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SEASONAL VARIATION IN ECOLOGICAL AND TAPHONOMIC PROCESSES RECORDED IN SHELLY DEATH ASSEMBLAGES

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ABSTRACT

Modern valves of *Lucina pensylvanica* (Bivalvia: Lucinidae) were analyzed for $^{18}O/^{16}O$ ratios, drilling predation traces, biometric measurements, and taphonomic descriptors to explore seasonal variations in ecological and taphonomic processes within a death assemblage from Grand Bahama Island. The $\delta^{18}O$ values at the shell margin (=last growth episode) were used as a proxy for temperature at the time closest to the organism's death. Temperature estimates suggest that most individuals died in warmer months, whereas mortality appeared to have been lower during cooler seasons (<24 °C). Only drilled valves yielded the coldest temperatures at the shell margin (~18.1–21.3 °C), whereas exclusively undrilled valves exhibited the hottest temperatures at the last growth episode (~25.5–26.5 °C). Drilled valves were significantly smaller and exhibited higher taphonomic alteration than undrilled valves, pointing to postmortem transport and sorting. While seasonal variations in predation and growth rates may have affected the observed patterns to some extent, the results, at least partly, reflect hydrodynamic variations throughout the year, which may have induced seasonal variation in postmortem sorting of drilled and undrilled valves. This study illustrates that, by combining geochemical proxies and quantitative paleoecological data, more informed ecologic and taphonomic interpretations can be achieved for subfossil and fossil assemblages.

INTRODUCTION

Drill holes made by gastropods in shells are produced *in vivo* and typically result in the death of the prey. Consequently, drill holes preserved in fossil and subfossil mollusk shells have been used widely to explore predator-prey interactions (for reviews and references, see Vermeij, 1983; Kitchell, 1986; Kabat, 1990; Kowalewski and Kelley, 2002; Harper, 2006). In particular, the frequency of drill holes preserved in hard skeletons, including mollusks and other shell-bearing taxa, have been measured to examine trends in predation intensity in ancient ecosystems from local to global scales (e.g., Kelley, 1988; Kowalewski et al., 1998, 2000; Leighton, 2002; Harper, 2003; Kelley and Hansen, 2006; Harries and Schopf, 2007; Hauser et al., 2008; Hasegawa and Sato, 2009; Yanes and Tyler, 2009; and references therein). One aspect of predator-prey interactions inherently difficult to assess in the fossil record, however, is the seasonality in predation intensity. In this study, we combine geochemical approaches (stable isotopes) and drilling predation data to assess seasonal changes in ecological and taphonomic aspects of drilling predation.

Observations in modern ecosystems suggest that activity of drilling predators varies seasonally as a response to several abiotic (e.g., temperature, salinity, wave-exposure) and biotic (e.g., predator competition, prey abundances, prey accessibility) factors. For example, previous field studies suggest that in modern marine ecosystems naticid gastropods drill bivalve shells more frequently during the warmest season of the year (e.g., Edwards and Huebner, 1977; Quijón et al., 2007). Similarly, experimental studies by Garton and Stickle (1980) showed that muricids drilled prey shells more frequently at relatively high temperature and salinity. This is in agreement with subsequent field studies that recorded a lower intensity of predation for muricid gastropods during winter months (e.g., Rilov et al., 2001).

The intensity of taphonomic processes is also expected to vary seasonally, for example, in response to changes in the frequency and magnitude of storm events. Unfortunately, due to pervasive time averaging (e.g., Flessa et al., 1993; Kowalewski et al., 1998; Kidwell et al., 2005; Kosnik et al., 2007; Krause et al., 2010), neither the fossil record of shell-bearing organisms nor surficial shell assemblages found on modern depositional surfaces are resolved sufficiently to separate specimens by season. Not surprisingly, previous studies of the preservation potential of drilled and undrilled shells have not addressed the issue of seasonality. Some previous studies reported that drilled and undrilled specimens did not differ significantly in terms of their preservational potential (e.g., Nebelsick and Kowalewski, 1999; Kaplan and Baumiller, 2000), whereas other studies suggested that taphonomic biases may affect the fossil record of drilling predation to various degrees (e.g., Roy et al., 1994; Harper et al., 1998; Zuschin and Stanton, 2001; Yanes and Tyler, 2009). Similarly, field studies have demonstrated that drilled and undrilled shells respond differently to hydrodynamic processes, due, most likely, to differences in entrainment velocity (e.g., Lever et al., 1961; Kaplan and Baumiller, 2000).

Drilled shells not only offer direct evidence for predation events, but they also may yield information about the environmental conditions existing at the time an organism was preyed upon. In particular, the stable oxygen isotopic composition of biogenic carbonates has been a useful tool as a paleothermometer due to the temperature dependence of equilibrium oxygen isotope exchange between water and biogenic aragonite (e.g., Grossman and Ku, 1986). Indeed, numerous studies have demonstrated the usefulness of the oxygen isotopic signatures of modern and fossil shells for reconstructing high-resolution climatic and or environmental variations (i.e., ocean water $\delta^{18}O$ and temperature) through an organism's life as well as for evaluating shell growth and metabolic rates (e.g., Goodwin et al., 2001, 2003, 2008; Kobashi et al., 2001; Dietl et al., 2002; Ivany et al., 2003; Kobashi and Grossman, 2003; Surge et al., 2003; Schöne et al., 2003, 2006; Jones et al., 2005; Fenger et al., 2007; Schöne and Feibig, 2009; and references therein).

In the present study, oxygen stable isotope analyses, drilling predation patterns, body size estimates, and taphonomic data were collected jointly using surficial dead valves of *Lucina pensylvanica* from a sandy shore of Port Lucaya, Grand Bahama Island. Using this multifaceted approach, stable isotope estimates of the approximate seasonal time closest to an organism's death, drilling predation patterns, and taphonomic features of shells were explored together.

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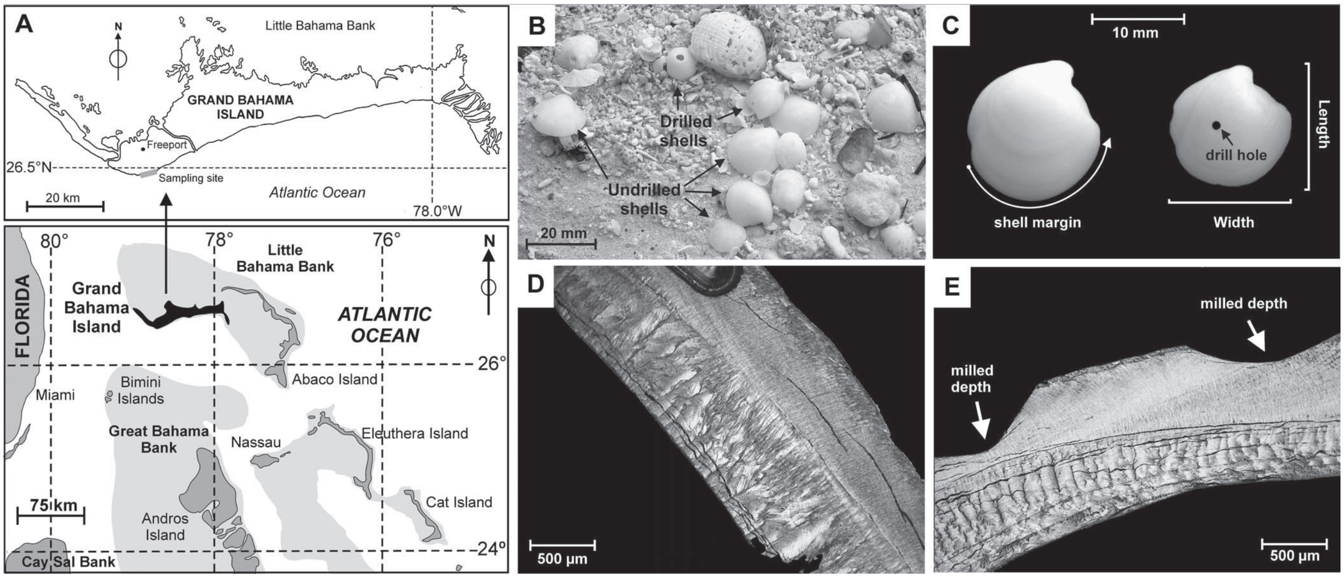

