



Quaternary interglacial environmental stability in San Salvador Island (Bahamas): A land snail isotopic approach

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ABSTRACT

The $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ ratios of modern and fossil shells of two ecologically-distinct land snail taxa (Cerionidae and Annularidae) from San Salvador Island were analyzed to estimate the interglacial Pleistocene and Holocene paleoenvironmental conditions in the Bahamas. The average $\delta^{13}\text{C}$ value of *Cerion* was $-5.0 \pm 1.8\text{‰}$ for modern (~ 0 – 0.1 ka) specimens, $-4.3 \pm 0.7\text{‰}$ for late Holocene (~ 2 – 4.6 ka) individuals, $-3.4 \pm 1.6\text{‰}$ for middle Holocene (~ 5 – 6.3 ka) shells, $-4.0 \pm 1.5\text{‰}$ for ~ 85 or ~ 110 ka specimens, and $-3.6 \pm 0.4\text{‰}$ for individuals that grew during OIS 5e (~ 125 ka). Annularidae specimens displayed average $\delta^{13}\text{C}$ values of $-6.3 \pm 2.5\text{‰}$, $-6.1 \pm 1.0\text{‰}$, $-2.4 \pm 1.0\text{‰}$, $-4.4 \pm 1.1\text{‰}$, and $-5.0 \pm 2.9\text{‰}$, respectively. These results suggest that snails consumed C_3 and C_4 plants arbitrarily through time, however, higher proportion of C_4 plants may have been consumed in the past compared to the present. *Cerion* was $\sim 1\text{‰}$ higher in average $\delta^{13}\text{C}$ value than Annularidae specimens for some time-intervals, indicating greater C_4 plant consumption and/or higher ingestion of carbonate-rich sediments. The average $\delta^{18}\text{O}$ value of *Cerion* was $-0.5 \pm 0.8\text{‰}$ for modern individuals, $-0.5 \pm 0.5\text{‰}$ for late Holocene specimens, $-0.8 \pm 0.2\text{‰}$ for middle Holocene shells, $-0.4 \pm 0.6\text{‰}$ for ~ 85 or ~ 110 ka specimens, and $-0.3 \pm 0.6\text{‰}$ for OIS 5e individuals. Annularidae individuals exhibited average $\delta^{18}\text{O}$ values of $-0.7 \pm 0.8\text{‰}$, $-0.5 \pm 0.9\text{‰}$, $-0.9 \pm 0.3\text{‰}$, $-0.3 \pm 0.6\text{‰}$, and $-0.9 \pm 0.9\text{‰}$, respectively. These results point to similar atmospheric conditions over time-intervals when shell was deposited. The shell $\delta^{18}\text{O}$ values did not significantly differ between species despite the apparent differences in lifestyle. Calculations from a snail evaporative steady-state flux balance model and proxy data suggest that modern individuals deposited shell at air temperatures of ~ 24 – 25°C , ambient water $\delta^{18}\text{O}$ values between -4.5‰ and -3.5‰ (SMOW), and relative humidity of ~ 87 – 89% . Late to middle Holocene and interglacial late Pleistocene shells appear to have precipitated under a similar environmental setting. Overall, atmospheric conditions during these Quaternary interglacial time-intervals at coastal sites of San Salvador were largely comparable to the present. This apparent environmental similarity is consistent with the relatively comparable snail richness and diversity observed at those same locales and time-intervals.

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1. Introduction

Land snail assemblages are increasingly used as an effective retrospective proxy for paleoenvironmental and paleoecological conditions at both spatial and temporal scales. It has been repeatedly demonstrated that variations in the isotopic signature (e.g., Yapp, 1979; Balakrishnan and Yapp, 2004), taxonomic composition and taphonomic feature (e.g., Yanes et al., 2008a, 2011a; Yanes, 2012), and body size (e.g., Hearty and Schellenberg, 2008; Huntley et al., 2008; Hearty, 2010) of land snails are linked to fluctuations of abiotic and biotic factors.

Land snails are an abundant and diverse fauna of ocean islands worldwide (Solem, 1984) and, thanks to their calcareous hard parts, they are frequently well-preserved in the Quaternary fossil record

(e.g., Goodfriend, 1992, 1999). San Salvador Island, an isolated platform on the eastern Bahamas, located ~ 640 km southeast from Miami, Florida (Fig. 1), is a tropical ($24^\circ 00' \text{ N}$, $74^\circ 30' \text{ W}$), low-altitude (> 40 m a.s.l.) and carbonate-rich island that contains an exceptional native terrestrial malacofauna which has been preserved in local Quaternary eolian sediments and paleosols (e.g., Rosse, 1989; Baldini et al., 2007; Hearty and Schellenberg, 2008). The popular tropical pulmonate *Cerion* (Gastropoda: Cerionidae) (Fig. 2A–B) is highly abundant in the Caribbean, and it exhibits an extraordinary morphological diversity that is well-preserved in Quaternary rocks (e.g., Gould et al., 1975; Goodfriend and Gould, 1996; Gould, 1988; Hearty and Schellenberg, 2008; Hearty, 2010). Besides *Cerion*, many other taxa, such as those of the family Annularidae, e.g., *Opisthosiphon coloni* (Fig. 2C) or *Colonella watlingensis* (Fig. 2D), are also relatively abundant, overlap in distribution with *Cerion* and have been preserved in the local sedimentary record. However, they have traditionally received much less scientific attention than *Cerion*. Such shell material provides a superb opportunity to explore

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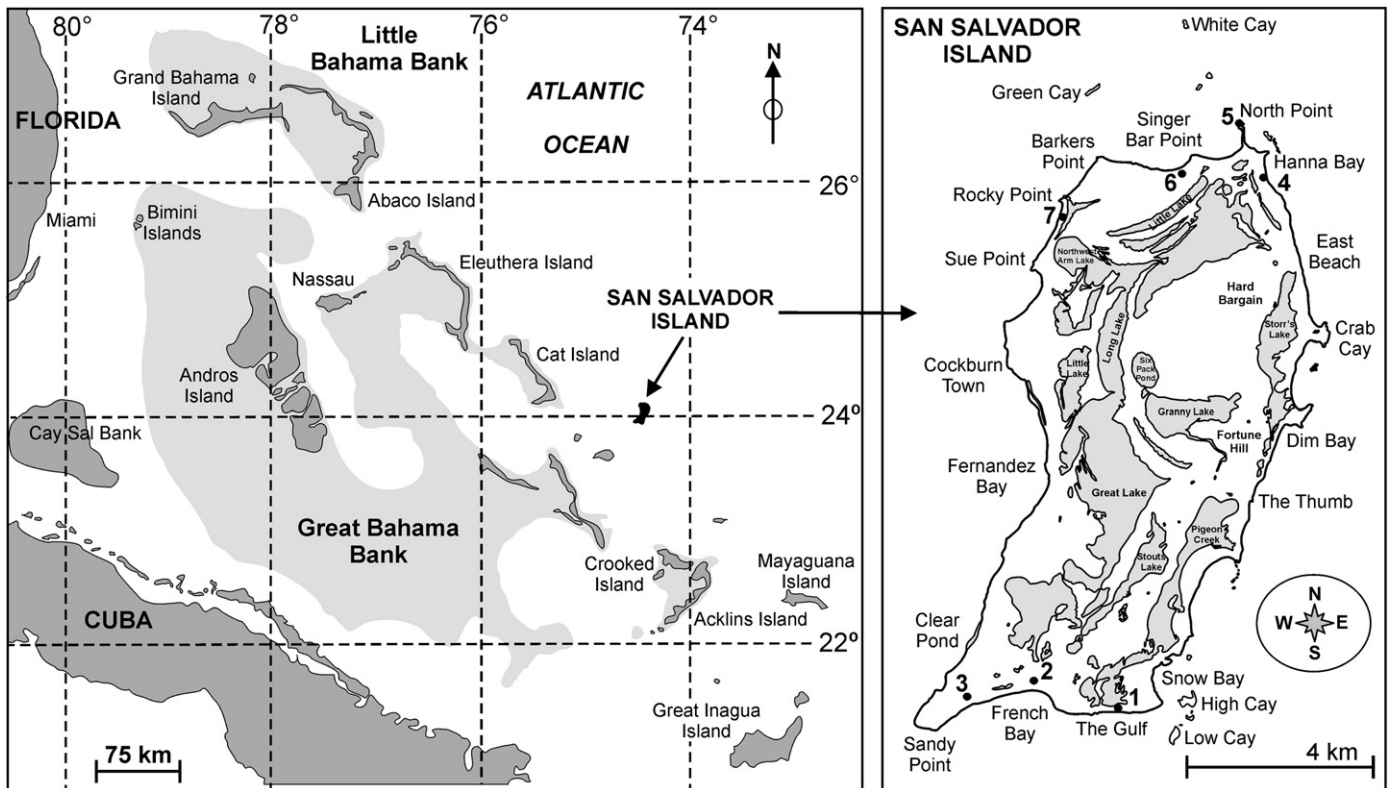


Fig. 1. Geographical setting and sampling sites of modern and fossil land snails. Late Pleistocene specimens were collected at The Gulf (1) and Watling's Quarry (2). Middle to late Holocene individuals were recovered from Hanna Bay (4) and North Point (5). Modern snails were gathered from the soil surface at The Gulf (1), French Bay (3), North Point (5), Singer Bay (6) and Rocky Point (7). Adapted from Yanes (2012).

atmospheric conditions and vegetation dynamics (e.g., C_3/C_4 plant ratio) when snails lived and grew using stable isotope records in their shells. Assessing the paleoenvironmental context is important for paleoclimatologists who want to better understand past climatic conditions and for paleontologists who wish to evaluate the effects of climate upon organisms.

The stable isotope composition of land snail shells has been gradually more used as an effective paleoenvironmental proxy (see reviews in Goodfriend, 1992, 1999). Specifically, land snails from low-latitude oceanic systems appear to faithfully trace the environmental information of the habitat where they live in the form of isotope codes (Baldini et al., 2007; Yanes et al., 2008b, 2009, 2011b). Baldini et al. (2007) studied living *Cerion* specimens from San Salvador Island. Their findings indicate that the isotope composition of modern shells track efficiently the local environmental conditions during calcification. The carbon isotope composition of the shell records the $\delta^{13}C$ values of plants consumed by individuals (Stott, 2002; Metref et al., 2003). Shifts in snail diet primarily reflect variations in the natural proportions of C_3 – C_4 plant in the foraging range, which in turn, are linked to climatic fluctuations (e.g., Goodfriend and Ellis, 2000, 2002). The oxygen isotope values of the shell document the dominant atmospheric conditions (i.e., $\delta^{18}O$ value of rainfall and water vapor, relative humidity and temperature) when land snails are active and precipitate shell material (Yapp, 1979; Balakrishnan and Yapp, 2004). Accordingly, it is possible to explore environmental variations that dominated ancient terrestrial ecosystems at the time of shell deposition using a land snail isotopic approach (e.g., Balakrishnan et al., 2005; Colonese et al., 2007, 2010a,b, 2011; Kehrwald et al., 2010; Yanes et al., 2011b,c).

