island (Fig. 1B) supports scattered vegetation of the *Coccothrinax*-shrub Subcommunity on the inland side of the locality and Sand Strand and *Uniola* Community on the seaward side (Smith, 1993). *Cerion* were collected on the seaward side of this site.

MATERIALS AND METHODS

Sample Collection and Analysis

Cerion.—In May 1999, live *Cerion* were collected from six plant species (two C₄- and four C₃-type plants) that occurred at more than one sampling locality (Table 1, Fig. 3). When present, a minimum of five adult *Cerion* of approximately equivalent size (e.g., 9 ± 1 whorls), were collected from each plant at each locality, resulting in a total of 64 adult *Cerion* sampled for this study. Juvenile *Cerion* were scarce at most localities, thus relatively few samples were collected. A total of 15 shell carbonate samples of juvenile *Cerion* were collected, including live snails, whole dead snails, and the last-deposited carbonate of living snails, breaking off of the most recent shell growth from the juvenile shell (Table 1). All juveniles observed and collected in this study were of approximately equivalent size (4 ± 1 whorls and a protoconch). No juveniles were observed at the Grotto Beach locality.

To verify the isotopic composition of the snails' potential food source, 28 plant organ samples in association with *Cerion* were collected and analyzed, including grass-blade, whole-leaf, leaf-epidermis, and bark samples. When present, *Cerion* feces samples (n = 4) were also collected and isotopically analyzed to further verify the *Cerion* diet. All samples were kept frozen between the time of collection and analysis.

A total of 69 whole-shell carbonate samples—63 adult and 6 juvenile—and 9 last-deposited juvenile shell carbonate samples were analyzed for δ¹³C and δ¹⁸O. In preparation for whole-shell isotopic analysis, frozen *Cerion* were thawed in a desiccator overnight. Once the soft parts were extracted, each shell was placed in a beaker of 30% H₂O₂ solution and heated for 10 hours at 70°C in a warming oven to remove shell organic matter and all foreign contamination (after Magaritz and Heller, 1983). Shells were then rinsed with deionized water and dried in a vacuum oven at 70°C for 15 minutes. Whole-shell samples were pulverized using a mortar and pestle until homogenous, and a 10 mg aliquot was obtained for isotope analysis. Last-deposited juvenile shell samples were also pulverized, and each entire sample was used for isotopic analysis. Shell samples were placed in reaction vessels containing 100% H₃PO₄ and, once under vacuum, allowed to react with the acid at a constant temperature of 50°C for 2 hours (McCrea, 1950). The ¹³C/¹²C and ¹⁸O/¹⁶O ratios of the evolved CO₂ were determined using a Finnegan-MAT model Delta E mass spectrometer. A phosphoric acid fractionation factor (α = 0.990780597) was used to determine δ¹⁸O (Sharma and Clayton, 1965). The carbon and oxygen isotope compositions are reported

per mil (‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard (Craig, 1957) as delta (δ) according to the following equations:

$$\delta^{13}\text{C} = \frac{(^{13}\text{C}/^{12}\text{C}) \text{ sample} - (^{13}\text{C}/^{12}\text{C}) \text{ standard}}{(^{13}\text{C}/^{12}\text{C}) \text{ standard}} \times 1000, \quad (1)$$

and

$$\delta^{18}\text{O} = \frac{(^{18}\text{O}/^{16}\text{O}) \text{ sample} - (^{18}\text{O}/^{16}\text{O}) \text{ standard}}{(^{18}\text{O}/^{16}\text{O}) \text{ standard}} \times 1000. \quad (2)$$

The precision of whole-shell δ¹³C and δ¹⁸O analyses was ±0.04‰ and ±0.06‰, respectively, based on six replicate analyses of the University of Georgia working standard for carbonate.

One adult *Cerion* shell was retained for sequential-rib analysis to determine the degree to which δ¹³C and δ¹⁸O values vary through ontogeny. Gastropod shells that lack apparent growth lines or regular ornamentation are sampled typically at fixed intervals of ≥1.5 mm, depending on shell size, along the whorls following ontogenetic growth from the apex to the aperture (Jones and Allmon, 1995; Purton and Brasier, 1997; Leng et al., 1998). *Cerion* shells, however, are ornamented by a series of well-defined ribs that increase in size, and consequently spacing, through ontogeny (Fig. 4A). Alternating ribs and troughs precluded fixed interval sampling because one sample might constitute a rib and another a trough, unnecessarily introducing noise to the data. We chose ribs instead of troughs because the shell material is isolated from the animal and thus less prone to resorption (Fig. 4B). Thus, shell ribs were analyzed sequentially from terminal lip to protoconch to determine δ¹³C and δ¹⁸O variations throughout shell growth.

Sample preparation was similar to that for whole-shell analysis, but we desiccated the organism in lieu of removing it with tweezers to avoid damaging the integrity of the ribs. The shell was then placed in 30% H₂O₂ at 70°C for 10 hours to remove organic matter, rinsed with deionized water, and dried in a vacuum oven at 70°C for 15 minutes. We took special care not to contaminate rib samples with material from adjacent troughs or the next rib in the sequence. A shell carbonate sample was obtained along the length of each rib using a dental drill with a 0.4 mm drill bit. Ribs were sequentially drilled starting with the rib adjacent to the terminal lip and proceeding helically to the protoconch (Fig. 4A). A total of 150 ribs (whorls 1–6) were individually drilled; shell carbonate samples varied in weight from 0.8 mg near the terminal lip to negligible weights (i.e., below the sensitivity of the scale) closer to the protoconch. Ribs 151 (whorl 6) to rib 170 (whorl 7) were sampled in pairs to increase the volume of shell carbonate and thus the precision of mass spectrometer readings. The remaining ribs from rib 171 (whorl 7) to the protoconch were divided into eight composite samples of relatively equal volume. Ribs toward the protoconch were poorly defined and, in some cases, indistinguishable. Therefore, each composite sample was estimated to represent eight ribs resulting in a rib count for the entire shell of ~234.

We reacted sequential-rib samples with 100% H₃PO₄ following the



FIGURE 3—*Cerion* on five of the six plant species from which they were collected for this study. White arrows point to living *Cerion*. A) *Cerion* on the C_4 plant *Sporobolus domingensis* at the Sue Point locality. B) *Cerion* on the C_4 plant *Cenchrus incertus* at the Sue Point locality. C) *Cerion* on the C_3 plant *Reynosia septentrionalis* at the Sue Point locality. D) *Cerion* on the C_3 plant *Sabal palmetto* at the Hard Bargain locality. E) *Cerion* on the C_3 plant *Coccoloba uvifera* at the Sue Point locality.