FIGURE 1—Location of the study site and bivalve species selected. A) Geographic setting of the sampling locality in Grand Bahama Island. B) Drilled and undrilled bivalves photographed *in situ*. C) Detailed view of one drilled and one undrilled valve of *Lucina pensylvanica*, indicating length and width measurements taken from each specimen. White arrow indicates the area from which carbonate dust was generated along valve margin (i.e., the most recent shell material secreted prior to the organism's death). D–E) Thin sections of *Lucina pensylvanica* showing shell microstructure.

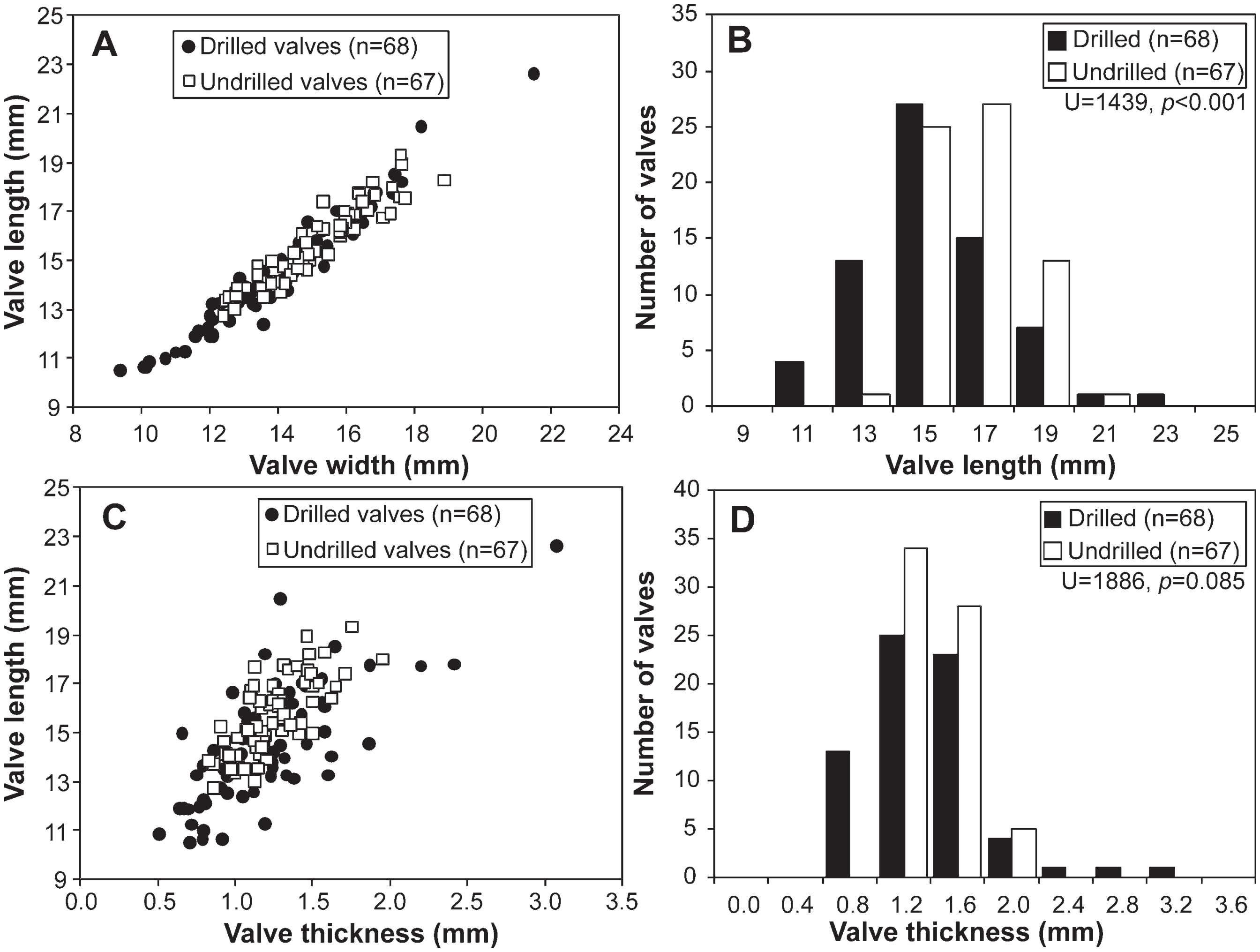

FIGURE 2—Valve size of *Lucina pensylvanica*. A) A scatter plot of valve length and valve width of drilled (black circles) and undrilled (open boxes) specimens. B) A scatter plot of valve length and valve thickness of drilled (black circles) and undrilled (open boxes) specimens. C) Size-frequency distribution of valve length of drilled (black bars) and undrilled (open bars) specimens. D) Size-frequency distribution of valve thickness of drilled (black bars) and undrilled (open bars) specimens.

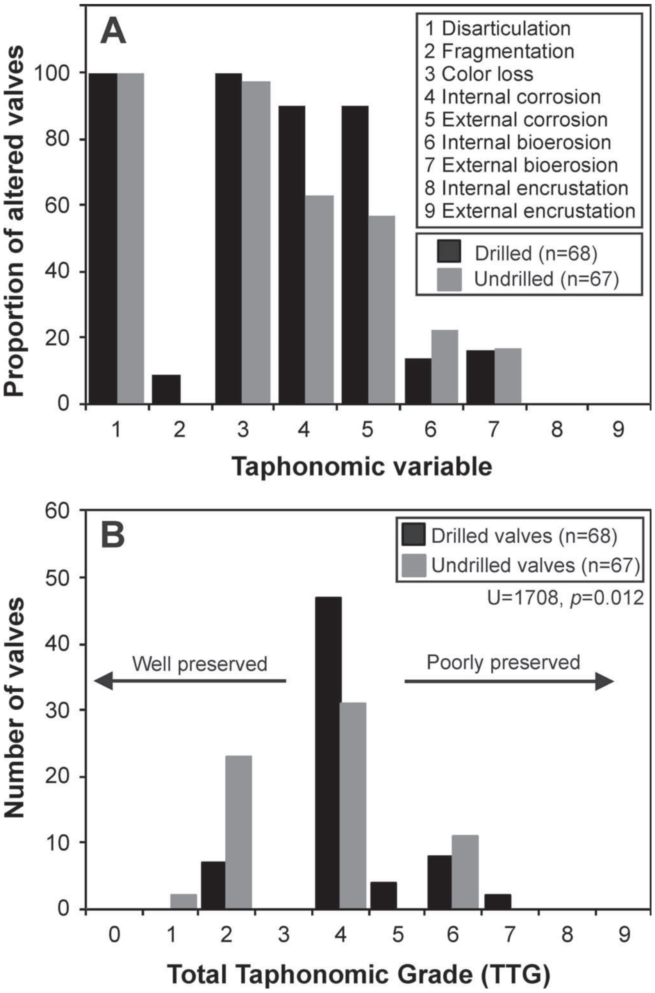

FIGURE 3—Taphonomic comparison of drilled and undrilled valves of *Lucina pensylvanica*. A) Proportion of drilled and undrilled valves displaying nine types of taphonomic alterations. B) Frequency distribution of the total taphonomic grade (TTG) of drilled and undrilled valves.