In the present study, carbon and oxygen stable isotope compositions of interglacial late Pleistocene, middle to late Holocene, and modern land snail shells of two ecologically-distinct taxa (*Cerionidae*

and *Annularidae*) were studied to better understand past interglacial Pleistocene–Holocene environmental conditions on coastal sites of San Salvador Island (Bahamas). Paleoenvironmental inferences derived from these data are in turn relevant for a better understanding of the relationship between climate and the evolution of the terrestrial malacofauna in the Caribbean.

2. Field stratigraphy and geochronology of San Salvador Island

The stratigraphic model by Carew and Mylroie (1985, 1987, 1995a,b, 1997) indicates that subaerial rocks exposed on San Salvador (and other Bahamian islands) are eolianites and intertidal and subtidal facies which were deposited during several middle to late Quaternary interglacial cycles. Various interglacial poorly-developed carbonate-rich paleosols (Fig. 3A–H), with relatively abundant and well-preserved terrestrial fossils (i.e., land snail shells, vegemorphs, land crab remains, etc.), formed within some eolianites during sedimentation pauses (e.g., Hearty and Schellenberg, 2008).

Three major units, bounded by an unconformity (i.e., allostratigraphic units), are identified based on field data combined with multiple age-dating techniques (Carew and Mylroie, 1985, 1987, 1995a,b, 1997): (1) Rice Bay formation, which includes Hanna Bay and North Point members, dated at middle to late Holocene (OIS 1); (2) Grotto Beach formation, which includes Cockburn Town and French Bay members, deposited at OIS 5e (~125 ka); and (3) Owl's Hole formation, deposited during OIS 7 (~220 ka), 9 (~320 ka), or 11 (~410 ka). The late Quaternary subaerial rocks of San Salvador are, hence, younger than ~500 ka (e.g., Carew and Mylroie, 1985, 1987, 1995a,b,c, 1997; Mylroie, 2008; Mylroie and Carew, 2008) and do not show evidence of tectonic deformation (Carew and Mylroie, 1995c). An alternative stratigraphic interpretation of San Salvador Island was presented by Hearty and Kindler (1993), Kindler and Hearty (1997), and Hearty and Schellenberg (2008),

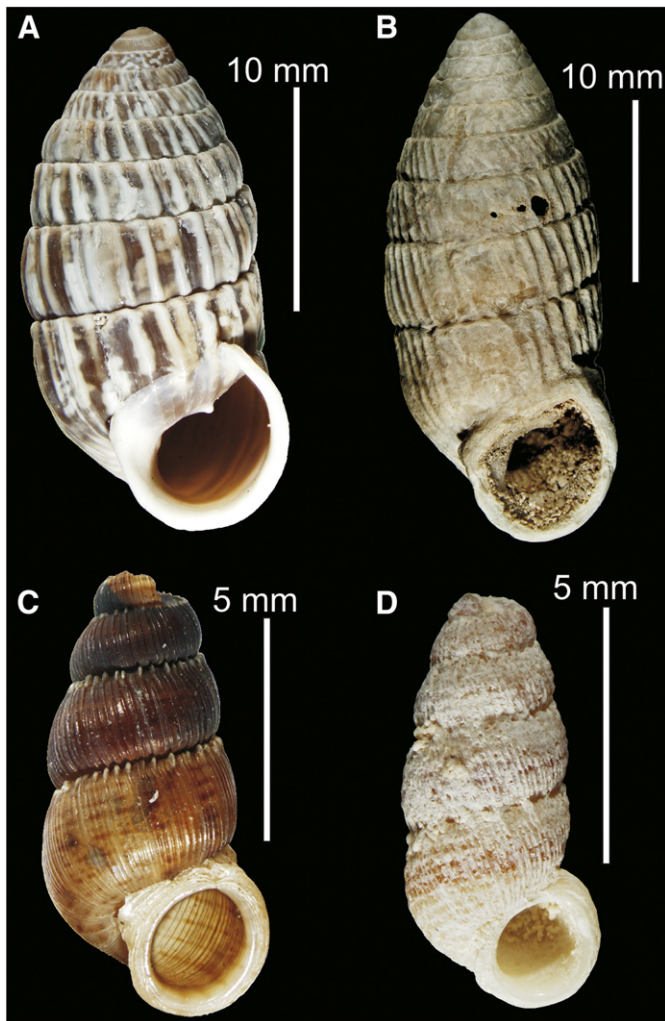


Fig. 2. Photographs of the land snail taxa used in this study. (A) Shell of a recently dead *Cerion* specimen collected from the soil surface at North Point. (B) Late Holocene (buried) *Cerion* shell collected at Hanna Bay protosol. (C) Shell of a recently dead Annulariidae individual (*Opisthosiphon coloni*) collected from the soil surface at The Gulf. (D) Late Pleistocene (buried) Annulariidae shell (*Colonella watlingensis*) collected from The Gulf paleosol. Note that photographs of shells were taken prior to shell cleaning procedure because that process requires shell breakage.

in which five new stratigraphic units were identified (East Bay member, Upper and Lower members of the Almgreen Cay formation, Fernandez Bay formation and Fortune Hill formation) in addition to those proposed by Carew and Mylroie (1985, 1987). These assignments were primarily based on morphostratigraphy and amino acid racemization data. Discussions about the stratigraphy and geochronology of San Salvador can be found in Carew and Mylroie (1994), Hearty and Kindler (1994) and Carew and Mylroie (1995d).

The oldest eolianites from Owl's Hole formation (OIS 7, 9 or 11) are capped by a terra rossa paleosol and overlain by eolianites of the Grotto Beach formation, this last mostly deposited during OIS 5e (e.g., Carew and Mylroie, 1985, 1987, 1995a,b, 1997; Mylroie, 2008; Mylroie and Carew, 2008). The older member of the Grotto Beach formation is the French Bay member (Fig. 3G–H), which represents an eolianite transgressive-phase deposited at ~125 ka (e.g., Carew and Mylroie, 1997; Mylroie and Carew, 2008). The younger unit of the Grotto Beach formation is the Cockburn Town member (Fig. 3E–F), characterized by complex subtidal and intertidal facies covered by an eolianite regressive-phase of OIS 5e, which was deposited about 15 ka later than the French Bay member. In contrast, eolianites from the Cockburn Town member have been assigned to OIS 5a (Hearty and Schellenberg, 2008).

The Grotto Beach formation is overlain by the Rice Bay formation, which is Holocene (OIS 1) in age, also separated by a terra rossa paleosol (e.g., Carew and Mylroie, 1985, 1987, 1995a,b, 1997; Mylroie, 2008; Mylroie and Carew, 2008). The oldest member of Rice Bay is the North Point member (Fig. 3C–D), which represents an eolianite transgressive-phase radiocarbon dated at ~5.3 ka by Carew and Mylroie (1987). Recent amino acid-dated *Cerion* shells and sediments of the lower part of the North Point protosol ranged from ~5 to ~6.3 ka (see figure 8 in Hearty and Kaufman, 2009). Laterally, the younger Hanna Bay member (Fig. 3A–B) of the Rice Bay formation is characterized by intertidal facies and eolianites deposited in equilibrium with modern sea level (e.g., Carew and Mylroie, 1985; Mylroie and Carew, 2008). Radiocarbon ages of the Hanna Bay member range from ~0.4 to ~3.3 ka (e.g., Carew and Mylroie, 1987). Latest amino acid and radiocarbon dates of *Cerion* shells and carbonate-rich sediments suggest that the Hanna Bay protosol is older than 2 ka, most samples ranging in age from ~2 to ~4.6 ka (see figure 8 in Hearty and Kaufman, 2009).

3. Methods

3.1. Present climate

Air temperature data from San Salvador was taken from Gamble et al. (2004). Precipitation data for the recording period between 2001 and 2011 was provided by D.W. Gamble (personal communication, 2012). Average relative humidity data for the recording period 2001–2011 was only available from the Nassau International Airport meteorological station, managed by the Bahamas Meteorology Department (<http://www.bahamasweather.org.bs/>). Maximum relative humidity data were not available. Monthly average air temperature ranges from 22 °C in January–February to 28 °C in July–August (Fig. 4A). The mean annual air temperature is 25 °C. Monthly precipitation ranges from 47 mm in February to a maximum of 199 mm in October (Fig. 4A–B). The rainy months are from April to June, and from September to November (see also Baldini et al., 2007). The mean temperature during the rainy seasons at night, when snails are expected to be more active and grow shell, is ~24 °C. Average monthly relative humidity in Nassau ranges from ~74% in April to ~80% in September (Fig. 4B). The annual average relative humidity value is ~77%. The $\delta^{18}\text{O}$ value of rainfall was adopted from Baldini et al. (2007). The rain $\delta^{18}\text{O}$ values range from –4.5‰ to –1.2‰ (SMOW). The amount-weighted mean annual $\delta^{18}\text{O}$ value for rain is –3.5‰ (SMOW), while the amount-weighted mean $\delta^{18}\text{O}$ value for the rainy months is –4.5‰ (SMOW).

The vegetation of San Salvador is shaped by shrubs and grasses which follow either C_3 or C_4 photosynthetic pathways. The C_3 photosynthetic pathway dominates at all localities, e.g., *Reynosa septentrionalis*, *Sabal palmetto*, *Lantana involucrata* and *Coccoloba uvifera*, although *Cerion* has been observed attached to the graminoid C_4 plants *Cenchrus incertus* and *Sporobolus domingensis* as well (Baldini et al., 2007).

3.2. Field sampling procedure

Modern shells of *Cerion* ($n=27$) and Annulariidae ($n=7$) were collected from 5 sites: North Point, Rocky Point, Singer Bay, The Gulf and French Bay (Fig. 1; Table 1). Only shells from dead animals were collected to protect the native terrestrial malacofauna. Modern shells were collected from the soil surface at sites with dense populations of living land snails. Recent shells exhibit a fresh-looking appearance (i.e., high color preservation, presence of periostracum, absence of carbonate crust, body tissue remains, etc.) with little taphonomic alteration (Fig. 2; see also Yanes, 2012). Hence, we are confident that only decadal to centennial old shells were collected for this study.