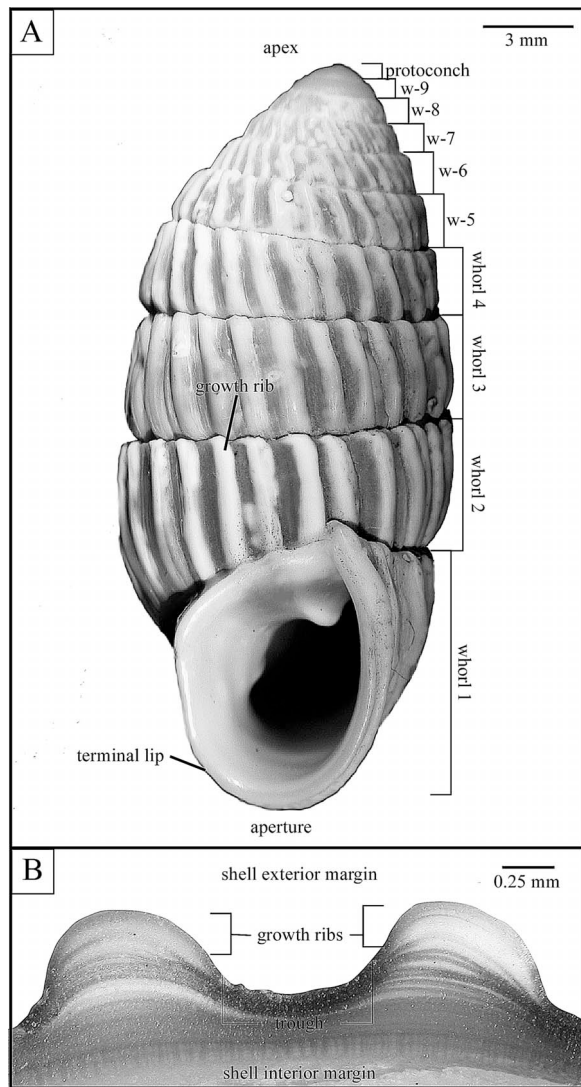


FIGURE 4—Anatomy of a San Salvador *Cerion* shell. A) External shell features include well-defined growth ribs and nine whorls between the aperture and protoconch. Sequential-rib analysis started with the first rib adjacent to the terminal lip and proceeded helically toward the protoconch. B) Internal features of a cross-sectioned *Cerion* shell. Sampling restricted to material identified as growth ribs in order to avoid material prone to resorption near the interior shell margin.

same technique described for whole-shell samples and determined the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values using a Finnegan-MAT 252 mass spectrometer. The precision of all sequential-rib carbonate analyses for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is $\pm 0.14\text{‰}$ and $\pm 0.03\text{‰}$, respectively, based on 15 replicate analyses of the University of Georgia working standard for carbonate.

Vegetation.—To verify the isotopic composition of the snails' potential food source, we obtained $\delta^{13}\text{C}$ values of whole-leaf samples from two plants with the C_4 photosynthetic pathway (*Cenchrus incertus* and *Sporobolus domingensis*) and various plant organs (i.e., whole leaf, leaf epidermis, and bark) from four plants with the C_3 photosynthetic pathway (*Reynosa septentrionalis*, *Sabal palmetto*, *Coccoloba wifera*, and *Lantana involucrata*). Because the *Cerion* diet is largely uncertain, we analyzed specific plant organs to determine the amount of carbon isotope variation within individual plants. (Variations of up to a few tenths per mil have been previously observed between plant organs; see O'Leary, 1981.) Additionally, we characterized plant tissue as living or nonliving at the time of collection. We photographed all plants and confirmed field identifications using Correll and Correll (1982), Kass (1991), and Smith (1993).

We analyzed all vegetation samples for total percent carbon and $\delta^{13}\text{C}$ relative to the VPBD standard. Prior to analysis, vegetation samples were dried in a drying oven at 80°C for 24 hours and then ground using a Spex Industries 8000 ball mill to less than $250\ \mu\text{m}$ particle size. Homogenized samples weighing $<2\ \text{mg}$ each were then transformed to gas phase by flash combustion, and the $\delta^{13}\text{C}$ value of the ionized combustion product (CO_2) was determined using a Total Nitrogen & Carbon Elemental Analyzer connected to a Finnegan-MAT Delta C mass spectrometer. The precision of vegetation $\delta^{13}\text{C}$ analyses is $\pm 0.1\text{‰}$ based on 14 replicate analyses of the University of Georgia bovine standard for vegetation.

Precipitation and Surface Water.—Because no direct measurements of San Salvador precipitation $\delta^{18}\text{O}$ values existed, we tried to collect samples from as many rain events as possible during the brief field visits in May 1999 ($n = 10$) and January 2000 ($n = 7$; see Fig. 1B). In December 2000, a total of 14 surface water samples were collected from San Salvador water bodies to determine if the island's hypersaline lakes were enriched in ^{18}O relative to ocean water. We obtained samples from four inland lakes (Storr's Lake, Little Lake, Long Lake, and Stouts Lake), one tidal creek (Pigeon Creek), and three eastern bays (Rice Bay, Dim Bay, and Snow Bay; see Fig. 1B).

We collected rainwater samples from five locations on San Salvador (Fig. 1B) using 60 ml bottles equipped with 10-cm-diameter funnels. Gaps between the funnel and bottle opening were sealed with tape, and samples were collected within 24 hours of each rain event to minimize fractionation due to evaporation. All water samples were transferred to airtight low-density polyethylene bottles that were filled to the top, leaving no airspace, and refrigerated prior to analysis. Water samples were prepared according to standard laboratory procedures for oxygen extraction from water using equilibration with CO_2 . Using a clean, dry syringe, we extracted 1.2 ml of water from the storage container and injected the water sample into an evacuated vial filled with CO_2 gas. We then placed samples in a shaker bath at 25°C for <3 hours and allowed them to equilibrate. We analyzed samples using the Finnegan-MAT model Delta E mass spectrometer to determine the oxygen isotope composition relative to Vienna Standard Mean Ocean Water (VSMOW) according to equation (2) above. The precision of all water analyses was $\pm 0.35\text{‰}$ based on six replicate analyses of the University of Georgia working standard for water.

RESULTS

Whole-Shell Analysis

Carbon Isotopes.—The $\delta^{13}\text{C}$ from whole-shell analysis (see Supplementary Data 2¹) of 63 adult *Cerion* ranges from -6.9‰ to 1.7‰ with a mean of -3.4‰ (Figs. 5A–F). Adult *Cerion* collected from C_4 plants exhibit a higher mean $\delta^{13}\text{C}$ and a broader range of $\delta^{13}\text{C}$ values (min = -6.5‰ , max = 1.7‰ , mean = -1.9‰ , $\sigma = 2.7\text{‰}$; Figs. 5A–B) than adult *Cerion* collected from C_3 plants (min = -6.9‰ , max = -0.7‰ , mean = -3.9‰ , $\sigma = 1.3\text{‰}$; Figs. 5C–F). The $\delta^{13}\text{C}$ values of the plants from which *Cerion* were collected are presented later. A Student t-test of the means assuming unequal variances (based on the results of an F-test) confirmed that the mean $\delta^{13}\text{C}$ of *Cerion* shell carbonate collected from C_4 plants and the mean $\delta^{13}\text{C}$ of *Cerion* shell carbonate collected from C_3 plants are significantly different ($p = 0.01$). Mean $\delta^{13}\text{C}$ values used in the Student t-tests comprised all adult *Cerion* collected from each plant type (C_3 and C_4) regardless of plant species and sample location. No geographic trend in $\delta^{13}\text{C}$ of *Cerion* shell carbonate is apparent at a 95% confidence level. For example, 95% confidence intervals calculated for the mean $\delta^{13}\text{C}$ values of *Cerion* collected from the same plant species at different sample localities were overlapping and thus revealed no significant difference between sample groups.