MATERIALS AND METHODS

Study Area

The Bahamas archipelago includes over 2,700 low-latitude islands, cays, and rocks that are located to the southeast of the coast of Florida. The Bahamas began to form about 200 myr, as emerging shallow carbonate banks surrounded by abyssal ocean. The islands are characterized by relatively flat landscapes, with the highest elevation reaching only 30–60 m above sea level (a.s.l.) (Carew and Mylroie, 1995a, 1995b, 1997). The Bahamian islands contain multiple habitat types including wetlands, saline lagoons, mangrove swamps, coastal flats, and inter-tidal mudflats. Although the dominant vegetation is low and dense with abundant herb and shrub forms, the northern islands include tree-size vegetation. The islands are covered by upper Pleistocene eolianite deposits varying in thickness from 10 to 45 m (e.g., Carew and Mylroie, 1995a, 1995b, 1997; Mylroie and Carew, 1995). The climate of the Bahamas is characterized by wet summers and relatively dry winters.

This study focuses on shells collected on Grand Bahama Island, an approximately 116-km-long and 25-km-wide island (Fig. 1A), located about 100 km southeast off the coast of Florida. In West Palm Beach, Florida, located at 26°42′ latitude north, less than 100 miles west from Grand Bahama Island, a meteorological station regulated by the National Oceanic and Atmospheric Administration (NOAA) indicates that the current mean monthly air temperatures range from ~18.7 °C in January to ~28.3 °C in August (http://www.ncdc.noaa.gov/cdo-web/search). Sea surface temperatures (SST) were downloaded from the station LKWF1 (also regulated by NOAA), located in Lake Worth, Florida, at 26°36′ latitude north. Measured monthly SST, for the 1990–2006 recording period, ranged from ~20.3 ± 1.9 °C in February to as much as ~30.9 ± 0.5 °C in August. Monthly SST extreme values ranged from 14.6 °C in February of 1996 to 32.0 °C in August of 2006 (http://www.ndbc.noaa.gov/data/climatic/LKWF1.txt). Mean monthly SST suggests that fall–winter months are represented by temperatures cooler than ~24 °C whereas spring–summer seasons are characterized by temperatures warmer than ~24 °C.

Lucina pensylvanica.—The species targeted in this study is *Lucina pensylvanica* (Linnaeus, 1758) (Figs. 1B–C), which was the dominant species at the studied site and showed evidence of drilling predation, most likely by naticid gastropods. *L. pensylvanica* inhabits sandy sea-grass areas from 0 to 3 m water depth, ranges in latitude from 9° to 35°N, and is known from the fossil record extending back to the Pleistocene (e.g., Schweimanns and Felbeck, 1985).

L. pensylvanica belongs to the Lucinidae (Bivalvia), a family that contains a large number of species that inhabit diverse habitats and occur over a wide latitudinal range (from 60°N to 55°S). The Indo-West Pacific and Atlantic reef environments exhibit the highest diversity of lucinids (Taylor and Glover, 2006; Glover and Taylor, 2007). Lucinids can occupy a broad range of settings, including mangrove muds, intertidal and offshore muds and sands, seagrass areas, and organic-rich settings (Taylor and Glover, 2006; Glover and Taylor, 2007).

Little is known about the biology of *L. pensylvanica*. This taxon appears to burrow with the anterior part of the shell pointing upward (Taylor et al., 2004). A detailed shell structure study by Taylor et al. (2004) suggests that live-collected *L. pensylvanica* from Florida Keys deposits shell material quickly and constantly until reaching ~18 mm in shell length. At sizes above ~18 mm, growth rates appear to slow down and become sporadic (Taylor et al., 2004).

Sample Processing and Specimen Description

Numerous dead bivalve specimens (including both left and right valves) of *L. pensylvanica* (Figs. 1B–C) were collected along the sandy shore of Port Lucaya, the southern shore of Grand Bahama Island (Fig. 1A). Shells were collected by hand along a ~2 km transect parallel to the shoreline by two researchers. All encountered individuals were picked up regardless of their size.

For each specimen, valve size was estimated using linear morphometric measurements (Table 1), including (1) maximum valve length, from umbo to shell margin (Fig. 1C); (2) maximum valve width, perpendicular to valve length (Fig. 1C); and (3) valve thickness, which was estimated at the anterior valve margin. All measurements were acquired to the nearest 0.02 mm using a digital caliper (Fig. 1C).

Several shells were thin-sectioned in the Department of Earth and Environmental Sciences (University of Kentucky) from the umbo to the margin along the axis of maximum growth using a low-speed saw to study the internal architecture of shell layers. Shell microstructure was then evaluated under a petrographic microscope in the Instituto Andaluz de Ciencias de la Tierra (CSIC-Universidad de Granada) (Fig. 1D).

Each valve was described in terms of six taphonomic features scored under a binocular microscope. These included disarticulation, fragmentation, color loss, corrasion, bioerosion, and encrustation. The taphonomic data were recorded as binomial variables, where (=1) was assigned for poorly preserved valves and (=0) was assigned for well-preserved valves. Detailed explanation of the taphonomic analysis used here is described by Yanes and Tyler (2009). The Total Taphonomic Grade (TTG) was recorded for each valve as the sum of all the taphonomic features. The possible array of TTG in this study varied from 0, which means that shells are nearly pristine (=well preserved) to 9, which translates that shells are strongly taphonomically damaged (=poorly preserved).

TABLE 1—Size, Total Taphonomic Grade (TTG), δ^{18}O values and temperature estimates at the shell margin of undrilled (=0) and drilled (=1) valves of *Lucina pensylvanica* from Grand Bahama Island.