Fossil land snail shell material was recovered from four well-known sites: Hanna Bay, North Point, The Gulf and Watling's Quarry (Figs. 1

Age	Stratigraphy	General view of the sampling site	Detailed view of the sampling site
HOLOCENE	Rice Bay Formation (OIS 1)	Hanna Bay member	Carbonate-rich protosol of Hanna Bay (~2 – 4.6 ka)
		North Point member	Carbonate-rich protosol of the North Point (~5 – 6.3 ka)
	Grotto Beach Formation (OIS 5)	Cockburn Town member	Complex paleosol of The Gulf (~85 or ~110 ka)
		French Bay member	Upper eolianite of the Watling's Quarry (~125 ka)
LATE PLEISTOCENE	Rice Bay Formation (OIS 1)	Hanna Bay member	Carbonate-rich protosol of Hanna Bay (~2 – 4.6 ka)
		North Point member	Carbonate-rich protosol of the North Point (~5 – 6.3 ka)
	Grotto Beach Formation (OIS 5)	Cockburn Town member	Complex paleosol of The Gulf (~85 or ~110 ka)
		French Bay member	Upper eolianite of the Watling's Quarry (~125 ka)

Fig. 3. Photographs of the studied late Quaternary sites from San Salvador Island. (A–B) Protosol of the Hanna Bay member of the Rice Bay formation. (C–D) Protosol of the North Point member of the Rice Bay formation. (E–F) Complex paleosol of The Gulf, which belongs to the Cockburn Town member of the Grotto Beach formation. Note that [Hearty and Schellenberg \(2008\)](#) propose an age of ~85 ka (OIS 5a) whereas [Carew and Mylroie \(1995a,b\)](#) suggest an age of ~110 ka (OIS 5e) (see text). (G–H) Upper eolianite of the Watling's Quarry of the French Bay member, Grotto Beach formation. Asterisks in photographs A, C, E and G denote where snail shells were collected. Stratigraphic and geochronological context was adapted from [Carew and Mylroie \(1985, 1995a\)](#).

and 3). Shells from the outer surface of the deposits were not considered to prevent potential shell reworking. Fossil shells were collected via dry-sieving sediments through 1-mm mesh diameter. A total of 65 fossil adult shells of Cerionidae (n = 35) and Annularidae (n = 30), the two most abundant taxa, were selected for stable isotope analyses. Various samples of associated eolianite sediments (n = 10) were collected for subsequent analysis as well.

At Hanna Bay, shells were collected from a protosol (Fig. 3A–B) in middle to late Holocene rocks, ~2–4.6 ka ([Hearty and Kaufman, 2009](#)). At North Point, shells were gathered from the lower part of the protosol (Fig. 3C–D) overlying middle Holocene rocks (e.g., [Carew and Mylroie, 1987](#)), and they are ~5–6.3 ka ([Hearty and Kaufman, 2009](#)). At The Gulf, shells were collected from a complex paleosol (Fig. 3E–F) that developed on the top of a coral reef. This

site is considered a regressive phase dune of OIS 5e ([Carew and Mylroie, 1985, 1987, 1995a,b, 1997](#)). Alternatively, [Hearty and Schellenberg \(2008\)](#) suggest that this site is younger, dated at OIS 5a. At Watling's Quarry, considered a transgressive phase eolianite of the French Bay member ([Carew and Mylroie, 1985, 1987; Hearty and Kindler, 1993; Carew and Mylroie, 1995a,b, 1997](#)), snail shells were gathered from the upper eolianite unit (Fig. 3G–H) dated at ~125 ka (see also [Hearty and Schellenberg, 2008](#)).

3.3. Land snail species selection

Shells of the families Cerionidae (Fig. 2A–C) and Annularidae (Fig. 2D–F) were selected for this study because they are highly abundant, they overlap in space and time around San Salvador, and

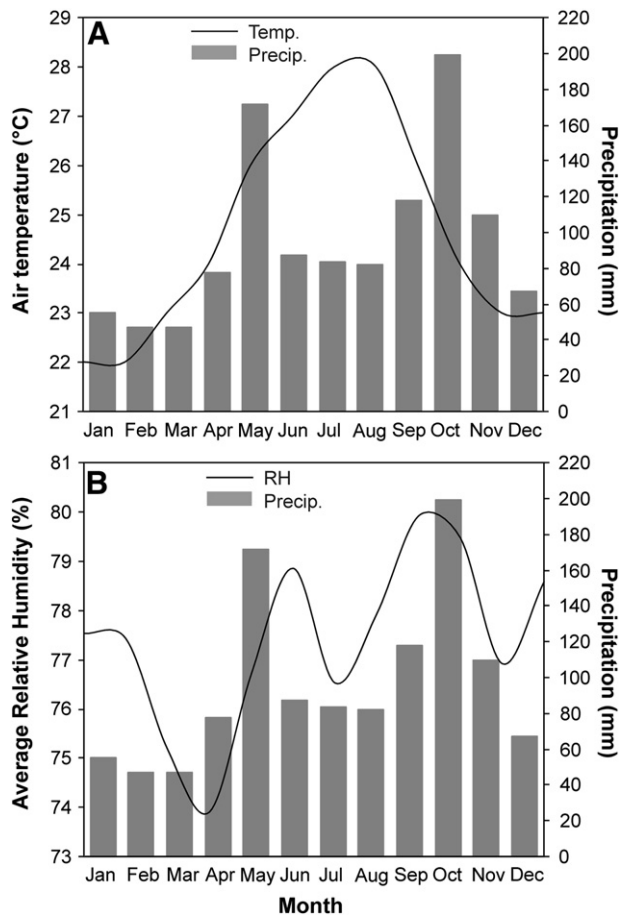


Fig. 4. Climatic context of San Salvador, Bahamas. (A) Mean monthly air temperature and monthly precipitation. (B) Mean monthly relative humidity and monthly precipitation. Data was adapted from Gamble et al. (2004), Gamble (personal communication, 2012), and the Nassau International Airport Station of the Bahamian Meteorological Department.

they appear to display noticeably different microhabitat preferences. *Cerion* is by far, the dominant taxon throughout the Quaternary. *Cerion* species are difficult to identify based solely on the hard skeleton due to their large phenotypic diversity, in addition to frequent hybridization between species (e.g., Gould et al., 1975; Rosse, 1989; Goodfriend and Gould, 1996; Baldini et al., 2007). Hence, *Cerion* specimens were not identified at the species level to minimize taxonomic errors. Little is known about *Cerion* dietary habits and life-cycle. Earlier studies observed that *Cerion* species forage on vascular plants, decaying plant material, mold, lichens and fungi (Rosse, 1989 and references therein). A recent stable isotope study at San Salvador indicated that living *Cerion* specimens follow a varied diet that includes both C_3 and C_4 plant types that are consumed in proportion to their availability in the landscape (Baldini et al., 2007).

Coastal *Cerion* individuals (Fig. 2A–B) rest attached to plants (mostly shrubs and palms) between 1/2 and 1 m above the ground surface during the day (e.g., tree-dwelling), whereas they become active preferentially at night or during rain events (personal field observations, 2010). Adult *Cerion* specimens from San Salvador display a relatively large and thick (highly durable) shell, with a maximum length that ranges from 17.5 to 26.4 mm ($n = 10$).

Opisthosiphon and *Colonella* species (Fig. 2C–D) were all considered jointly as Annulariidae specimens to prevent potential taxonomic errors. From hereafter, we will refer to them as Annulariidae. Little information exists regarding the ecological preferences of Annulariidae specimens from San Salvador. Individuals were often found resting on or buried

Table 1
Carbon and oxygen stable isotope values of Cerionidae ($n = 62$) and Annulariidae ($n = 37$) land snail entire shells from San Salvador, Bahamas.