Juvenile *Cerion* $\delta^{13}\text{C}$ values range from -7.1‰ to 1.1‰ with a mean of -2.9‰ ($\sigma = 2.2\text{‰}$) for whole-shell and last-deposited carbonate (Figs. 5A–F; Supplementary Data 2¹). Juvenile *Cerion* collected from C_4

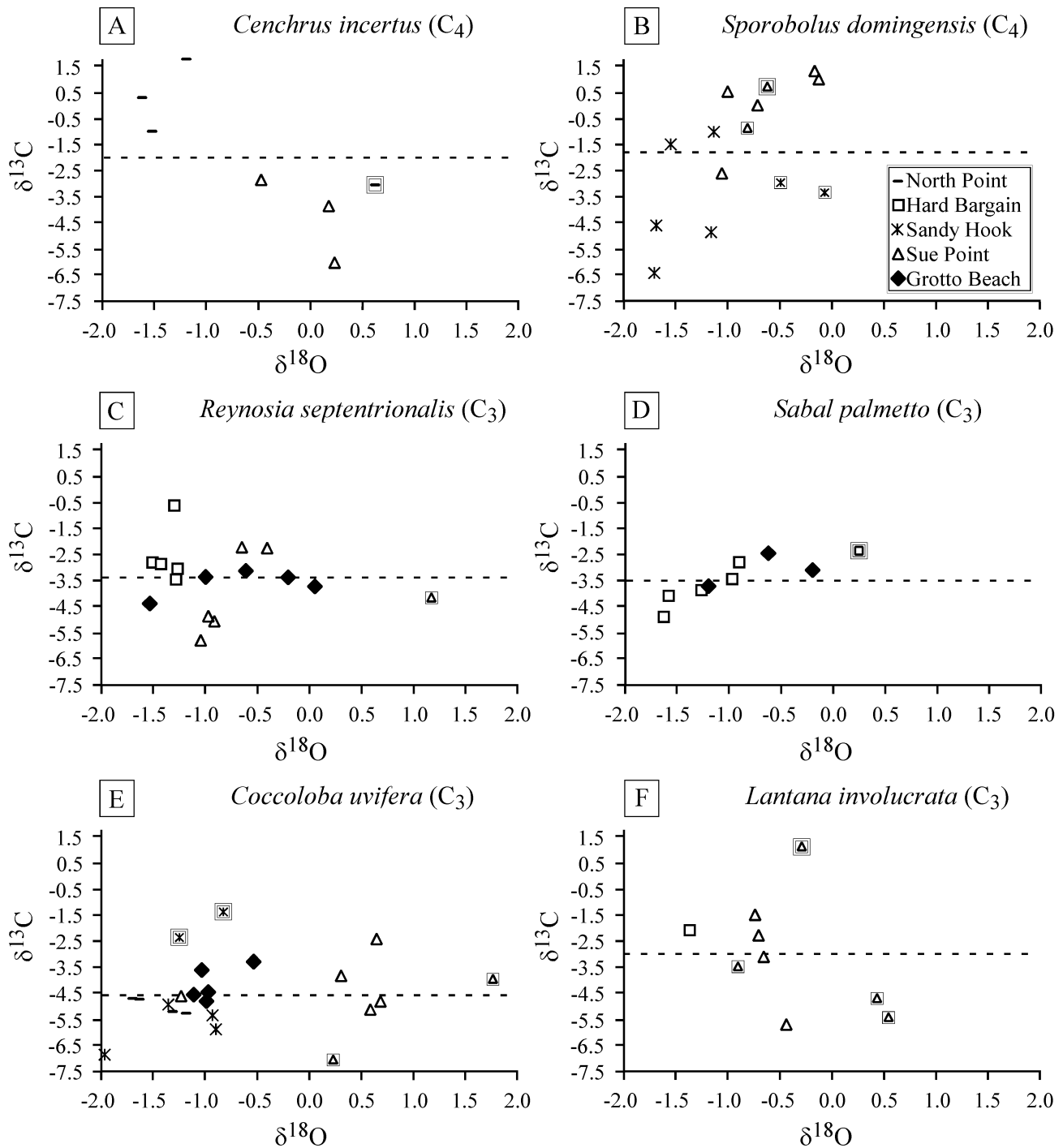


FIGURE 5—The $\delta^{13}\text{C}$ values of *Cerion* shell carbonate from each of the six host plants sampled. C_4 plants: A) *Cenchrus incertus*, B) *Sporobolus domingensis*. C_3 plants: C) *Reynosa septentrionalis*, D) *Sabal palmetto*, E) *Coccoloba uvifera*, F) *Lantana involucrata*. Horizontal dashed lines represent the mean of $\delta^{13}\text{C}$ values of shell carbonate associated with each of the six plant species sampled. Adult *Cerion* from C_4 plants exhibit a broader range and higher mean $\delta^{13}\text{C}$ values than *Cerion* collected from C_3 plants. Symbols enclosed within double squares represent whole-juvenile-shell carbonate samples and symbols within single squares represented last-deposited juvenile shell carbonate samples (see text).

plants exhibit $\delta^{13}\text{C}$ values that are within the range observed for adult *Cerion*. A Student t-test to compare the mean $\delta^{13}\text{C}$ of adults ($n = 10$) and juveniles ($n = 4$) collected from the C_4 plant, *Sporobolus domingensis*, confirms this observation ($p > 0.05$). Likewise, juveniles collected from two of the C_3 plants, *Reynosa septentrionalis* and *Sabal palmetto*, exhibit $\delta^{13}\text{C}$ values that are within the range observed for adults from the same plants. Of the 15 juveniles sampled, only three last-deposited juvenile shell carbonate samples exhibit $\delta^{13}\text{C}$ values that are high-

er than the $\delta^{13}\text{C}$ range for the adults, specifically, two juveniles from the C_3 plant, *Coccoloba uvifera*, and one juvenile from the C_3 plant, *Lantana involucrata*. Student t-tests, however, revealed no significant difference between the mean $\delta^{13}\text{C}$ values of juvenile *Cerion* and that of adult *Cerion* collected from *Coccoloba uvifera* or *Lantana involucrata* ($p > 0.05$). The limited number of juveniles ($n \leq 2$) collected from the remaining plants (*Cenchrus incertus*, *Reynosa septentrionalis*, *Sabal palmetto*) precluded the use of Student t-tests to compare the mean $\delta^{13}\text{C}$ values of