Valve #	Valve side	Length (mm)	Width (mm)	Thickness (mm)	Drill hole	Total Taphonomic Grade (TTG)	Shell margin δ^{18}O‰ (PDB)	Calculated temperature (°C)
1	L	17.78	16.90	2.41	1	4	−0.9	25.3
2	L	16.19	15.29	1.37	1	4	−0.7	24.5
4	R	17.75	16.80	1.87	1	4	−0.4	23.3
5	L	17.71	17.36	2.20	1	4	−0.4	23.1
6	R	22.62	21.49	3.07	1	4	−0.7	24.6
7	R	16.62	16.43	0.98	1	4	−0.5	23.8
8	L	18.50	17.43	1.64	1	4	−0.3	22.9
9	L	20.48	18.19	1.29	1	4	−0.8	24.9
11	L	16.21	15.95	1.56	1	4	−0.7	24.4
12	L	16.55	14.88	1.27	1	4	−0.7	24.5
13	R	15.58	15.44	1.13	1	4	0.1	21.1
14	L	16.91	15.97	1.45	1	4	−0.5	23.5
15	R	16.54	16.50	1.11	1	4	−0.4	23.5
16	R	12.57	12.08	1.12	1	4	0.1	21.3
17	L	14.03	13.39	1.62	1	4	−0.7	24.8
18	L	14.17	14.04	1.22	1	4	−0.1	22.1
19	R	13.12	13.35	1.38	1	4	0.2	20.8
20	R	16.04	16.20	1.58	1	4	−0.6	24.2
21	L	14.55	14.42	1.46	1	4	−0.3	23.0
22	L	15.02	14.09	1.58	1	4	−0.6	24.2
23	R	17.00	16.44	1.26	1	4	−0.5	23.8
24	R	15.12	14.82	1.14	1	4	−0.5	23.8
25	R	15.71	14.63	1.43	1	4	0.3	20.1
26	L	15.44	14.58	1.08	1	4	−0.8	25.2
27	L	18.20	17.63	1.19	1	4	−0.7	24.8
28	L	14.10	14.15	1.02	1	6	−0.1	22.0
29	R	13.58	13.70	1.24	1	4	0.2	20.6
30	R	13.50	13.05	0.95	1	5	0.4	20.0
31	R	14.20	14.11	1.25	1	4	−0.3	22.7
32	R	12.38	13.58	1.05	1	6	−0.2	22.6
33	R	14.00	13.69	1.18	1	4	−0.7	24.5
34	R	17.20	16.74	1.56	1	4	−0.6	24.1
35	R	13.52	13.79	0.93	1	4	−0.9	25.2
36	R	13.76	13.27	0.97	1	4	−0.4	23.2
37	R	17.01	15.72	1.43	1	7	−0.5	23.7
38	L	14.44	13.40	1.15	1	6	−0.8	24.8
39	R	13.21	13.26	1.23	1	4	0.3	20.1
40	R	13.25	12.24	1.33	1	7	−0.7	24.8
41	R	13.23	12.08	0.95	1	5	−0.7	24.5
42	R	13.80	14.27	1.24	1	2	−0.2	22.4
43	R	13.62	13.20	0.79	1	4	0.6	18.9
44	L	13.25	12.84	0.75	1	4	−0.2	22.3
45	L	11.86	12.03	0.70	1	2	0.4	20.0
46	L	14.53	13.58	1.86	1	4	−0.6	24.0
47	R	16.64	16.24	1.35	1	2	−0.8	25.2
48	L	12.72	12.00	0.91	1	4	0.3	20.3
49	L	11.90	11.57	0.67	1	2	−0.4	23.3
50	R	14.98	14.94	0.66	1	2	−0.6	24.2
51	R	13.48	13.08	0.95	1	4	0.5	19.5
52	L	14.26	12.88	0.86	1	5	−0.8	24.8
53	L	10.67	10.08	0.92	1	6	−0.3	23.0
54	L	12.10	11.68	0.81	1	4	0.0	21.4
55	R	15.81	15.12	1.06	1	6	−0.8	25.0
56	L	10.86	10.23	0.51	1	4	−0.9	25.4
57	R	11.92	12.09	0.64	1	4	0.1	21.0
58	R	13.26	12.37	1.60	1	6	−0.6	24.3
59	R	10.52	9.38	0.71	1	6	−0.5	23.5
60	L	11.29	11.28	1.19	1	4	−0.5	23.5
61	R	12.24	11.95	0.80	1	4	−0.2	22.6
62	L	11.01	10.70	0.80	1	4	−0.2	22.2
63	R	11.97	12.09	0.77	1	4	0.8	18.1
64	L	10.66	10.15	0.79	1	4	0.2	20.6
65	R	11.25	10.99	0.72	1	2	−0.7	24.6
66	L	14.12	14.22	1.04	1	2	−0.8	25.2
67	L	12.53	12.58	0.95	1	4	0.3	20.2
68	R	13.95	13.01	1.32	1	5	−0.6	24.0
69	L	14.75	15.35	1.05	1	4	−0.2	22.2
70	L	14.47	14.42	1.29	1	6	−0.8	25.2
71	R	16.44	15.81	1.09	0	4	−0.9	25.7
72	L	15.08	14.56	1.30	0	6	0.0	21.6

TABLE 1—Continued.

Valve #	Valve side	Length (mm)	Width (mm)	Thickness (mm)	Drill hole	Total Taphonomic Grade (TTG)	Shell margin δ^{18}O‰ (PDB)	Calculated temperature (°C)
73	L	13.68	12.78	1.02	0	2	−0.9	25.3
74	R	15.33	14.48	1.36	0	4	−1.0	25.7
75	R	13.51	13.56	0.97	0	4	−1.1	26.4
76	R	14.39	14.36	1.14	0	4	−0.4	23.4
77	L	16.87	16.10	1.65	0	4	−0.6	24.3
78	L	14.65	14.35	0.93	0	4	−0.7	24.7
79	R	14.06	14.20	1.01	0	4	−0.8	25.1
80	R	15.39	15.10	1.42	0	2	−0.2	22.5
81	L	17.40	16.47	1.49	0	4	−0.9	25.2
82	L	16.74	17.06	1.10	0	4	−1.0	25.7
83	L	15.98	15.82	1.17	0	4	−0.3	22.8
84	R	14.66	14.56	1.13	0	4	−0.9	25.5
85	L	17.71	16.36	1.40	0	4	−0.3	23.0
87	L	17.05	16.62	1.45	0	2	−0.8	25.1
88	L	18.00	17.35	1.95	0	1	−0.3	22.7
89	L	18.28	18.88	1.58	0	1	−0.8	24.9
90	L	15.00	14.92	1.46	0	2	−0.5	23.5
91	R	13.88	12.79	1.20	0	6	−0.5	23.8
92	R	16.18	15.79	1.28	0	4	−0.7	24.4
93	R	14.04	13.79	0.96	0	2	−0.9	25.6
94	R	13.54	12.77	1.15	0	2	−0.6	24.1
95	R	14.61	14.85	1.18	0	2	0.0	21.5
96	L	16.33	15.87	1.24	0	2	−1.0	25.9
97	R	16.39	15.15	1.62	0	2	−0.9	25.6
98	R	17.01	15.95	1.54	0	4	−0.9	25.4
99	L	16.25	15.85	1.50	0	4	−0.8	25.1
100	L	17.58	17.54	1.34	0	4	−0.2	22.4
101	L	14.15	14.03	0.94	0	4	−0.2	22.4
103	R	16.92	17.30	1.12	0	4	−1.0	26.0
104	R	15.26	15.46	0.91	0	4	−0.4	23.4
105	R	17.67	16.84	1.13	0	4	−0.4	23.4
106	R	14.95	13.82	1.50	0	6	−0.7	24.5
107	L	13.89	13.02	0.98	0	2	−0.5	23.8
108	L	14.98	14.61	1.41	0	2	−1.0	26.0
109	L	16.57	15.97	1.28	0	2	−0.7	24.4
110	L	16.88	16.21	1.50	0	4	−0.5	23.6
111	L	12.72	12.40	0.86	0	4	−0.7	24.6
112	R	15.10	14.60	1.08	0	4	−0.9	25.4
113	L	17.75	16.38	1.31	0	6	−0.2	22.2
114	L	14.11	13.71	1.16	0	2	0.0	21.3
115	R	15.71	14.83	1.31	0	4	−0.6	24.3
116	L	16.12	15.82	1.22	0	6	−0.4	23.4
117	L	18.21	16.77	1.48	0	6	−0.2	22.2
118	R	13.01	12.72	1.13	0	4	−0.3	22.7
119	L	16.27	15.32	1.29	0	2	−0.7	24.7
120	R	13.84	13.50	0.83	0	2	−0.7	24.6
121	R	14.41	13.39	1.17	0	4	−1.0	26.0
122	R	14.80	13.40	1.02	0	2	−0.8	25.0
123	R	19.31	17.59	1.75	0	2	−0.8	25.0
124	L	15.13	14.56	1.30	0	4	0.1	21.3
125	L	14.86	14.27	1.19	0	2	−0.7	24.6
126	L	17.53	17.73	1.47	0	6	−0.5	23.6
127	L	13.36	12.44	1.00	0	2	−0.8	24.8
128	R	18.91	17.61	1.46	0	6	−0.5	23.9
129	R	16.07	14.70	1.28	0	6	−0.6	24.2
130	R	13.50	12.54	1.06	0	6	−0.5	23.7
131	R	17.42	15.32	1.71	0	4	−0.9	25.2
132	R	15.25	14.88	1.14	0	4	−0.7	24.4
134	L	16.93	16.01	1.24	0	2	−0.4	23.1
135	R	15.07	14.74	1.17	0	4	0.0	21.7
136	L	14.77	14.15	1.11	0	2	−1.0	25.7
137	L	15.40	15.15	1.24	0	4	−0.9	25.4
138	L	16.28	16.22	1.16	0	2	−0.6	24.0
139	L	13.69	14.07	0.86	0	2	−0.2	22.2
140	R	15.14	14.59	1.07	0	6	−0.8	24.8