Sample #	Sample ID	Taxa	Locality	~Age (ka) ^a	$\delta^{13}C_{\text{‰}}$ (PDB)	$\delta^{18}O_{\text{‰}}$ (PDB)
1	NPM-1	<i>Cerion</i>	North Point	0–0.1	–3.3	–0.1
2	NPM-2	<i>Cerion</i>	North Point	0–0.1	–5.3	–0.8
3	NPM-3	<i>Cerion</i>	North Point	0–0.1	–5.0	0.1
4	NPM-4	<i>Cerion</i>	North Point	0–0.1	–6.3	–0.5
5	NPM-5	<i>Cerion</i>	North Point	0–0.1	–3.4	–2.1
6	NPM-6	<i>Cerion</i>	North Point	0–0.1	–6.7	–0.5
7	NPM-7	<i>Cerion</i>	North Point	0–0.1	–2.9	–2.1
8	SB-1	<i>Cerion</i>	Singer Bay	0–0.1	–6.2	–1.7
9	SB-2	<i>Cerion</i>	Singer Bay	0–0.1	–9.1	–0.7
10	SB-3	<i>Cerion</i>	Singer Bay	0–0.1	–6.3	–1.1
11	SB-4	<i>Cerion</i>	Singer Bay	0–0.1	–9.7	–0.4
12	SB-5	<i>Cerion</i>	Singer Bay	0–0.1	–5.2	–1.0
13	RP-1	<i>Cerion</i>	Rocky Point	0–0.1	–3.9	0.5
14	RP-2	<i>Cerion</i>	Rocky Point	0–0.1	–4.1	–0.8
15	RP-3	<i>Cerion</i>	Rocky Point	0–0.1	–4.3	0.1
16	RP-4	<i>Cerion</i>	Rocky Point	0–0.1	–2.9	0.0
17	RP-5	<i>Cerion</i>	Rocky Point	0–0.1	–4.3	0.7
18	TGM-1	<i>Cerion</i>	The Gulf	0–0.1	–4.2	0.4
19	TGM-2	<i>Cerion</i>	The Gulf	0–0.1	–6.5	0.8
20	TGM-3	<i>Cerion</i>	The Gulf	0–0.1	–4.4	–0.2
21	TGM-4	<i>Cerion</i>	The Gulf	0–0.1	–5.4	–1.4
22	TGM-5	<i>Cerion</i>	The Gulf	0–0.1	–7.0	–0.8
23	TGM-6	<i>Cerion</i>	The Gulf	0–0.1	–5.4	–1.4
24	FB-1	<i>Cerion</i>	French Bay	0–0.1	–3.0	–0.9
25	FB-2	<i>Cerion</i>	French Bay	0–0.1	–3.5	0.4
26	FB-3	<i>Cerion</i>	French Bay	0–0.1	–3.0	0.2
27	FB-4	<i>Cerion</i>	French Bay	0–0.1	–3.7	–0.7
28	HB-21	<i>Cerion</i>	Hanna Bay	2–4.6	–3.9	0.4
29	HB-22	<i>Cerion</i>	Hanna Bay	2–4.6	–5.0	–0.8
30	HB-23	<i>Cerion</i>	Hanna Bay	2–4.6	–5.2	–0.9
31	HB-24	<i>Cerion</i>	Hanna Bay	2–4.6	–3.6	–0.6
32	HB-25	<i>Cerion</i>	Hanna Bay	2–4.6	–3.8	–0.6
33	NP-1	<i>Cerion</i>	North Point	5–6.3	–3.4	–0.5
34	NP-2	<i>Cerion</i>	North Point	5–6.3	–5.0	–1.0
35	NP-3	<i>Cerion</i>	North Point	5–6.3	–0.8	–0.4
36	NP-4	<i>Cerion</i>	North Point	5–6.3	–4.5	–0.6
37	NP-5	<i>Cerion</i>	North Point	5–6.3	–2.7	–0.7
38	NP-6	<i>Cerion</i>	North Point	5–6.3	–5.2	–0.8
39	NP-7	<i>Cerion</i>	North Point	5–6.3	–3.7	–0.9
40	NP-8	<i>Cerion</i>	North Point	5–6.3	–4.9	–0.9
41	NP-9	<i>Cerion</i>	North Point	5–6.3	–0.6	–0.8
42	NP-10	<i>Cerion</i>	North Point	5–6.3	–2.8	–1.2
43	TGF-1	<i>Cerion</i>	The Gulf	85 or 110	–4.0	0.4
44	TGF-2	<i>Cerion</i>	The Gulf	85 or 110	–3.0	–0.9
45	TGF-3	<i>Cerion</i>	The Gulf	85 or 110	–0.9	0.4
46	TGF-4	<i>Cerion</i>	The Gulf	85 or 110	–5.2	0.1
47	TGF-5	<i>Cerion</i>	The Gulf	85 or 110	–4.9	–1.5
48	TGF-6	<i>Cerion</i>	The Gulf	85 or 110	–5.9	–0.9
49	TGF-7	<i>Cerion</i>	The Gulf	85 or 110	–5.0	–0.7
50	TGF-8	<i>Cerion</i>	The Gulf	85 or 110	–2.3	–0.2
51	TGF-9	<i>Cerion</i>	The Gulf	85 or 110	–4.5	–0.2
52	TGF-10	<i>Cerion</i>	The Gulf	85 or 110	–4.0	–0.4
53	WQ-1	<i>Cerion</i>	Watling's Quarry	125	–3.3	1.1
54	WQ-2	<i>Cerion</i>	Watling's Quarry	125	–3.3	–0.2
55	WQ-3	<i>Cerion</i>	Watling's Quarry	125	–3.5	–0.1
56	WQ-4	<i>Cerion</i>	Watling's Quarry	125	–3.4	–1.0
57	WQ-5	<i>Cerion</i>	Watling's Quarry	125	–3.0	0.1
58	WQ-6	<i>Cerion</i>	Watling's Quarry	125	–3.9	0.1
59	WQ-7	<i>Cerion</i>	Watling's Quarry	125	–4.5	–0.2
60	WQ-8	<i>Cerion</i>	Watling's Quarry	125	–3.5	–0.8
61	WQ-9	<i>Cerion</i>	Watling's Quarry	125	–4.1	–0.9
62	WQ-10	<i>Cerion</i>	Watling's Quarry	125	–3.5	–0.8
63	NPM-7	Annulariidae	North Point	0–0.1	–2.4	–0.8
64	NPM-8	Annulariidae	North Point	0–0.1	–5.4	0.6
65	TGM-6	Annulariidae	The Gulf	0–0.1	–7.9	–1.2
66	TGM-7	Annulariidae	The Gulf	0–0.1	–8.1	–0.7
67	TGM-8	Annulariidae	The Gulf	0–0.1	–4.6	–1.2
68	TGM-9	Annulariidae	The Gulf	0–0.1	–9.7	0.0
69	TGM-10	Annulariidae	The Gulf	0–0.1	–6.3	–1.9
70	HB-1	Annulariidae	Hanna Bay	2–4.6	–6.4	0.7
71	HB-2	Annulariidae	Hanna Bay	2–4.6	–7.4	–1.7
72	HB-3	Annulariidae	Hanna Bay	2–4.6	–5.8	0.6
73	HB-4	Annulariidae	Hanna Bay	2–4.6	–5.9	–1.3
74	HB-5	Annulariidae	Hanna Bay	2–4.6	–6.3	–1.8

Table 1 (continued)

Sample #	Sample ID	Taxa	Locality	~Age (ka) ^a	δ ¹³ C‰ (PDB)	δ ¹⁸ O‰ (PDB)
75	HB-6	Annularidae	Hanna Bay	2–4.6	−4.0	−0.9
76	HB-7	Annularidae	Hanna Bay	2–4.6	−6.7	0.4
77	HB-8	Annularidae	Hanna Bay	2–4.6	−7.0	0.2
78	HB-9	Annularidae	Hanna Bay	2–4.6	−5.1	−0.2
79	HB-10	Annularidae	Hanna Bay	2–4.6	−6.3	−0.6
80	NP-11	Annularidae	North Point	5–6.3	−3.5	−1.2
81	NP-12	Annularidae	North Point	5–6.3	−1.1	−0.5
82	NP-13	Annularidae	North Point	5–6.3	−3.1	−0.8
83	NP-14	Annularidae	North Point	5–6.3	−1.2	−0.9
84	NP-15	Annularidae	North Point	5–6.3	−1.5	−0.7
85	NP-16	Annularidae	North Point	5–6.3	−3.2	−0.5
86	NP-17	Annularidae	North Point	5–6.3	−3.7	−1.5
87	NP-18	Annularidae	North Point	5–6.3	−1.6	−1.3
88	NP-19	Annularidae	North Point	5–6.3	−2.7	−0.8
89	NP-20	Annularidae	North Point	5–6.3	−2.2	−1.3
90	TG-11	Annularidae	The Gulf	85 or 110	−4.4	−0.2
91	TG-12	Annularidae	The Gulf	85 or 110	−4.6	0.1
92	TG-13	Annularidae	The Gulf	85 or 110	−2.6	0.2
93	TG-14	Annularidae	The Gulf	85 or 110	−4.7	−0.5
94	TG-15	Annularidae	The Gulf	85 or 110	−5.6	−1.3
95	WQ-11	Annularidae	Watling's Quarry	125	−6.2	−0.3
96	WQ-12	Annularidae	Watling's Quarry	125	−4.6	−2.0
97	WQ-13	Annularidae	Watling's Quarry	125	−0.1	−1.3
98	WQ-14	Annularidae	Watling's Quarry	125	−6.8	0.2
99	WQ-15	Annularidae	Watling's Quarry	125	−7.2	−1.2

^a Approximate age taken from Carew and Mylroie (1995a,b, 1997); Hearty and Schellenberg (2008) and Hearty and Kaufman (2009). Note that shells from The Gulf have been assigned to OIS 5e (Carew and Mylroie, 1995a,b, 1997) or to OIS 5a (Hearty and Schellenberg, 2008).

in the upper 5 cm of the soil, among leaf litter or under rocks (e.g., ground-dwelling), and feeding upon living and/or decaying plant tissues (personal field observations, 2010). Adult Annularidae shells are relatively small and thin, with a maximum length that ranges between 6.8 and 10.3 mm (n=6).

3.4. Stable isotope analyses

Land snail shells and eolianite sediments were prepared and analyzed in the Department of Earth and Environmental Sciences at the University of Kentucky (USA). Fossil shells were evaluated for diagenetic alteration prior to stable isotope analysis. X-ray diffraction analysis on two randomly selected finely pulverized shells showed that they retained their original aragonite composition, suggesting that diagenetic alteration was unlikely. Each entire shell was cleaned ultrasonically in deionized water to remove any adhering particles, and pulverized by hand with an agate mortar and pestle. Organic matter was removed by placing the powdered samples in a 3% hydrogen peroxide solution for 24 h at room temperature (~22 °C). Subsequently, the powders were rinsed three times with deionized water and dried in an oven at 40 °C overnight.

Bulk carbonate sediments were prepared for isotope analysis as described above for the shells. The stable isotope composition of the carbonate matrix permits the geochemical characterization of local carbonate-rich eolianites for comparison to buried fossil shells (Yanes et al., 2011b).

Carbonate powder (~150 µg) was placed in a 6 ml Exetainer™ vial that was subsequently flushed with helium to replace the headspace. The carbonate was then converted to CO₂ gas by adding 0.5 ml of 105% phosphoric acid (H₃PO₄) at 25 °C. The resulting CO₂ was analyzed isotopically after 24 h using a GasBench II attached to a Finnigan Delta^{plus} XP isotope ratio mass spectrometer (IRMS), which was operated in continuous flow mode. All stable isotope results are reported in δ notation relative to the international standard Pee Dee

Belemnite (PDB) for carbonate and SMOW for water. The δ value is defined as:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 (\text{‰})$$

where X = ¹³C for R = ¹³C/¹²C, or X = ¹⁸O for R = ¹⁸O/¹⁶O. Carbon and oxygen isotope values were calibrated against the international standard NBS-19 and in-house standards. The precision of the analyses was better than ±0.1‰ (1σ standard deviation) for carbon and oxygen isotopes based on the repeated measurement (n=30) of the NBS-19 and in-house standards. Replicate analyses of aliquots of powdered snail shells had an overall precision of ±0.2‰ for both oxygen and carbon isotopes.

3.5. Statistical treatment

Statistical analyses were performed using PAST 1.38b software (Hammer et al., 2001), assuming a significance level of α=0.05. Non-parametric (rank-based) tests were computed to test samples for statistical differences. Spearman correlation was used to test whether two variables showed a statistical relationship. The Mann Whitney-U test and Kruskal Wallis test were used to estimate whether or not groups of samples showed similar median distribution values.

4. Results

4.1. Modern shells

Twenty seven modern specimens of *Cerion* displayed a range of δ¹³C values from −9.7‰ to −2.9‰, and a range of δ¹⁸O values from −2.1‰ to +0.8‰ (Table 1). Seven modern individuals of Annularidae exhibited δ¹³C values from −9.7‰ to −2.4‰, and δ¹⁸O values from −1.9‰ to +0.6‰ (Table 1). While average δ¹⁸O values were comparable between species, Annularidae showed an average δ¹³C value which was ~1‰ lower than *Cerion*. However, no statistical differences were observed in δ¹³C or δ¹⁸O values between species (Mann Whitney-U test, p>0.05).