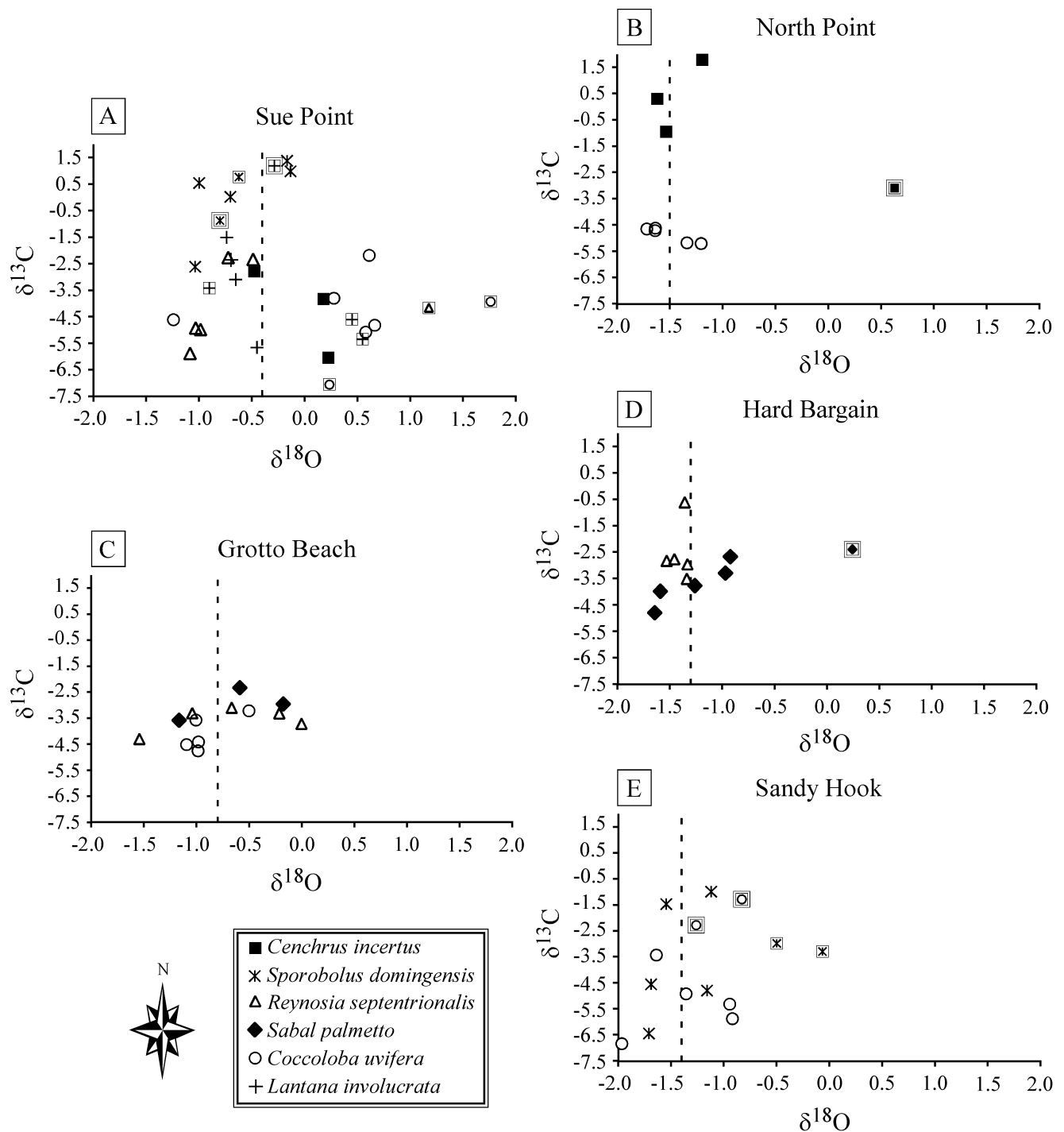


FIGURE 6—The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of *Cerion* shell carbonate from each of the five sampling localities: A) Sue Point, B) North Point, C) Grotto Beach, D) Hard Bargain, E) Sandy Hook. Graphs A–E are arranged according to geographic position on the island, with North Point positioned to the northeast and Grotto Beach to the southwest. Vertical dashed lines represent the mean of $\delta^{18}\text{O}$ values of *Cerion* shells at each locality and reveal higher values for *Cerion* sampled from western localities relative to eastern localities. Symbols enclosed within double squares represent whole-juvenile-shell carbonate samples, and symbols within single squares represent last-deposited juvenile shell carbonate samples (see text).

juveniles to coexisting adults. Finally, the mean $\delta^{13}\text{C}$ value of all whole-juvenile-shell carbonate samples ($n = 6$) is significantly different from that of last-deposited juvenile shell carbonate samples ($n = 9$; Student t -test of equal variances, $p < 0.05$).

Oxygen Isotopes.—The $\delta^{18}\text{O}$ values from whole-shell analysis of 63 adult *Cerion* range from -2.0‰ to 0.7‰ with a mean of -0.9‰ ($\sigma = 0.6\text{‰}$; Figs. 6A–E; Supplementary Data 2¹). The mean $\delta^{18}\text{O}$ value of adult *Cerion* shell carbonate is heavier by 2.5‰ relative to the Online

Isotopes in Precipitation Calculator model-generated weighted-annual mean $\delta^{18}\text{O}$ of San Salvador precipitation (-3.4‰). Mean $\delta^{18}\text{O}$ values of *Cerion* shell carbonate from western localities, Sue Point and Grotto Beach, are -0.4‰ ($\sigma = 0.6\text{‰}$) and -0.8‰ ($\sigma = 0.4\text{‰}$), respectively (Figs. 6A, C). *Cerion* collected from eastern localities—North Point, Hard Bargain, and Sandy Hook—exhibit mean $\delta^{18}\text{O}$ values of -1.5‰ ($\sigma = 0.2\text{‰}$), -1.3‰ ($\sigma = 0.2\text{‰}$), and -1.4‰ ($\sigma = 0.4\text{‰}$), respectively (Figs. 6B, D, E). Contours of mean $\delta^{18}\text{O}$ of shell carbonate illustrate the

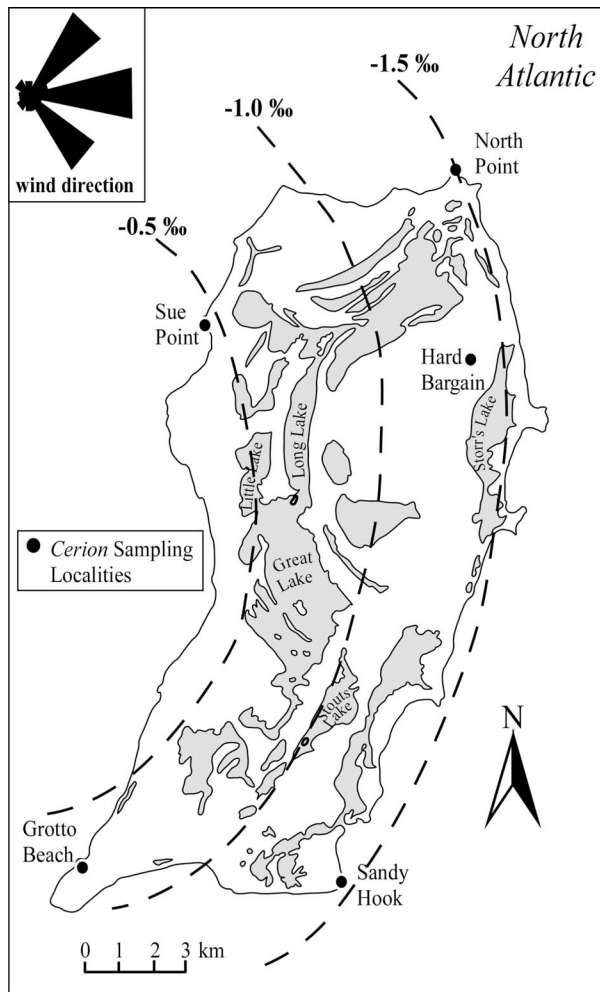


FIGURE 7—Contours of mean $\delta^{18}\text{O}$ values of adult *Cerion* shell carbonate illustrating a trend toward ^{18}O enrichment on the leeward coast of San Salvador relative to the windward coast. The prevailing wind is from the east (Shaklee, 1996).

trend toward ^{18}O enrichment on the west (leeward) side of the island relative to the east (windward) side (Fig. 7). Windward (North Point, Hard Bargain, Sandy Hook) *Cerion* samples are significantly depleted in ^{18}O at the 95% confidence level relative to leeward (Sue Point, Grotto Beach) samples (Fig. 8). No significant difference exists in shell carbonate $\delta^{18}\text{O}$ between leeward sites or in shell carbonate $\delta^{18}\text{O}$ between windward sites.

Juvenile *Cerion* $\delta^{18}\text{O}$ values range from -1.3‰ to 1.8‰ (both from the Sue Point locality) with a mean of 0.0‰ ($\sigma = 0.8\text{‰}$) for whole-shell and last-deposited carbonate (Figs. 6A, B, D, E; Supplementary Data 2¹). A Student t-test of equal variances comparing mean $\delta^{18}\text{O}$ of juvenile *Cerion* at Sue Point to adults at the same locality determined these two groups to be significantly different ($p = 0.05$), with juveniles enriched in ^{18}O relative to adults by an average of 0.6‰ . Juveniles from the Sandy Hook locality were also significantly different from adults ($p < 0.01$), with $\delta^{18}\text{O}$ values higher by an average of 0.7‰ . No Student t-tests were performed to compare adults and juveniles from North Point and Hard Bargain because we collected only one juvenile from each site. Juvenile shells, however, are clearly enriched in ^{18}O relative to adults at both localities (Figs. 6B, D). A Student t-test of equal variances comparing the mean $\delta^{18}\text{O}$ of whole-juvenile-shell carbonate to last-deposited juvenile shell carbonate revealed no significant difference ($p > 0.05$).