L=left valve, R=right valve; 1=drilled valve, 0=undrilled valve.

TABLE 2—Intrashell oxygen stable isotope profiles along the growth axis (from shell margin toward the umbo).

Sample ID	Intrashell $\delta^{18}O$‰ (PDB)	Calculated temperature (°C)	Distance from shell margin (mm)	Length (mm)	Width (mm)
GBPL-undrilled-4-1	−0.3	22.6	shell margin	18.07	17.61
GBPL-undrilled-4-2	−0.4	23.4	1		
GBPL-undrilled-4-3	−0.6	24.0	2		
GBPL-undrilled-4-4	0.0	21.7	3		
GBPL-undrilled-4-5	−0.1	21.8	4		
GBPL-undrilled-4-6	−0.1	21.8	5		
GBPL-undrilled-4-7	0.2	20.5	6		
GBPL-undrilled-4-8	1.0	17.3	7		
GBPL-undrilled-4-9	0.6	19.0	8		
GBPL-undrilled-4-10	0.0	21.7	9		
GBPL-undrilled-4-11	0.1	21.0	10		
GBPL-undrilled-4-12	−0.2	22.3	11		
GBPL-undrilled-5-1	−0.6	24.0	shell margin	16.14	17.02
GBPL-undrilled-5-2	−1.1	26.2	1		
GBPL-undrilled-5-3	−0.1	21.9	2		
GBPL-undrilled-5-4	0.6	19.0	3		
GBPL-undrilled-5-5	1.0	17.3	4		
GBPL-undrilled-5-6	0.9	17.7	5		
GBPL-undrilled-5-7	0.0	21.5	6		
GBPL-undrilled-5-8	−0.6	24.3	7		
GBPL-undrilled-5-9	0.6	18.7	8		
GBPL-undrilled-5-10	0.5	19.5	9		
GBPL-undrilled-6-1	0.1	21.2	shell margin	13.47	12.93
GBPL-undrilled-6-2	−1.0	26.1	1		
GBPL-undrilled-6-3	0.0	21.6	2		
GBPL-undrilled-6-4	0.7	18.3	3		
GBPL-undrilled-6-5	0.1	20.9	4		
GBPL-undrilled-6-6	0.0	21.4	5		
GBPL-undrilled-6-7	0.2	20.8	6		
GBPL-drilled-1-1	−0.8	25.1	shell margin	17.33	16.95
GBPL-drilled-1-2	−1.0	26.0	1		
GBPL-drilled-1-3	0.2	20.5	2		
GBPL-drilled-1-4	0.2	20.6	3		
GBPL-drilled-1-5	−0.1	22.1	4		
GBPL-drilled-1-6	−0.3	22.7	5		
GBPL-drilled-1-7	0.1	21.0	6		
GBPL-drilled-1-8	−0.7	24.7	7		
GBPL-drilled-1-9	−0.7	24.7	8		
GBPL-drilled-1-10	0.2	20.8	9		
GBPL-drilled-2-1	−1.5	28.1	shell margin	13.88	14.13
GBPL-drilled-2-2	−0.4	23.3	1		
GBPL-drilled-2-3	−0.9	25.6	2		
GBPL-drilled-2-4	−0.4	23.1	3		
GBPL-drilled-2-5	−0.4	23.3	4		
GBPL-drilled-2-6	−0.4	23.3	5		
GBPL-drilled-2-7	−0.3	22.7	6		
GBPL-drilled-2-8	−0.5	23.6	7		
GBPL-drilled-2-9	−0.7	24.6	8		
GBPL-drilled-2-10	−0.7	24.7	9		
GBPL-drilled-3-1	−0.1	21.9	shell margin	12.54	12.26
GBPL-drilled-3-2	−1.7	28.9	1		
GBPL-drilled-3-3	−0.5	23.8	2		
GBPL-drilled-3-4	−0.2	22.5	3		
GBPL-drilled-3-5	1.1	16.9	4		
GBPL-drilled-3-6	0.2	20.8	5		
GBPL-drilled-3-7	−0.7	24.6	6		
GBPL-drilled-3-8	0.2	20.7	7		

Two seawater samples were collected in the summer of 2008 from the shallow waters of Port Lucaya coast using plastic vials that were immediately sealed to prevent evaporation.

Analytical Methods

All samples, including sea water and bivalve shells were prepared and analyzed in the Savannah River Ecology Laboratory (University of Georgia) using a Finnigan Delta^{PLUS} XL continuous flow isotope ratio mass spectrometer (CF-IRMS). All stable isotope results are reported in δ notation relative to the international standard Standard Mean Ocean Water (SMOW) for seawater or Pee Dee Belemnite (PDB) for shell carbonate. The δ values are defined as:

$$\delta^{18}O = \left[\left({}^{18}O/{}^{16}O_{\text{sample}}\right)/\left({}^{18}O/{}^{16}O_{\text{standard}}\right) - 1\right] \times 1000(‰)$$

Stable Oxygen Isotopic Analysis of Sea Water

Twelve ml exetainers™ containing a small aliquot (<0.2 ml) of 100% H_3PO_4 acid were flushed with 0.3% CO_2 in He to replace air in the headspace. One half ml of water was then injected through a septum