Modern shells collected at northern and southern sites differed significantly (Kruskal Wallis, H=13.6; p=0.0086) in δ¹³C values (Fig. 5A). Shells from Rocky Point and French Bay showed considerably higher δ¹³C values and a smaller range of δ¹³C values than samples from the other coastal sites (Fig. 5A). In contrast, modern shells from different localities of San Salvador Island did not generally show significant differences (Kruskal Wallis, H=6.13, p=0.19) in δ¹⁸O values (Fig. 5B).

4.2. Fossil shells

Late Holocene (~2–4.6 ka) shells of *Cerion* (n=5) from the Hanna Bay protosol ranged from −5.2‰ to −3.6‰ for δ¹³C, and from −0.9‰ to +0.4‰ for δ¹⁸O (Table 1), while Annularidae individuals (n=10) ranged from −7.4‰ to −4.0‰ for δ¹³C, and from −1.8‰ to +0.7‰ for δ¹⁸O (Table 1). Late Holocene individuals of both species did not differ in the carbon and oxygen isotope composition of their shells (Mann Whitney-U test, p>0.05).

Middle Holocene (~5–6.3 ka) shells of *Cerion* (n=10) recovered from the lower part of the North Point protosol ranged from −5.2‰ to −0.6‰ for δ¹³C, and from −1.2‰ to −0.4‰ for δ¹⁸O (Table 1). Annularidae individuals (n=10) ranged from −3.7‰ to −1.1‰ for δ¹³C, and from −1.5‰ to −0.5‰ for δ¹⁸O (Table 1). Both species exhibited similar carbon and oxygen isotope compositions in their shells (Mann Whitney-U test, p>0.05).

Interglacial Pleistocene *Cerion* shells (n=10) from The Gulf, dated at ~85 ka by Hearty and Schellenberg (2008) or at ~110 ka according

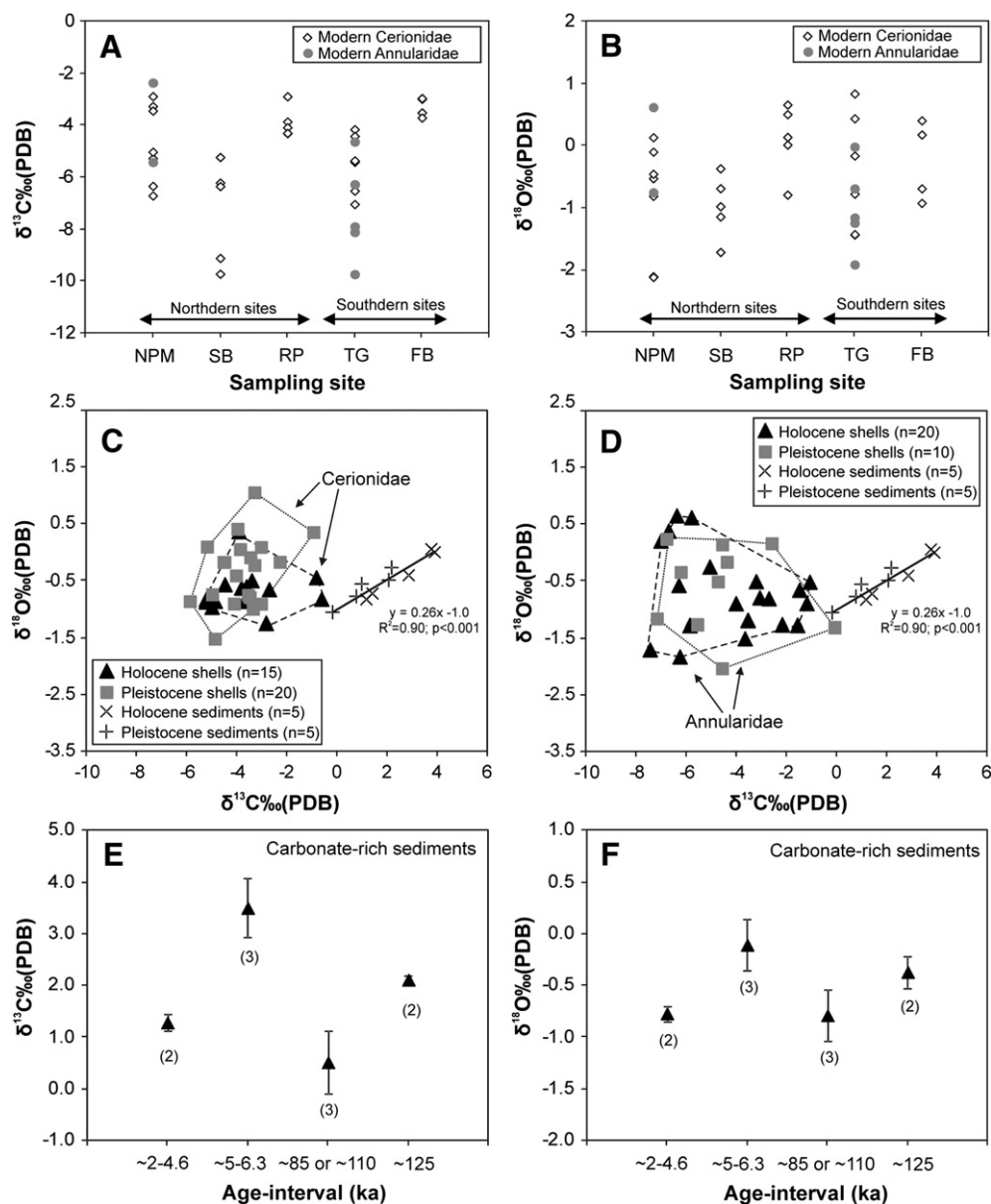


Fig. 5. Stable isotopic composition of modern and fossil land snail shells and carbonate-rich sediments from San Salvador, Bahamas. (A–B) Carbon and oxygen isotopic composition of modern land snail shells collected at different coastal sites. (C–D) Relationship between carbon and oxygen stable isotope values of fossil land snail shells and ancient sediments in which shells were preserved. (E–F) Carbon and oxygen stable isotope values of carbonate-rich sediments per time-interval.

to Carew and Myroie (1987, 1995a,b, 1997), ranged from -5.9‰ to -0.9‰ for $\delta^{13}\text{C}$, and from -1.5‰ to $+0.4\text{‰}$ for $\delta^{18}\text{O}$ (Table 1), while Annularidae shells ($n=5$) ranged from -5.6‰ to -2.6‰ and from -1.3‰ to $+0.2\text{‰}$, respectively. No significant differences are observed between species regarding carbon and oxygen isotope values (Mann Whitney- U test, $p>0.05$).

Interglacial Pleistocene *Cerion* shells ($n=10$) from the Watling's Quarry (~ 125 ka) ranged from -4.5‰ to -3.0‰ for $\delta^{13}\text{C}$, and from -1.0‰ to $+1.1\text{‰}$ for $\delta^{18}\text{O}$ (Table 1). Annularidae shells ($n=5$) ranged from -7.2‰ to -0.1‰ and from -2.0‰ to $+0.2\text{‰}$, respectively. Shells of both species from the Watling's Quarry did not significantly differ in carbon and oxygen stable isotope values (Mann Whitney- U test, $p>0.05$).

The carbon and oxygen stable isotope values of land snails did not correlate for either snail species (Fig. 5C–D).

When evaluating the stable isotope data through time, modern, Holocene and late Pleistocene $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the shell overlapped substantially (Fig. 6A–D), exhibiting comparable average values for both species across time-intervals (Table 2).

4.3. Bulk carbonate sediments

Late Holocene sediments of the Hanna Bay protocol displayed $\delta^{13}\text{C}$ values of $+1.2\text{‰}$ and $+1.4\text{‰}$, and $\delta^{18}\text{O}$ values of -0.8‰ and -0.7‰ (Table 3; Fig. 5E–F). Middle Holocene sediments ($n=3$) from the protocol at North Point exhibited $\delta^{13}\text{C}$ values from $+2.9\text{‰}$ to $+3.9\text{‰}$, and $\delta^{18}\text{O}$ values from -0.4‰ to $+0.1\text{‰}$ (Table 3; Fig. 5E–F). Late Pleistocene sediments ($n=3$) from The Gulf paleosol (OIS 5a or e) had $\delta^{13}\text{C}$ values that ranged from -0.2‰ to $+1.0\text{‰}$ and $\delta^{18}\text{O}$ values that ranged from -1.1‰ to -0.6‰ (Table 3; Fig. 5E–F). Late Pleistocene carbonate-rich sediments from the Watling's Quarry (~ 125 ka) had $\delta^{13}\text{C}$ values from $+2.1\text{‰}$ to $+2.2\text{‰}$ and $\delta^{18}\text{O}$ values from -0.5‰ to -0.3‰ (Table 3; Fig. 5E–F).

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of sediments correlated positively (Fig. 5C–D). The isotopic signature of bulk carbonate sediments was significantly different from that of snail shells (Fig. 5C–D). Bulk carbonate-rich sediments from the Watling's Quarry and North Point exhibited higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values than samples from Hanna Bay and The Gulf (Fig. 5E–F).