Sequential-Rib Analysis

Sequential analysis of ~ 234 ribs from the terminal lip to the protoconch revealed $\delta^{13}\text{C}$ values from -6.5‰ to -1.4‰ with a mean of

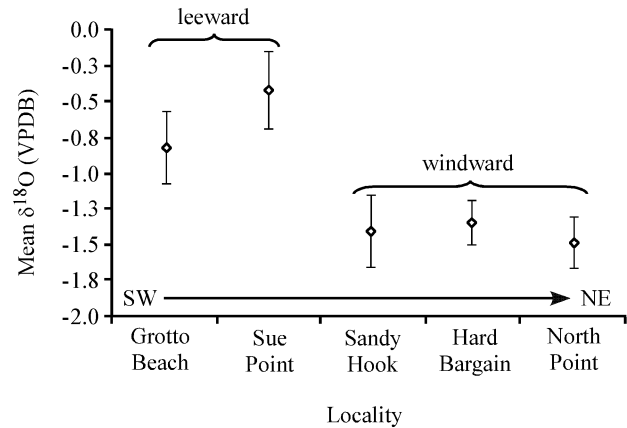


FIGURE 8—Mean $\delta^{18}\text{O}$ values of adult *Cerion* shell carbonate with 95% confidence intervals. The graph shows a clear west to east trend across the island with *Cerion* shell carbonate enriched in ^{18}O on the west (leeward) side relative to shell carbonate collected from the east (windward) side of San Salvador. Mean $\delta^{18}\text{O}$ values represent all adult *Cerion* collected from each location regardless of plant type. VPDB = Vienna Pee Dee Belemnite standard.

-4.6‰ ($\sigma = 0.8\text{‰}$) and $\delta^{18}\text{O}$ values from -3.0‰ to 1.7‰ with a mean of -0.3‰ ($\sigma = 0.9\text{‰}$; see Fig. 9; Supplementary Data 3¹). The mean $\delta^{18}\text{O}$ of sequentially analyzed ribs is consistent with, but slightly higher than, the mean $\delta^{18}\text{O}$ from whole-shell analysis of the five remaining *Cerion* collected from the same plant (*Coccoloba wifera* at Grotto Beach; mean = -0.9‰ ; $\sigma = 0.2\text{‰}$). Ribs closer to the aperture (i.e., whorls 1–3) are consistently enriched in ^{18}O relative to this mean. The mean $\delta^{13}\text{C}$ of sequentially analyzed ribs is slightly lower than that observed for the remaining five *Cerion* from the same plant (mean = -4.2‰ ; $\sigma = 0.7\text{‰}$).

Vegetation and *Cerion* Feces Analysis

The $\delta^{13}\text{C}$ values of vegetation in association with *Cerion* range from -28.8‰ to -11.9‰ . Plant organ $\delta^{13}\text{C}$ values varied by less than 2.0‰ between samples taken from the same plant (Fig. 10). The $\delta^{13}\text{C}$ values of grass-blade samples obtained from *Cenchrus incertus* and *Sporobolus domingensis* range from -13.3‰ to -11.9‰ , falling within the expected range for C_4 plants. The $\delta^{13}\text{C}$ values of various plant organs from *Reynosia septentrionalis*, *Sabal palmetto*, *Coccoloba wifera*, and *Lantana involucrata* range from -28.8‰ to -24.7‰ , within the expected values for C_3 plants. Four *Cerion* feces samples exhibited $\delta^{13}\text{C}$ values from -25.6‰ to -23.0‰ . Although one feces sample was collected from the C_4 plant *Sporobolus domingensis*, all feces samples exhibited $\delta^{13}\text{C}$ values typical of a C_3 plant diet (Fig. 10).

Water Analysis

The $\delta^{18}\text{O}$ values of 10 rainwater samples collected in May 1999 range from -4.1‰ (Inland Caves) to 0.3‰ (Sue Point) with a mean of -2.3‰ (Fig. 1B; also see Supplementary Data 4¹). Rainwater samples ($n = 7$) collected in January 2000 yielded $\delta^{18}\text{O}$ values from -5.7‰ (Bahamian Field Station) to -1.1‰ (Hard Bargain) with a mean of -5.2‰ . The mean $\delta^{18}\text{O}$ values of rainwater collected from eastern and western locations demonstrate no significant difference between samples collected during the same month (Student t-test of equal variance, $p = 0.5$).

Inland-lake $\delta^{18}\text{O}$ values ranged from -1.3‰ (lower Storr's Lake) to 1.5‰ (middle Long Lake; see Fig. 1B). Tidal creek samples obtained from upper and middle Pigeon Creek exhibited a consistent $\delta^{18}\text{O}$ value of 0.6‰ . The $\delta^{18}\text{O}$ values of ocean water samples obtained from Rice Bay in the northeast, Dim Bay to the east, and Snow Bay to the southeast were 1.0‰ , 1.0‰ , and 0.9‰ , respectively. The $\delta^{18}\text{O}$ values of lake samples from the western interior of San Salvador are higher by as much as 0.6‰ relative to ocean water obtained from eastern bays.