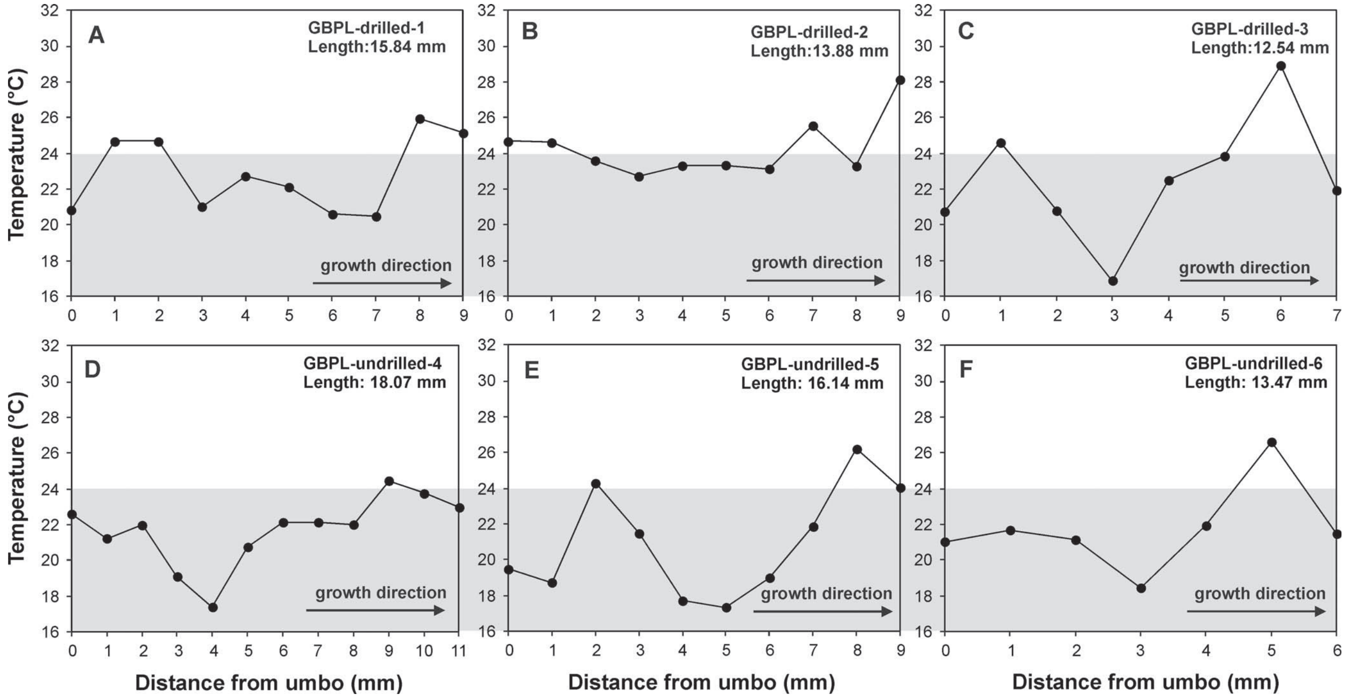

FIGURE 4—Temperature estimates from intrashell oxygen isotope profiles along the shell growth axis. A–C) Drilled valves. D–F) Undrilled valves. Gray band represents observed fall–winter temperatures on the sea surface in the study area (~18–24 °C). Note that shell carbonate precipitates throughout most seasons, except for the hottest months.

into the vial and left to equilibrate at 25 °C for 48 hours. The headspace was then analyzed using a Gas Bench II peripheral device connected to the CF-IRMS. Precision was ±0.1‰ (1σ standard deviation) based on multiple measurements of the international GISP and SMOW water standards, and in-house water standards (n = 6).

Stable Oxygen Isotopic Analysis of Shell Carbonate

Shells were rinsed with deionized water by ultrasonication for 30 minutes to remove sand and other debris, and thereafter air dried at room temperature for 48 hours.

Three drilled and three undrilled shells were sampled subsequently along the axis of maximum growth to attain complete intrashell oxygen isotope profiles parallel to growth direction. The isotope profiles were used to (1) explore the temperature range at which shell is deposited through life history of individual specimens (does *L. pensylvanica* precipitate shell across seasons in the Bahamas?), and (2) evaluate if the shell margin is a reasonable proxy for the temperature at the time closest to specimen death (does *L. pensylvanica* shell margin approximate the season closest to specimen death?).

Thin sections reveal that the skeleton microstructure of *L. pensylvanica* consists of three layers (Fig. 1D). The outer layer contains crystals of constant ~0.6–0.7 mm thickness. The middle layer comprises a thin crossed-lamellar structure of variable thickness. The inner layer consists of a prismatic structure also with varying thickness. Approximately 150 µg of shell carbonate was milled out of the outer shell surface (~0.5 mm deep) using a ~500-µm-diameter drill bit (Fig. 1E). Samples were collected every ~1 mm from the shell margin toward the umbo, parallel to shell growth direction. Posterior thin sections of the six studied shells confirmed that carbonate was milled out exclusively from the outer shell surface layer (Fig. 1E).

A total of 135 valves were sampled afterward solely along the ventral margin of the valve edge, which is assumed to represent the carbonate deposited closest to the time of death. Approximately 150 µg of carbonate powder was milled out from the valve margin using an electronic dremel, which was passed slowly along the margin of each shell (see arrow in Fig. 1C).

Carbonate powder samples were placed in 6 ml exetainer™ vials that were subsequently flushed with helium to replace the headspace. The carbonate was then converted to CO_2 gas by adding 0.5 ml of 100% H_3PO_4 at 25 °C. The resulting CO_2 was analyzed isotopically after 24 hours using the GasBench II and the CF-IRMS. Oxygen isotope values were calibrated against the international standard NBS-19 and in-house standards. The precision of the analyses were better than ±0.1‰ (1σ standard deviation) based on the repeated measurement of the NBS-19 and in-house standards (n = 20).

Temperature estimates (Table 2) were obtained by applying the measured $\delta^{18}O$ values of both the local sea water (+0.6‰ vs. SMOW; n = 2) and *L. pensylvanica* shells into the modified temperature equation proposed by Grossman and Ku (1986):

$$T(^{\circ}C) = 19.7 - 4.34\left[\left(\delta^{18}O_{aragonite}\right) - \left(\delta^{18}O_{water} - 0.2\right)\right]$$

Modifications to the equation included (1) the calibration to Standard Mean Ocean Water (SMOW), and (2) the 0.2‰ subtraction of the measured $\delta^{18}O_{water}$ value (e.g., Dettman et al., 1999; Goodwin et al., 2001).

Statistical Analysis

Nonparametric (rank-based) tests were conducted using PAST 1.38b software (Hammer et al., 2001). A significance level of $\alpha = 0.05$ was assumed. Spearman rho correlation was computed to evaluate the potential rank-correlations between variables. The Mann-Whitney U test was used to estimate potential differences in central tendency among *a priori* defined groups of observations (e.g., drilled against undrilled specimens).

RESULTS

Valve Size and Valve Preservation

Valves of *L. pensylvanica* ranged from 10.52 to 22.62 mm long, from 9.38 to 21.49 mm wide, and from 0.51 to 3.07 mm thick (Table 1).