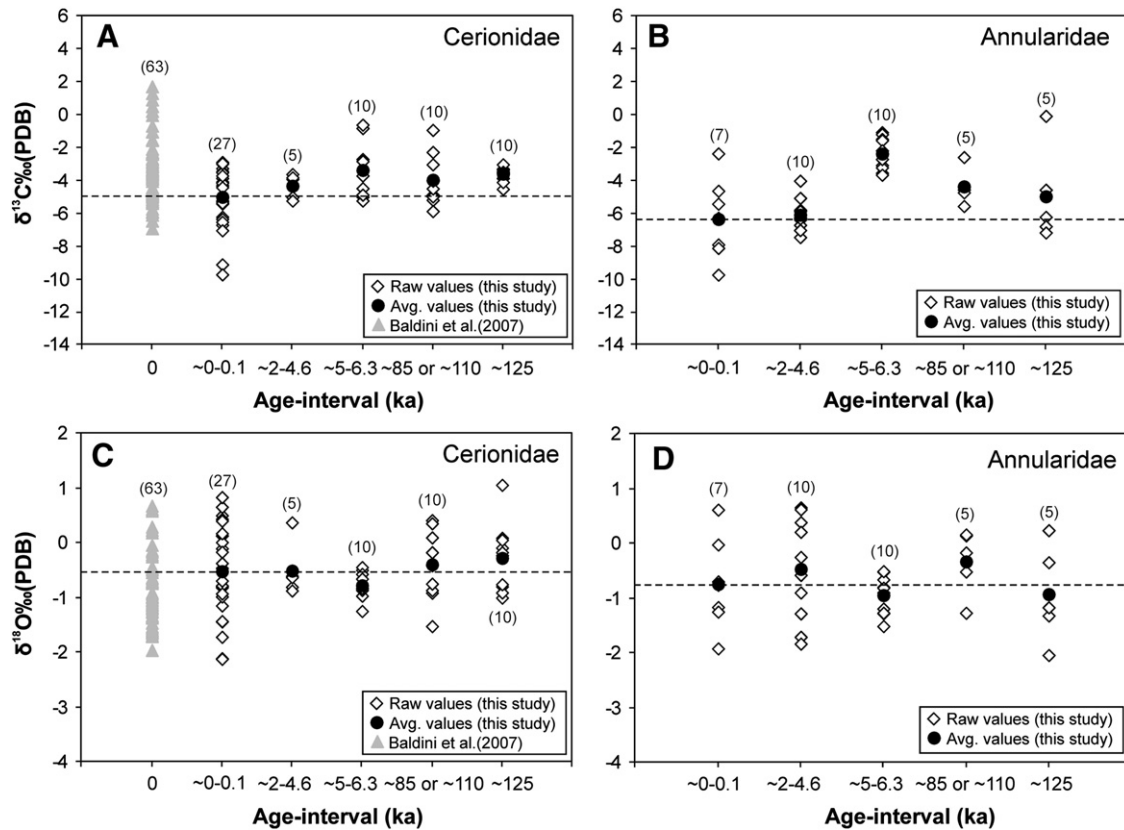


Fig. 6. Stable isotope composition of land snail shells from San Salvador, Bahamas. (A) Carbon isotope composition of *Cerion* shells. (B) Carbon isotope composition of Annularidae shells. (C) Oxygen isotope composition of *Cerion* shells. (D) Oxygen isotope composition of Annularidae shells.

5. Discussion

5.1. Environmental significance of $\delta^{13}\text{C}$ values of modern shells

The $\delta^{13}\text{C}$ values of modern specimens of *Cerion* from this study (from -9.7‰ to -2.9‰) may be compared to previously published data by Baldini et al. (2007) on modern (adult only) *Cerion* shells. The $\delta^{13}\text{C}$ values reported by Baldini et al. (2007) from -6.9‰ to $+1.7\text{‰}$ in part overlap with those from the present study, although many of the values are substantially higher (Fig. 6A). The differences in carbon isotope composition can be explained by an uneven distribution of C_3 and C_4 plants in San Salvador. Shells from the present study were collected at different localities than those collected by Baldini et al. (2007), except for shells from North Point. While Baldini et al. (2007) collected living specimens that were attached to either C_4 or C_3 plants, here only shells from recently dead individuals found on the soil surface were considered. Shell $\delta^{13}\text{C}$ values of modern specimens differed significantly across localities in this study. Specimens from Rocky Point and French Bay showed significantly higher $\delta^{13}\text{C}$ values than those from other locales (Fig. 5A), which may stress the significant variation in the proportional distribution of C_3 and C_4 plants around coastal sites of the island.

If the carbon content from the shell was derived exclusively from consumed vegetation (Stott, 2002; Baldini et al., 2007), modern *Cerion* individuals from this study should have consumed $\sim 39\%$ of C_4 plants, on average, based on the following assumptions: (1) a measured average $\delta^{13}\text{C}$ value for shell of -5.0‰ , (2) C_3 and C_4 plant endmember values of -26.7‰ and -12.6‰ , respectively (Tieszen et al., 1997; Baldini et al., 2007), (3) an isotopic offset between shell and body of -15.6‰ (Yanes et al., 2008b) and (4) an isotopic offset between body and diet of $\sim 1\text{‰}$ (DeNiro and Epstein, 1978). Viewed another, the *Cerion* specimen with the highest $\delta^{13}\text{C}$ value

of -2.9‰ translates to the consumption of as much as $\sim 51\%$ C_4 plants whereas the specimen with the lowest $\delta^{13}\text{C}$ value of -9.7‰ consumed as little as $\sim 3\%$ C_4 plants. This stresses the large variability of dietary habits of contemporaneous specimens living today on the island. The live-collected *Cerion* specimen from a C_4 plant by Baldini et al. (2007) with a shell $\delta^{13}\text{C}$ value of $+1.7\text{‰}$ may have consumed up to $\sim 84\%$ C_4 plants.

However, land snails that inhabit limestone areas frequently ingest carbonate minerals as a source of calcium to build their shells (e.g., Goodfriend and Hood, 1983; Goodfriend et al., 1999; Yanes et al., 2008b). In fact, Goodfriend and Gould (1996) performed radiocarbon analyses on *Cerion* shells from the Bahamas which were collected alive prior to thermonuclear bomb tests and observed an anomalous age of 1020 ± 430 years. This indicates that *Cerion* has the potential to incorporate significant amounts of carbon derived from local limestone.

In contrast to shells, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the sediments where shells were preserved exhibit a strong correlation (Fig. 5C–D), which suggests that two main carbonate sources, marine carbonates (higher $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values) and terrestrial carbonates (lower $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values), shape the eolianites of San Salvador. Bulk eolian sediments from San Salvador display an average $\delta^{13}\text{C}$ value of $+1.9 \pm 1.3\text{‰}$, and range from -0.2‰ to $+3.9\text{‰}$ (Table 3). The $\delta^{13}\text{C}$ values of bulk carbonate-rich sediments varied significantly across sites (Fig. 5E). Samples from North Point ($\sim 3.5\text{‰}$) and Watling's Quarry ($\sim 2.1\text{‰}$) were significantly higher in $\delta^{13}\text{C}$ values than those from Hanna Bay ($\sim 1.3\text{‰}$) and The Gulf ($\sim 0.5\text{‰}$), possibly suggesting higher contributions of marine rather than terrestrial carbon sources in the former sites. These fairly high carbon isotope values observed in local eolianites complicate the use of carbon isotope values from snail shells for paleovegetation estimates. Hence, the proportion of C_4 plants inferred from *Cerion* shell $\delta^{13}\text{C}$ values is most likely

Table 2

Average $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of Cerionidae and Annularidae land snail shells from San Salvador, Bahamas.

Sample ID	Snail taxa	Locality	n	~Age (ka) ^a	$\delta^{13}\text{C}\text{‰}$ (PDB)	$\delta^{18}\text{O}\text{‰}$ (PDB)
NPM	<i>Cerion</i>	North Point	7	0–0.1	-4.7 ± 1.5	-0.9 ± 0.9
SB	<i>Cerion</i>	Singer Bay	5	0–0.1	-7.3 ± 2.0	-1.0 ± 0.5
RP	<i>Cerion</i>	Rocky Point	5	0–0.1	-3.9 ± 0.6	0.1 ± 0.6
TGM	<i>Cerion</i>	The Gulf	6	0–0.1	-5.5 ± 1.1	-0.4 ± 1.0
FB	<i>Cerion</i>	French Bay	4	0–0.1	-4.2 ± 1.9	-0.6 ± 0.7
		Total	27	0–0.1	-5.0 ± 1.8	-0.5 ± 0.8
HB	<i>Cerion</i>	Hanna Bay	5	2–4.6	-4.3 ± 0.7	-0.5 ± 0.5
NP	<i>Cerion</i>	North Point	10	5–6.3	-3.4 ± 1.6	-0.8 ± 0.2
TG	<i>Cerion</i>	The Gulf	10	85 or 110	-4.0 ± 1.5	-0.4 ± 0.6
WQ	<i>Cerion</i>	Watling's Quarry	10	125	-3.6 ± 0.4	-0.3 ± 0.6
NPM	Annularidae	North Point	2	0–0.1	-3.9 ± 2.2	-0.1 ± 1.0
TGM	Annularidae	The Gulf	5	0–0.1	-7.3 ± 1.9	-1.0 ± 0.7
		Total	7	0–0.1	-6.3 ± 2.5	-0.7 ± 0.8
HB	Annularidae	Hanna Bay	10	2–4.6	-6.1 ± 1.0	-0.5 ± 0.9
NP	Annularidae	North Point	10	5–6.3	-2.4 ± 1.0	-0.9 ± 0.3
TG	Annularidae	The Gulf	5	85 or 110	-4.4 ± 1.1	-0.3 ± 0.6
WQ	Annularidae	Watling's Quarry	5	125	-5.0 ± 2.9	-0.9 ± 0.9

^a Approximate age taken from Carew and Mylroie (1995a,b, 1997), Hearty and Schellenberg (2008) and Hearty and Kaufman (2009); n = number of shells analyzed. Note that fossil shells from The Gulf have been assigned to OIS 5e (Carew and Mylroie, 1995a,b, 1997) or to OIS 5a (Hearty and Schellenberg, 2008).

overestimated by the unknown contribution of limestone in the study area (see also Yanes et al., 2008b).

Modern shells of Annularidae exhibit an average $\delta^{13}\text{C}$ value of -6.3‰ , which is 1.3‰ lower than *Cerion* (Fig. 6B). This can be explained by a differing dietary habit between species (e.g., Annularidae specimens preferentially consume more C_3 plants than *Cerion*). Alternatively, Annularidae individuals may ingest significantly lower (or negligible) amounts of limestone. Pigati et al. (2004, 2010) observed that many minute land snail species incorporate insignificant proportions of limestone into their shells. Considering that Annularidae shells exhibit a rather small body size (maximum length between 6 and 10 mm), similar to those studied by Pigati et al. (2004, 2010), it is possible that the contribution of carbon from carbonate sediments into the shell is minor. Although this hypothesis remains to be tested, the carbon isotope composition of the Annularidae shell may be more useful for paleovegetation reconstruction than that of *Cerion*.

Assuming a negligible contribution of limestone in Annularidae shells, and considering the same assumptions outlined above for *Cerion*, the proportion of C_4 plants consumed by modern Annularidae snails is predicted to be $\sim 27\%$, which seems to be a reasonable estimate for coastal sites on San Salvador. The Annularidae specimen with a shell $\delta^{13}\text{C}$ value of -2.4‰ could have ingested as much as $\sim 55\%$ C_4 plants whereas the shell with a $\delta^{13}\text{C}$ value of -9.7‰ may have consumed as little as $\sim 3\%$ C_4 plants. This substantial range of calculated values among modern specimens matches with those from *Cerion* and also emphasizes the large variability of dietary habits of land snails in present-day ecosystems from San Salvador. Both snail taxa are therefore generalized herbivorous.

5.2. Environmental significance of $\delta^{18}\text{O}$ values of modern shells

Modern specimens of *Cerion* and Annularidae showed similar ranges of stable oxygen isotope values despite the fact that *Cerion* appears to be a tree-dwelling taxon while Annularidae seems to be a ground-dwelling taxon at the coastal study sites.