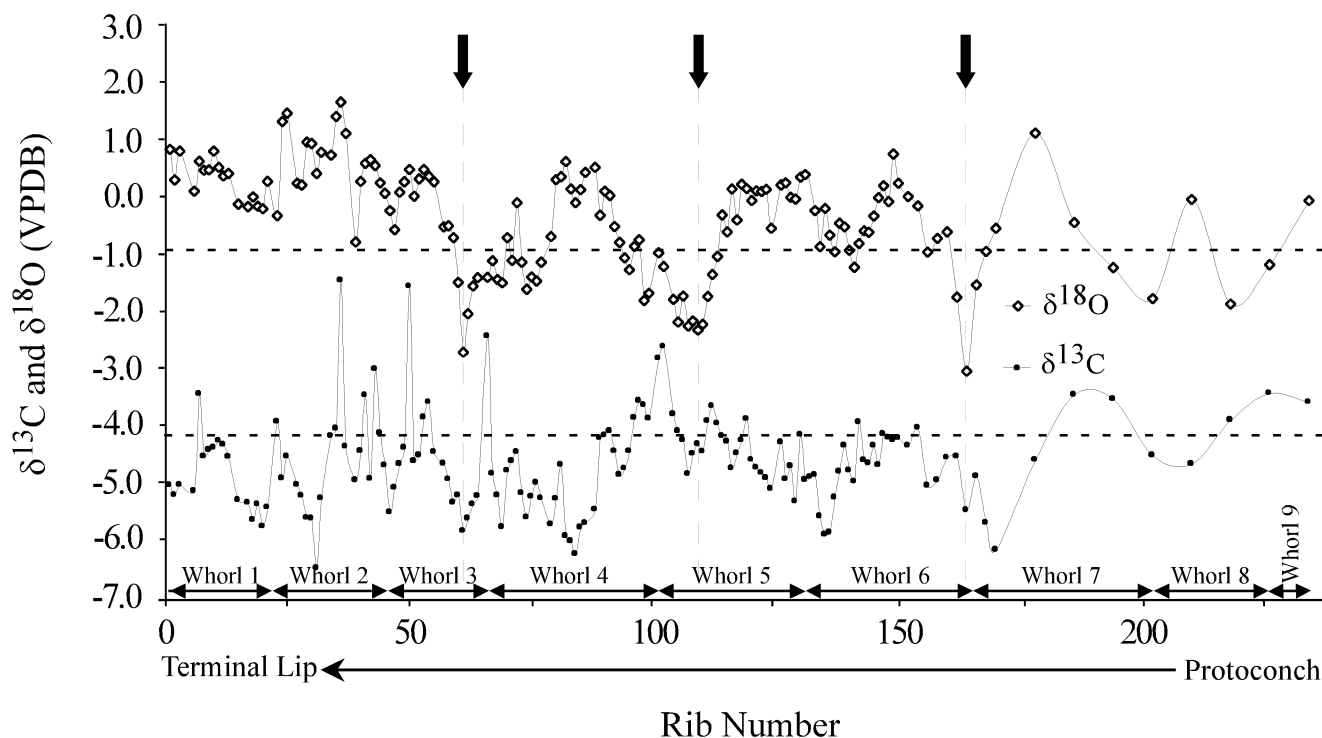


FIGURE 9—Carbon and oxygen isotope profile of ~234 consecutive ribs from the terminal lip to the protoconch (1–150: individual ribs; 151–170: rib pairs; 171–234: eight-rib composites) of one adult *Cerion* collected from *Coccoloba uvifera* at Grotto Beach. Horizontal dashed lines represent the mean $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values from whole-shell analysis of the five remaining *Cerion* collected from the same plant. Black arrows and vertical dashed lines correspond to three of the lowest $\delta^{18}\text{O}$ values in the profile that may represent shell deposition during the month of greatest rainfall, October. VPDB = Vienna Pee Dee Belemnite standard.

DISCUSSION

Shell Carbonate $\delta^{13}\text{C}$ and the *Cerion* Diet

Previous studies on the isotopic ecology of modern land snails living in their natural environment have reported $\delta^{13}\text{C}$ values of shell carbonate from -13.5‰ to 0.5‰ (Yapp, 1979; Magaritz and Heller, 1980; 1983; Magaritz et al., 1981; Lecolle, 1983; 1984; Goodfriend and Magaritz,

1987; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005b). In this study, $\delta^{13}\text{C}$ of adult land snails ranged from -6.9‰ to 1.7‰ , extending the upper limit of globally distributed land snail $\delta^{13}\text{C}$ by 1.2‰ . *Cerion* shell carbonate $\delta^{13}\text{C}$ values, however, are within the range (-24.3‰ to 2.5‰) observed for experimentally raised *Helix aspersa* that were fed diets of known C_3 and C_4 isotopic composition (Stott, 2002). The highest $\delta^{13}\text{C}$ value of 2.5‰ was recorded for a corn-fed snail (i.e., pure C_4 plant diet).

In this study, $\delta^{13}\text{C}$ values of *Cerion* collected from C_4 plants (Figs. 5A–B) were elevated by an average of 1‰ relative to *Cerion* collected from C_3 plants (Figs. 5C–F). Although the data suggest that half of *Cerion* sampled from C_4 plants fed predominantly on C_4 plants, the relatively broad range of $\delta^{13}\text{C}$ values suggests a mixed diet ($\text{C}_3 + \text{C}_4$ plants). This interpretation is supported by the results from feces analysis, in which *Cerion* feces collected from *Sporobolus domingensis* (C_4 plant) exhibited a carbon isotope signature more typical of a C_3 plant. Elevated $\delta^{13}\text{C}$ values (by 2‰ – 3‰) characterize snails living in mixed C_3 and C_4 plant communities relative to snails from pure C_3 plant communities (Goodfriend and Magaritz, 1987). In a study of experimentally raised snails (*Helix aspersa maxima*), Metref et al. (2003) found that snails fed a mixed diet (C_3 and C_4) were enriched by 2‰ relative to snails fed a pure C_3 plant diet. These results, however, were not consistent for all groups fed a mixed diet. Of the three groups fed a mixed diet, only one group exhibited $\delta^{13}\text{C}$ values more typical of mixed feeders, while the other two groups reflected a C_3 -dominated diet. Similar selective feeding patterns were observed in the Great Plains, USA, where snails were reported to favor certain grass species over others (Goodfriend and Ellis, 2002).

Adult *Cerion* collected from C_3 plants exhibit lower $\delta^{13}\text{C}$ values with a narrower range than *Cerion* collected from C_4 plants. Individuals collected from *Sabal palmetto* at the Grotto Beach and Hard Bargain localities exhibit the narrowest range of $\delta^{13}\text{C}$ values (2.4‰ ; Fig. 5D). The dominance of C_3 plants at both localities may explain this range (see Supplementary Data 1¹).

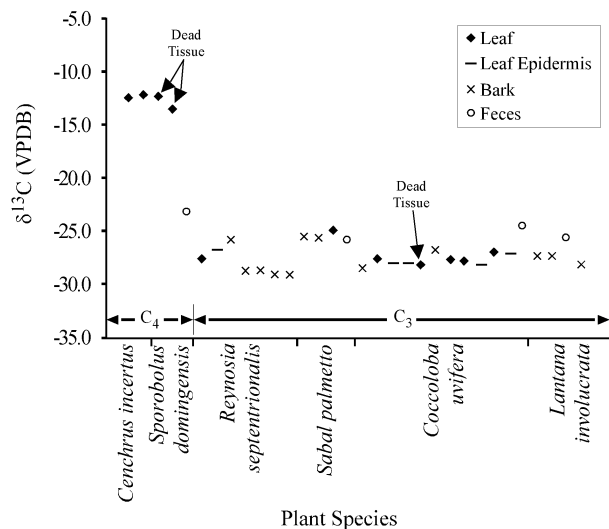


FIGURE 10— $\delta^{13}\text{C}$ values of C_3 and C_4 plants collected during this study. Such different plant tissues as leaf, leaf epidermis, and bark are identified to examine intraplant variations in $\delta^{13}\text{C}$. Arrows identify three samples of dead tissue demonstrating little to no variation in the isotopic signature of living versus necrotic plants. Data from four *Cerion* feces samples are also shown. VPDB = Vienna Pee Dee Belemnite standard.