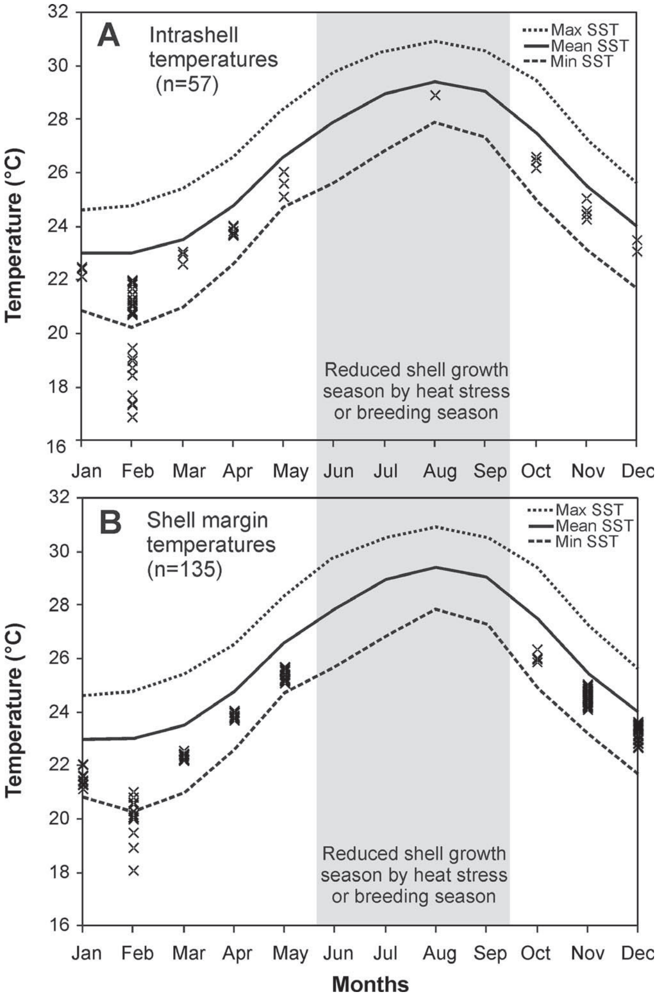

FIGURE 5—Temperature estimates from shell $\delta^{18}O$ values (symbols) and observed maximum, mean, and minimum SST (black lines) throughout the year. Gray band represents the plausible breeding season for *Lucina pensylvanica* (Bigatti et al., 2004), which coincides with time when heat stress is most likely to arrest the shell growth. A) Temperature estimates from $\delta^{18}O$ values from six individuals sampled along the growth axis. B) Temperature estimates based on $\delta^{18}O$ values at the shell margin collected from 135 specimens. Note that this figure merely represents a hypothetical number match between observed SST and calculated SST from the shell to graphically illustrate that most observed SST bins overlap with calculated values from shells.

Drilled and undrilled valves showed similar range of sizes (Figs. 2A–D), however, drilled valves were significantly smaller than undrilled ones (Fig. 2A, C) (Mann-Whitney U test; U = 1439, $p < 0.001$). Drilled valves were also marginally significantly thinner than undrilled valves (Mann-Whitney U test; U = 1886, $p = 0.087$). Of the 68 drilled valves, 32 were left valves whereas 36 were right valves. Such ratio (47:53) is not significantly different from a 50:50 ratio ($p = 0.54$, binomial test).

Valves were largely affected by various biostratinomic processes, including disarticulation, color loss, and internal and external corrosion (Fig. 3A). A small proportion of valves were affected by fragmentation and bioerosion, whereas no valves were affected by encrustation (Fig. 3A). Drilled valves exhibited slightly higher taphonomic alteration for some variables (Fig. 3A). When all variables were considered jointly, significant differences were observed between drilled and undrilled valves (Mann-Whitney U test; U = 1708, $p = 0.012$), with drilled valves exhibiting significantly higher TTG (i.e., appreciably higher taphonomic alteration) than undrilled valves (mean TTG = 4.2 vs. mean TTG = 3.6, respectively; Fig. 3B).

Temperature Estimates along Shell Growth Axis

Given that shells were collected from a sandy shoreline, which represents a setting experiencing intense taphonomic processes, valves exhibited variable degrees of alteration. Consequently, many specimens lacked prominent rhythmic banding patterns making age determinations difficult (see also Jones et al., 2005). Thus, sequential oxygen isotopic sampling along the shell growth axis was used to identify the range of temperature at which *L. pensylvanica* is capable of precipitating its shell (e.g., Jones and Quitmyer, 1996; Schöne et al., 2003; Jones et al., 2005). The intrashell $\delta^{18}O$ values (n = 57) of three drilled and three undrilled valves varied from −1.7 to +1.1‰, and temperature estimates ranged from 16.9 °C to 28.9 °C (Table 2). Such range of calculated temperatures is consistent with values estimated from modern *Donax variabilis* Say, 1822 (17–27 °C) from northeastern Florida (Jones et al., 2005). Both drilled (Figs. 4A–C) and undrilled (Figs. 4D–F) valves exhibited comparable $\delta^{18}O$ values and calculated temperatures (Table 2). Intrashell temperature estimates vary over a range of values that is comparable to the seasonal range of SST documented for the region (~20.0 °C to ~30.9 °C), excluding the hottest temperatures (Fig. 5A).

In order to evaluate growth rates of *L. pensylvanica* from the Bahamas in a rigorous manner, a higher resolution study would be required, preferably by combining higher-resolution oxygen isotope profiles with growth mark measurements. Nevertheless, the intrashell oxygen isotope profiles presented here are sufficient to estimate potential seasonal preferences for calcification at a coarse (seasonal rather than monthly-submonthly resolution) temporal scale. The results revealed that *L. pensylvanica* is capable of secreting shell throughout most of the year, except perhaps the hottest weeks or months of the year. Shell material was deposited during both fall–winter (16.9–24.0 °C; n = 45) and spring–early summer (24.3–28.9 °C; n = 14). Clearly, some preference for cooler over warmer months is perceptible (Table 2; Fig. 4). Although Taylor et al. (2004) tested that *L. pensylvanica* from Florida Keys displayed a relatively continuous growth across seasons for specimens smaller than ~18 mm, the present results suggest that *Lucina* from Bahamas exhibits some preferential growth during cooler months (Figs. 4–5).

Shackleton (1973) outlined several conditions required for using shell margin $\delta^{18}O$ values to identify the season at which organisms died, including: (1) shell is deposited in equilibrium with water and temperature, (2) the oxygen isotopic composition of the water remains nearly constant, (3) shell deposition occurs at sea surface temperatures, (4) shell deposits carbonate through the year relatively continuously, and (5) shell growth rate is sufficiently high to track variations in temperature up to the shell margin. Our results suggest that *L. pensylvanica* from Bahamas deposits shell throughout most seasons, matching with most observed SST values (Fig. 5). Accordingly, we propose that the $\delta^{18}O$ values obtained from the shell margin should represent the temporal markers that approximate the time of death for the specimens that died in the late fall through early summer months or, at worst, predate death events by 1–2 months for specimens that died in late summer or early fall.

Temperature Estimates at the Shell Margin

The $\delta^{18}O$ values of drilled valves at the shell margin ranged from −0.9 to +0.8‰, whereas undrilled valves ranged from −1.1 to +0.1‰ (Table 1; Figs. 6A, C). The $\delta^{18}O$ values of both drilled and undrilled valves showed a right-skewed distribution, indicating that the great majority of valves displayed low $\delta^{18}O$ values while valves with higher $\delta^{18}O$ values were gradually less frequent (Figs. 6A, C). Significant differences were observed between the $\delta^{18}O$ values of drilled and undrilled valves (Mann-Whitney U test; U = 1460; $p < 0.001$), with the drilled valves showing higher $\delta^{18}O$ values comparing with the undrilled ones (Figs. 6A, C).