The $\delta^{18}\text{O}$ values of modern *Cerion* specimens ranged from -2.1‰ to $+0.8\text{‰}$, which is consistent with $\delta^{18}\text{O}$ values reported by Baldini et al. (2007) from other localities on San Salvador (Fig. 6C). Combining

Table 3

Carbon and oxygen stable isotope values of ancient bulk eolian sediments from San Salvador, Bahamas.

Sample ID	Locality	~Age (ka) ^a	$\delta^{13}\text{C}\text{‰}$ (PDB)	$\delta^{18}\text{O}\text{‰}$ (PDB)
HB-Sed-1	Hanna Bay	2–4.6	1.4	-0.7
HB-Sed-2	Hanna Bay	2–4.6	1.2	-0.8
NP-Sed-1	North Point	5–6.3	3.9	0.0
NP-Sed-2	North Point	5–6.3	2.9	-0.4
NP-Sed-3	North Point	5–6.3	3.8	0.1
TG-Sed-1	The Gulf	85 or 110	1.0	-0.6
TG-Sed-2	The Gulf	85 or 110	0.8	-0.8
TG-Sed-3	The Gulf	85 or 110	-0.2	-1.1
WQ-Sed-1	Watling's Quarry	125	2.1	-0.5
WQ-Sed-2	Watling's Quarry	125	2.2	-0.3

^a Approximate age taken from Carew and Mylroie (1995a,b, 1997), Hearty and Schellenberg (2008) and Hearty and Kaufman (2009). Note that The Gulf has been assigned to OIS 5e (Carew and Mylroie, 1995a,b, 1997) or to OIS 5a (Hearty and Schellenberg, 2008).

this factor with the observation that there are not strong differences in shell $\delta^{18}\text{O}$ values among localities (Fig. 5B) suggests that shell $\delta^{18}\text{O}$ values may be a valuable record of environmental information. For example, relative humidity, rain and water vapor $\delta^{18}\text{O}$ values, and air temperature at the time of shell deposition may be estimated from the $\delta^{18}\text{O}$ value of the shell using the snail evaporative-steady state flux balance mixing model by Balakrishnan and Yapp (2004). Model calculations assume that water vapor is in isotope equilibrium with liquid water (rain) and that body water is lost through evaporation. Therefore, water vapor $\delta^{18}\text{O}$ values can be predicted from environmental water values and the isotopic fractionation factor between water and water vapor (Balakrishnan and Yapp, 2004). To test this model for the study site, the annual average temperature on San Salvador (25°C) and the amount-weighted mean annual $\delta^{18}\text{O}$ value for rain, -3.5‰ (SMOW), were used in the calculations, along with measured $\delta^{18}\text{O}$ values for modern *Cerion* shells to predict relative humidity at present-day. If snails in San Salvador are active and grow shell year round, modern shells with average $\delta^{18}\text{O}$ values of -0.5‰ should have precipitated when relative humidity was $\sim 89\%$ (see dashed line in Fig. 7A). This predicted value is higher than the observed average annual relative humidity ($\sim 77\%$) in the region. Nonetheless, land snails are mostly active and precipitate shell at night or during rain events, at the wettest times of the day (e.g., Cook, 2001; Pearce and Örstan, 2006). Accordingly, a relative humidity of $\sim 89\%$ looks reasonable for a low latitude oceanic island, and suggests that land snails record higher relative humidity values than mean values (see also Yanes et al., 2009, 2011a,b). Alternatively, if snails grew mostly during the rainy season, which has an average temperature of 24°C and an amount-weighted rain $\delta^{18}\text{O}$ value of -4.5‰ (SMOW), the predicted relative humidity is $\sim 87\%$, which is a plausible value as well. Because modern Annularidae shells exhibited $\delta^{18}\text{O}$ values similar to *Cerion*, the model calculates similar relative humidity values for both taxa. Equally, the model predicts comparable relative humidity values for living *Cerion* specimens measured by Baldini et al. (2007). Consequently, this model can be used to estimate environmental conditions from fossil shells on San Salvador with confidence.

5.3. Paleoenvironmental inferences

Carbonate sediment matrix in which shells were preserved displayed significantly different stable isotope values than fossil shells (Fig. 5C–D). This illustrates that potential contamination of carbonate sediment in shell samples should be minimal.

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossil shells clearly overlap with modern (both living and dead) snail values for both species (Fig. 6A–D). This finding suggests that the overall interglacial environmental conditions traced

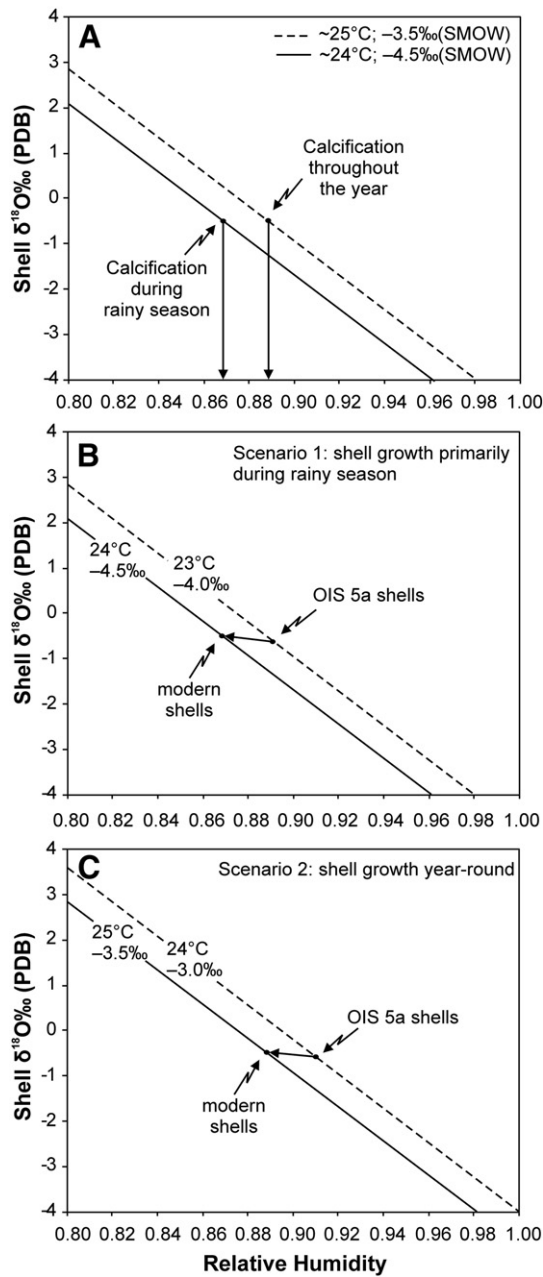


Fig. 7. Calculations of shell $\delta^{18}\text{O}$ values using the evaporative steady-state flux balance model of Balakrishnan and Yapp (2004), assuming (1) isotope equilibrium between environmental water and water vapor and (2) water loss by evaporation. (A) Modern shells. Dashed line represents the $\delta^{18}\text{O}$ values of shells that precipitate year round and track mean annual conditions (average annual temperature of 25 °C and environmental water $\delta^{18}\text{O}$ value of -3.5‰ vs. SMOW). Continuous line represents the $\delta^{18}\text{O}$ values of shells that precipitated mostly during the rainy months (from April to June and from September to October), using an average annual temperature of 24 °C and an environmental water $\delta^{18}\text{O}$ value of -4.5‰ (SMOW). Note that an equivalent environmental setting is predicted for both Cerionidae and Annularidae shells. Middle to late Holocene shells and OIS 5e shells likely precipitated under a comparable environmental scenario. (B) A possible paleoenvironmental scenario assuming that shells from The Gulf paleosol precipitated at ~85 ka (Hearty and Schellenberg, 2008) during rainy seasons only. (C) An alternative paleoenvironmental scenario if calcification of shells from The Gulf occurred at ~85 ka (Hearty and Schellenberg, 2008) throughout the year (see text). Note that even if shells from The Gulf precipitated during OIS 5a, atmospheric conditions appear to have been largely similar to the present.

by land snails while they have been active during several Holocene and late Pleistocene age-intervals in coastal sites of San Salvador were probably similar to those observed today. The relatively large dispersion of $\delta^{18}\text{O}$ values (Fig. 6C–D) at all age-intervals (including modern shells)

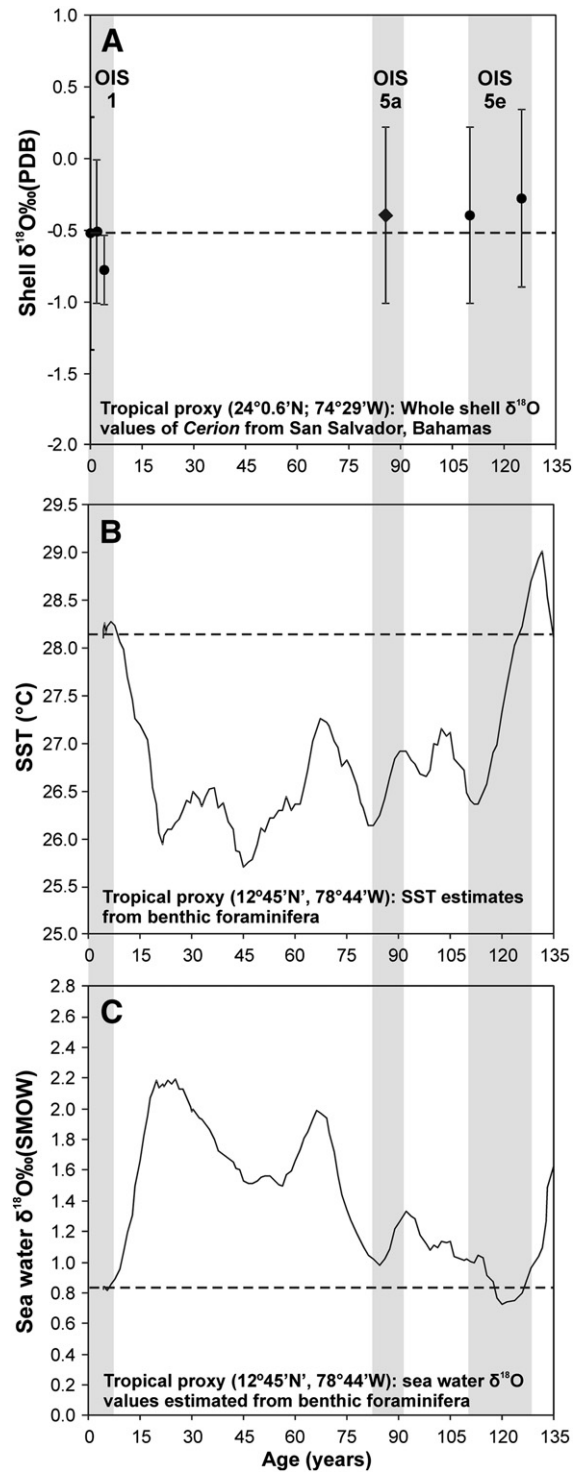


Fig. 8. Paleoclimatic proxies during OIS 5 and OIS 1 (gray bands). (A). Oxygen stable isotope values of Cerionidae shells from San Salvador Island (this study). (B) Tropical sea surface temperatures (SST) for western Caribbean region (Schmidt et al., 2004, 2006). (C) Estimates of seawater $\delta^{18}\text{O}$ values for western Caribbean region (Schmidt et al., 2004, 2006). Dashed lines represent modern values. Note that Hearty and Schellenberg (2008) dated shells from The Gulf paleosol (filled diamond) at ~85 ka (OIS 5a) whereas Carew and Mylroie (1995a,b) obtained an age of ~110 ka, i.e., regressive phase dune of OIS 5e (filled circle).