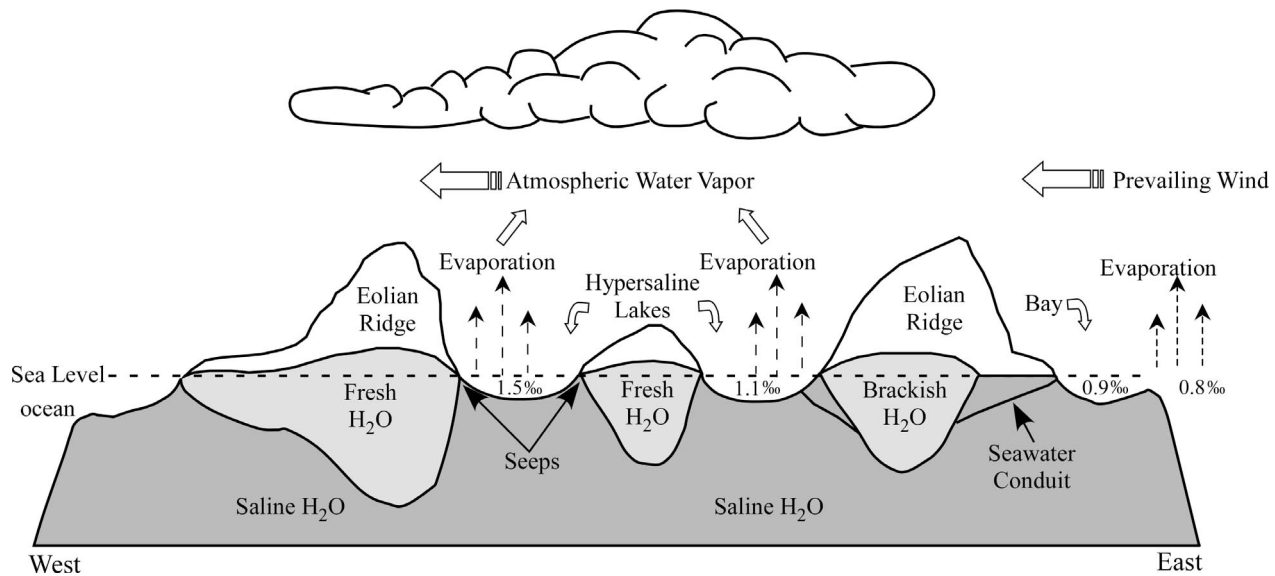


FIGURE 11—General model of San Salvador's hydrological system explaining the proposed inland-lake effect on the $\delta^{18}\text{O}$ of atmospheric water vapor (adapted from Davis and Johnson, 1990). The hypersaline lake on the right is conduit fed and has a $\delta^{18}\text{O}$ signature similar to ocean water. The hypersaline lake on the left is seep fed and is enriched in ^{18}O because of evaporation. Atmospheric water vapor migrates across the island in the direction of prevailing wind. Evaporation from hypersaline lakes results in enrichment of the air mass and the subsequent enrichment of *Cerion* shell carbonate on the west (leeward) side of the island relative to the east (windward) side.

Previous studies have speculated on the diet of *Cerion* (Bartsch, 1920; Mayr and Rosen, 1956; Quensen, 1981; Rose, 1989), and this isotopic study may resolve some of the uncertainties. The results of this study do not rule out the role of such heterotrophs as mold and fungi in the *Cerion* diet. Heterotrophs have carbon isotope signatures that are within 1‰–2‰ of their host plant (DeNiro and Epstein, 1978; Gleixner et al., 1993). A difference of 1‰–2‰ between host plant and saprophyte should have little effect on the correlation observed here because the $\delta^{13}\text{C}$ signature of C_3 and C_4 plants differs by as much as 14‰.

Rose (1989) suggested that *Cerion* also consume lichens. Lichens are symbiotic associations between fungi and photosynthetic autotrophs (algae and cyanobacteria; Douglas, 1994) with highly variable isotopic compositions. The carbon isotope signature of lichens is independent of the host plant because lichens obtain all of their nutrients from photosynthesis (Smith, 1980; Douglas, 1994). Therefore, the observed correlation of shell carbonate $\delta^{13}\text{C}$ values and the plant type (C_3 or C_4) from which *Cerion* were collected does not support a lichen-dominated diet.

Based on the results of this study, lichens do not contribute significantly to the *Cerion* diet. The question remains open, however, whether *Cerion* consume the plant or saprophytic mold or fungi that is growing on the plant. Regardless, *Cerion* reflect the proportion of C_3 and C_4 plants in their habitat, and thus, fossil *Cerion* should prove to be a valuable archive of C_3 and C_4 plant distribution in the past.

Shell Carbonate $\delta^{18}\text{O}$ Relative to Geographic Location

Published $\delta^{18}\text{O}$ values of modern globally distributed land snail shells range from -11.7‰ to 4.5‰ (Yapp, 1979; Magaritz and Heller, 1980; Magaritz et al., 1981; Lecolle, 1985; Goodfriend and Magaritz, 1987; Goodfriend et al., 1989; Sharpe et al., 1994; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005b). The $\delta^{18}\text{O}$ values of *Cerion* shell carbonate obtained in the current study are within the range of this global record. A geographic trend in the $\delta^{18}\text{O}$ of shell carbonate exists for San Salvador *Cerion*. The mean $\delta^{18}\text{O}$ values of adult shells collected from eastern (windward) localities were lower by an average of 0.8‰ compared to western (leeward) localities (Figs. 6A–E). Mean shell carbonate $\delta^{18}\text{O}$ values between eastern localities varied by less than 0.1‰ and between western localities by less than 0.4‰ . San Salvador's prevailing winds originate from the northeast, east, and southeast (Shaklee, 1996; see Fig. 7), and thus, the observed trend toward $\delta^{18}\text{O}$ enrichment westward across

the island is the opposite of that expected from a rainout effect—progressive depletion of precipitation ^{18}O as a moisture mass travels inland (Lécolle, 1985; Goodfriend and Magaritz, 1987; Sharpe et al., 1994). Local rainfall alone cannot explain the geographic trend in the $\delta^{18}\text{O}$ of *Cerion* shell carbonate based on limited event-based rainwater data.

Large inland lakes occupying approximately one-third of San Salvador's land surface may influence *Cerion* shell carbonate $\delta^{18}\text{O}$ values. In most geographic regions with a humid climate, the $\delta^{18}\text{O}$ of atmospheric water vapor is directly related to that of local rainfall (Bonadonna et al., 1999). Atmospheric water vapor ^{18}O enrichment relative to local rainfall can occur, however. Tzur (1971; cited in Goodfriend et al., 1989) observed this phenomenon in Israel, where rainfall is derived from a variety of sources while water vapor is affected locally by evaporation from the Mediterranean Sea. Land snail studies in this region have demonstrated a direct correlation between the isotopic composition of shell carbonate, body water, and local atmospheric water vapor that was slightly enriched in ^{18}O relative to rainwater (Goodfriend et al., 1989). A similar effect is likely on San Salvador because of its oceanic setting and abundance of shallow, hypersaline, and isotopically enriched inland lakes.

Daytime heating and evaporation from the ocean surface create very humid conditions on San Salvador, particularly in the summer and early autumn (Shaklee, 1996). Water vapor, produced by evaporation from the ocean surface, migrates across the island in the direction of the prevailing wind. As atmospheric water vapor passes over the many saline and hypersaline lakes that occupy the island's interior, evaporation from these water bodies may affect the air mass (Fig. 11). Because of evaporation, many of these inland lakes have salinities over twice that of seawater and $\delta^{18}\text{O}$ values that are an average of 1.1‰ higher relative to VSMOW. San Salvador's inland lakes are very shallow, typically 1–2 m deep (Davis and Johnson, 1990), and larger lakes tend to have a higher evaporation rate due to their greater surface-area-to-volume ratio. Evaporation from ^{18}O -rich hypersaline lakes could result in ^{18}O enrichment of atmospheric water vapor as it migrates in the direction of prevailing winds across San Salvador. This effect may explain the observed enrichment of *Cerion* shell carbonate on the leeward side of the inland lakes relative to the windward side.

Juvenile *Cerions*

We undertook a preliminary investigation of juveniles to evaluate the effect of life history and age on the isotope composition of *Cerion* shell

carbonate. We observed no significant difference in the $\delta^{13}\text{C}$ values of adult and juvenile *Cerion* collected from the same plant (Fig. 5), corroborating previous research from the Southern Great Plains, USA, where no age effect was observed in the $\delta^{13}\text{C}$ values of juvenile and adult *Vallonia* shells (Balakrishnan et al., 2005b). Other studies, however, have found a carbon isotope offset between adults and juveniles, which has been attributed to one of several factors, including differences in the surface-area-to-volume ratio between adults and juveniles, the tendency for juveniles to feed within ^{13}C -poor leaf litter, or ingestion of the ^{13}C -depleted albumen (yolk) by the snail embryo during shell building (Goodfriend and Hood, 1983; Magaritz and Heller, 1983; Metref et al., 2003). The lack of an observed carbon isotope offset between adult and juvenile *Cerion* suggests that the isotopic difference between C_3 and C_4 plants exerts a greater control over *Cerion* shell carbonate $\delta^{13}\text{C}$ values than age-related influences induced by ontogenetic variations in behavior and diet.

Juvenile *Cerion* exhibit the same geographic trend in $\delta^{18}\text{O}$ values as adults (i.e., lower $\delta^{18}\text{O}$ values on the windward side of the island relative to the leeward coast). At any one site, however, juveniles exhibited higher $\delta^{18}\text{O}$ values relative to adults. The observed offset between the $\delta^{18}\text{O}$ values of adult *Cerion* versus juvenile *Cerion* is unique because the only comparable study reported no oxygen isotope offset between adult and juvenile *Vallonia* shells (Balakrishnan et al., 2005b). While the greater surface-area-to-volume ratio of juveniles compared to adults did not significantly influence the $\delta^{13}\text{C}$ values of *Cerion* juveniles, it is feasible that the greater surface-area-to-volume ratio increased exchange with ^{18}O -rich atmospheric water vapor derived from the inland lakes and had a noticeable effect on the $\delta^{18}\text{O}$ values of juvenile shell carbonate. Such an effect could explain the ^{18}O enrichment of juvenile shells relative to adults while permitting juveniles and adults to follow the same geographic trend in isotope enrichment across the island.

Intrashell Isotopic Variations

High-resolution analyses of ~ 234 ribs from one *Cerion* shell revealed intrashell carbon and oxygen isotope variations through ontogeny. Accurate interpretation of the intrashell isotopic variations requires knowledge of the likely growth rates and overall lifespan of the snail. The best available estimates suggest that *Cerion* reaches reproductive and possibly developmental maturity between 2 and 3 years of age. While cyclicity in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is not apparent in the data, the pattern of variation appears nonrandom and, thus, warrants further discussion.

The maximum amplitude of intrashell $\delta^{18}\text{O}$ variations (4.7‰), determined through sequential-rib analysis of one *Cerion* shell, is similar to but slightly greater than the mean annual range (3.2‰) of San Salvador precipitation $\delta^{18}\text{O}$. To facilitate discussion, we have divided the $\delta^{18}\text{O}$ profile into four sections, separated by the three lowest $\delta^{18}\text{O}$ values in the data set (Fig. 9; black arrows). Because the amount effect is known to exist at oceanic island sites (Yapp, 1982) and is observed in the model-generated San Salvador precipitation $\delta^{18}\text{O}$ data (Fig. 2B), months of increased ^{18}O -poor rainfall on San Salvador should reduce the inland-lake effect. Thus, rib oxygen isotope minima (at ribs 61, 110 and 164) may point to snail shell carbonate deposition during periods of seasonal rainfall maxima on San Salvador (Figs. 2A–B). The variable spacing between rib $\delta^{18}\text{O}$ minima, from 61 to 49 ribs (between whorls 1 to 6; Fig. 9), most likely indicates changes in growth rate in response to interannual rainfall variability (Fig. 2A). Higher $\delta^{18}\text{O}$ values of ribs closer to the aperture (whorls 1–3) may be linked to decreasing total annual rainfall on San Salvador during the years that the snail was growing (Figs. 2C, 9).

Intrashell $\delta^{13}\text{C}$ values exhibit increasing variability through ontogeny with amplitudes as great as 5.1‰. These results for *Cerion* contrast markedly with the relatively constant intrashell $\delta^{13}\text{C}$ values observed in the Ethiopian land snail *Limicolaria* (Leng et al., 1998). The proportion of C_3 and C_4 plants in the *Cerion* diet appear to influence shell carbonate $\delta^{13}\text{C}$ values, based on the results from whole-shell analysis. Thus, intrashell $\delta^{13}\text{C}$ variations may suggest a change in food source through

ontogeny perhaps caused by movement between C_3 and C_4 plants in the snail's habitat. Other potential influences such as variations in the $\delta^{13}\text{C}$ value of ambient CO_2 and *Cerion* metabolic rate through ontogeny must also be considered.

CONCLUSIONS

The stable isotope composition of *Cerion* shell carbonate is a reflection of diet and environmental moisture on San Salvador. A difference of 1‰ exists between the mean $\delta^{13}\text{C}$ values of *Cerion* shells collected from C_4 plants relative to *Cerion* collected from C_3 plants. Although half of the *Cerion* collected from C_4 plants exhibited $\delta^{13}\text{C}$ values typical of an exclusively C_4 plant diet, the remainder exhibited values more indicative of a mixed diet. Juvenile *Cerion* $\delta^{13}\text{C}$ values are within the range observed for adults from the same plant. While the isotopic evidence largely supports a C_3 and C_4 plant diet for *Cerion*, a secondary contribution from saprophytic mold or fungi cannot be excluded. The data do not support a lichen-dominated diet for San Salvador *Cerion*, however. Future studies are necessary to build on the foundations of *Cerion* isotopic ecology presented here, with the ultimate goal of establishing fossil *Cerion* as a tool for reconstructing shifts in the distribution of C_4 to C_3 plants arising from climatic perturbations in the Quaternary.

The $\delta^{18}\text{O}$ values of live-collected adult *Cerion* shells from eastern (windward) localities on San Salvador were lower by an average of 0.8‰ compared to western (leeward) localities and are contrary to the expected pattern resulting from a rainout effect. Juvenile *Cerion* were enriched in ^{18}O relative to adults from the same locality but exhibited the same geographic trend as adults. The enrichment in ^{18}O of *Cerion* shells toward the western (leeward) coast of San Salvador is tentatively attributed to the influence of atmospheric water vapor derived from the evaporation of ^{18}O -rich inland hypersaline lakes. If this mechanism for ^{18}O enrichment of shell carbonate is corroborated by future investigations, then a paleoclimatic and paleohydrological reconstruction of San Salvador using oxygen isotopes in Holocene- and Pleistocene-age fossil *Cerion* is tenable. A study of the oxygen-isotope composition of fossil *Cerion* has the potential to provide an intermittent but long-term paleoenvironmental and palaeoclimatic record of the amount and isotopic composition of rainfall as well as changes in San Salvador's paleohydrology (i.e., the size, geographic position, and relative salinity of the inland hypersaline lakes) during the Pleistocene and Holocene epochs.

While more extensive field and laboratory observations of *Cerion* feeding habits and life cycle are warranted, the application of the isotopic compositions of *Cerion* shells as paleoenvironmental proxies for the Bahamas has considerable potential. A future study of experimentally raised *Cerion* under controlled environmental conditions is essential to elucidate the *Cerion* diet and lifespan. In the case of the latter, knowledge of the maximum age that *Cerion* may attain, the maximum age for deposition of the terminal lip and cessation of growth, and the growth rate of *Cerion* through ontogeny will enable detailed interpretation of the observed intrashell $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variations.

Seasonal rainfall maxima muting the inland-lake effect are likely responsible for regular sequential-rib $\delta^{18}\text{O}$ minima. A trend toward heavier $\delta^{18}\text{O}$ values through ontogeny is consistent with the decrease in San Salvador rainfall that occurred between 1994 and 1999 (i.e., the snail's likely growth period). The sequential-rib $\delta^{13}\text{C}$ profile exhibits pronounced variability through ontogeny with a maximum amplitude of 5.1‰ and may indicate movement between C_3 and C_4 plants during the snail's life cycle. Additional sequential-rib analyses are necessary to corroborate the pattern of intrashell $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variability observed in this study.

Finally, the proposed inland-lake effect is testable by implementing a long-term (≥ 1 year) monitoring program on San Salvador island to quantify the spatial and temporal variability of inland-lake evaporative ^{18}O enrichment and the flux of isotopically heavy water vapor in the direction of prevailing wind. The monitoring program should include weather sta-

tions compiling daily atmospheric conditions and inland-lake evaporation rates, as well as monthly oxygen isotope measurements of evaporation pan water and monthly integrated rainwater.

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