for both species reflect the large environmental variability at a microhabitat scale (e.g., Balakrishnan et al., 2005; Yanes et al., 2011b,c). Thus, daily and seasonal environmental variations, time-averaging, etc., contribute to the observed scatter of values. This stresses the crucial necessity of

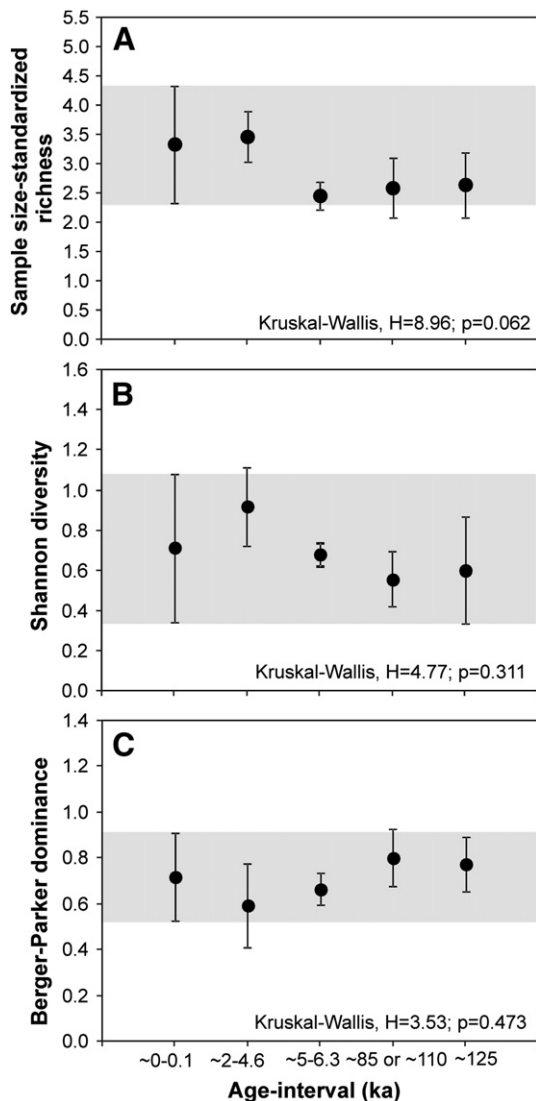


Fig. 9. Land snail richness and diversity per age-interval. (A) Sample-size standardized land snail richness. (B) Shannon diversity. (C) Berger–Parker simple dominance index. Filled circles represent average values whereas whiskers represent 1 σ standard deviation. Gray bands embrace the variation traced by modern specimens. Note that no convincing differences in snail richness and diversity are observed across age-levels. Data adapted from Yanes (2012).

analyzing a large number of specimens per sampling site and age-interval in paleoclimatic studies using land snails.

Conventional thought considers interglacial periods to be intervals of geologic time in which the atmospheric–oceanic circulation system fluctuated similar to that observed today (see review by Kukla et al., 2002). Schmidt et al. (2004, 2006) estimated sea surface temperatures (SST) by Mg/Ca paleothermometry combined with benthic foraminifera $\delta^{18}\text{O}$ values from a marine sediment core in the western Caribbean sea at latitude: 12° 45' N and longitude: 78° 44' W (Fig. 8B). SST at ~125 ka (OIS 5e) was similar to that observed today but ~1 °C lower during OIS 5a, at ~85 ka (Fig. 8B). Accordingly, it is reasonable to expect that air temperatures did not fluctuate substantially among these Pleistocene age-intervals on San Salvador. The oxygen isotopic composition of benthic foraminifera from the same core (Schmidt et al., 2004, 2006) also indicate that $\delta^{18}\text{O}$ values of the seawater did not vary considerably at those times (Fig. 8C). While seawater $\delta^{18}\text{O}$ values during OIS 5e were equivalent to present day values, seawater during OIS 5a was ~0.5‰ higher than today (Fig. 8C). According to this, rain water $\delta^{18}\text{O}$ values in tropical western Atlantic region may have experienced comparable magnitude of fluctuation of values.

If both Pleistocene sites studied here (Watling's Quarry and The Gulf) are respective eolianite transgressive and regressive phases of OIS 5e (Carew and Mylroie, 1985, 1995a,b 1997), both temperature and seawater $\delta^{18}\text{O}$ values (and possibly, rain water $\delta^{18}\text{O}$ values) were probably comparable to modern conditions (see Fig. 8B–C). Thus, late Pleistocene land snail shells may have precipitated at times when relative humidity conditions were similar to the present (~87–89%). If, however, shells from The Gulf precipitated during OIS 5a (Hearty and Schellenberg, 2008), temperatures were probably ~1 °C cooler (Fig. 8B) and rain water $\delta^{18}\text{O}$ values may have been ~0.5‰ higher (Fig. 8C) than today. In this second case, land snail shells preserved in The Gulf paleosol may have precipitated shell at times when relative humidity was just slightly higher (~89–91%) than today (Fig. 7B–C). Both paleoenvironmental possibilities (Fig. 7B–C) suggest that the overall environmental conditions in San Salvador during OIS 5a and/or OIS 5e were likely comparable to present conditions when snails were active and grew their shells.

Holocene conditions evaluated for various Caribbean islands have yielded controversial results. While some proxies have identified wetter conditions during the middle Holocene, others observed drier conditions than today. For example, pollen records from continental lake sediments showed that the middle Holocene (7–3.2 ka) in Haiti was characterized by high lake levels and the greatest relative abundance of pollen from moist forest taxa (Higuera-Gundy et al., 1999). The $\delta^{18}\text{O}$ values from a stalagmite from Barbados suggest that precipitation was enhanced during the period from 6.7 to 3.0 ka (Mangini et al., 2007). Other continental proxies from central Mexico (Metcalf et al., 1991) and Haiti (Curtis and Hodell, 1993) have revealed middle Holocene moisture conditions as well. In contrast, Costa Rican stalagmite $\delta^{18}\text{O}$ values suggest that the middle Holocene was a dry period in the Caribbean region (Lachniet et al., 2009). Holmes et al. (1995) concluded that the geochemical signature of ostracod shells from lakes in Jamaica revealed that between ~8 and 5 ka, conditions became drier in Jamaica. Inconsistent results may be explained by local (site-specific) temporal or spatial influencing factors such as summer precipitation and the influence of continental versus coastal conditions (e.g., Mangini et al., 2007). The presented data here suggest however that middle and late Holocene land snail shells appear to have precipitated under a very similar environmental scenario than today, that is, temperatures between ~24 and 25 °C, rain $\delta^{18}\text{O}$ values between –3.5‰ and –4.5‰ and relative humidity values of ~87–89% (Fig. 7A).

Other measures of apparent climatic stability on San Salvador include the statistically-equivalent sample-size standardized land snail richness (Fig. 9A), snail diversity (Fig. 9B), and simple dominance (Fig. 9C) observed by Yanes (2012). In addition, Gould (1988) recognized noticeable stability in *Cerion* populations on several Bahamian islands from the late Pleistocene to recent. Such perceptible expressions of interglacial environmental stability may have partly shaped land snail diversity on the island. Climatic stability in the Jamaican Pleistocene sedimentary record has been suggested to have favored local land snail evolutionary processes (Goodfriend and Mitterer, 1988). Dynesius and Jansson (2000) pointed out that climatically stable conditions have the potential to favor natural selection against dispersion because organisms are better adapted to the local habitat than to environments far away. This scenario may reduce gene flow which, in turn, may enhance speciation and specialization processes. Accordingly, it is possible that the inferred environmental stability here during these interglacial time-intervals on the Bahamas has in part facilitated land snail evolution in the Caribbean.

6. Conclusions

The carbon and oxygen stable isotope composition of well-preserved fossil shells of land snails from the Bahamas has the potential to record valuable environmental information during calcification. Tree-dwelling (Cerionidae) and ground-dwelling (Annularidae) snails from coastal sites of San Salvador Island suggest that paleoenvironmental conditions

during OIS 5e and/or OIS 5a and OIS 1 were largely similar to conditions prevailing currently. The $\delta^{13}\text{C}$ values indicate that snails followed a mixed diet that included C_3 and C_4 plants of variable proportions. If $\delta^{13}\text{C}$ values of shells were merely influenced by $\delta^{13}\text{C}$ values of the vegetation, modern snails consumed from as little as ~3% to as much as ~55% C_4 plants. Fossil shells suggest that the proportion of C_4 plants was greater during the late (~2–4.6 ka) and middle (~5–6.3 ka) Holocene and the late Pleistocene (~85 ka or ~110 ka, and ~125 ka) than today. The $\delta^{18}\text{O}$ values of the shell exhibited substantial scatters (up to ~3‰) at all sites and age-intervals linked to environmental variability at microhabitat scale. Similarity in the magnitude of the isotopic scatter across age-intervals implies comparable seasonal environmental variations. Calculations from a published snail flux balance mixing model and independent proxy data suggest that modern shells precipitated at times when temperature was ~24–25 °C, rain water $\delta^{18}\text{O}$ values were from –3.5‰ to –4.5‰, and relative humidity was ~87–89%. Shell $\delta^{18}\text{O}$ values suggest that such atmospheric conditions likely dominated during OIS 5e and/or OIS 5a and OIS 1 on coastal sites of San Salvador. The inferred atmospheric similarity across various Quaternary interglacial times matches well with the apparent similarity in snail richness, dominance and diversity at those locales and times. Because environmental stability appears to prevent dispersion and favors speciation and specialization, it is likely that the perceptible interglacial climatic stability here has driven to some extent the evolution of Caribbean terrestrial malacofaunas.

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