Drilled valves displayed an estimated range of temperatures at the shell margin from ~18.1 °C to ~25.3 °C (n = 68), whereas undrilled valves ranged from ~21.3 °C to ~26.4 °C (n = 67) (Figs. 5B, 6B, D). Calculated temperatures exhibited a left-skewed frequency distribution, indicating that the majority of specimens died during warmer temperatures (at least ~24–25 °C, or higher, if death post-dated secretion of the terminal shell layer; see above) while specimens that died during cooler temperatures (<24 °C) were gradually less abundant (Figs. 6B, D). Drilled and undrilled valves differed significantly in temperature values at the shell margin (Mann-Whitney U test; U = 1467; $p < 0.001$). Indeed, although drilled and undrilled valves displayed a comparable range of temperatures, solely drilled valves tracked the coldest temperatures (~18.1–21.3 °C) at the shell margin (Fig. 6D) while only undrilled valves traced the hottest temperatures (~25.5–26.4 °C during the last growth episode (Fig. 6B). Note that the observed difference is a conservative estimate because the undrilled shells recording hottest temperatures (probably representing May–June growth; Fig. 5) may have died at even higher temperatures later in the year, as the shell growth may have been arrested during the summer–early fall months.

Drilled left and right valves did not differ in size or temperature. Undrilled left and right valves were also statistically indistinguishable in terms of those variables. Moreover, no significant differences were observed across TTG classes with respect to valve size or temperature estimates closest to death (Figs. 7A–B). Strongly and weakly taphonomically altered valves exhibited a comparable range of sizes and $^{18}O/^{16}O$ ratios at the shell margin. Thus, differing degree of taphonomic alteration among shells did not affect notably the observed patterns.

Finally, although some size classes of drilled and undrilled valves overlapped along similar temperatures (Figs. 8A–B), the largest valves were only drilled during the hottest temperatures (~24.5–25.5 °C), whereas small valves were preyed upon at times of both cooler and warmer temperatures (Fig. 8B). In contrast, no consistent size patterns were observed for size classes of undrilled valves (Fig. 8A).

PALEOECOLOGICAL IMPLICATIONS

Prey Size Selection, Valve Preference, and Taphonomy

Drilled valves were significantly smaller than the undrilled valves (Figs. 2A–D), pointing to preferential drilling predation for smaller and thinner individuals. This is consistent with previous laboratory-studies in which some naticids target thinner-shelled preys (e.g., Grey et al., 2007). Such size-selective behavior has a potential influence on the prey population size structure through the reduction of vulnerable prey size classes (e.g., Kelley, 1988).

The fact that the number of left and right drilled valves was comparable suggests no valve preference by drilling organisms, as expected for equivalved shelly skeletons. Even though a few field studies have observed a naticid-drilling preference for the left valve of the bivalve prey (e.g., Hasegawa and Sato, 2009), the majority of previous studies have observed that naticid gastropods drill left and right valves indiscriminately (e.g., Kingsley-Smith et al., 2003).

Taphonomic alterations of shells can be induced by multiple abiotic and biotic factors, including water energy, sedimentation rate, bioturbation, bioerosion, and predation. Also, intrinsic characteristics such as mode of life and type and size of shell can influence the shell taphonomy (e.g., Best and Kidwell, 2000a, 2000b). Drilled shells are likely to have different hydrodynamic behavior (e.g., entrainment velocity) and may be also more vulnerable to taphonomic destruction than undrilled shells (e.g., Zuschin and Staton, 2001; see also Roy et al., 1994). The higher taphonomic alteration observed among drilled valves (Fig. 2) suggests that drill holes (which make shells easier to lift by water currents and more susceptible to physical damage) influenced, at least partly, the taphonomic history of *L. pensylvanica* valves.

Seasonal Variations Recorded in the Death Shelly Assemblage

The differences between drilled and undrilled valves in temperature estimates at the shell margin, assumed here to approximate or predate (for summer months) the season during which specimens died, may be explained by: (1) an ecological hypothesis (i.e., seasonal changes in predation intensity), (2) a preferential temperature hypothesis (i.e., preferential growth at certain temperatures), or (3) a taphonomic hypothesis (i.e., taphonomic bias due to differential seasonal transport of drilled against undrilled valves).

Ecological Hypothesis.—This hypothesis postulates a seasonal increase of attack frequency by drilling organisms, or alternatively, a seasonal increase of durophagous predation by crushing crabs or shell-transporting birds (e.g., Cadée, 1989, 1994). In the latter case, during the times when shell-crushing predators are more active, undrilled valves may have been destroyed making drilled specimens appear relatively more frequent. While this hypothesis cannot be evaluated with the data presented here, such ecological hypothesis cannot account for the observed patterns alone. Even if mortality from drilling predation was 100% during the coldest months (~18–21 °C), half of the valves from drilled bivalves would bear no drill holes (i.e., only one valve out of two will contain drill holes). Undrilled valves recorded the hottest temperatures (~25.5–26.5 °C), whereas no drilled valves tracked such high temperatures at the last growth episode (Fig. 6). This finding may be explained by a heat stress experienced by drilling predators during the hottest temperatures. Boring gastropods could have ceased drilling bivalves at temperatures higher than ~25.5 °C in the study area. Thus, those undrilled specimens that recorded the hottest temperatures may have died by heat stress. While small specimens were preyed upon throughout most seasons, larger specimens were progressively preyed upon more intensively at warmer conditions (Fig. 8B). If so, this could suggest that larger specimens may be more easily drilled at warmer temperatures. According to this interpretation, naticid gastropods in Bahamas appear to drill bivalves more frequently as sea surface temperature rises, but never above ~25.5 °C (Fig. 6D, 8B). On the other hand, drilled valves did not yield temperatures below ~18 °C at the shell edge (Fig. 6D). This may reflect (1) sampling deficiencies (if more specimens were sampled such shells would have been found) or (2) a cold temperature stress for local drilling predators (i.e., naticids may stop drilling at temperatures <18 °C in the region). The fact that undrilled specimens did not die at temperatures below ~21 °C also suggests that winter (cold) temperature was not a major cause of death.

Preferential Temperature Hypothesis.—This hypothesis postulates that warmer temperature estimates will be preferentially detected as organisms age. Growth rates and growth histories of different specimens can vary substantially based on size. Many bivalves grow continuously across seasons while they are juveniles, but often restrict their growth to the optimum season (i.e., summer) as they get older (e.g., Jones and Quitmyer, 1996; Jones et al., 2005; Goodwin et al., 2001, 2003; Schöne et al., 2003). The intrashell $\delta^{18}O$ profiles, however, indicate that calcification of *L. pensylvanica* from the Bahamas occurred throughout most seasons, except the hottest months (Figs. 4–5A), a pattern not unexpected for tropical settings. Slower (minimized) summer growth (Fig. 5) may be explained by either (1) reproduction, as observed for some species of bivalves from the tropics (e.g., Berg and Alatalo, 1985), including *L. pensylvanica* from Florida Keys (Bigatti et al., 2004), or (2) a heat stress threshold above which shells cannot grow (e.g., Schöne et al., 2003). Also, larger specimens did not always exhibit the hottest temperatures at the shell margin (Figs. 8A–B), suggesting that growth histories were not strongly biased by individual's sizes or preferential growth during warmer temperatures. Indeed, neither drilled nor undrilled valves recorded temperatures expected for the hottest

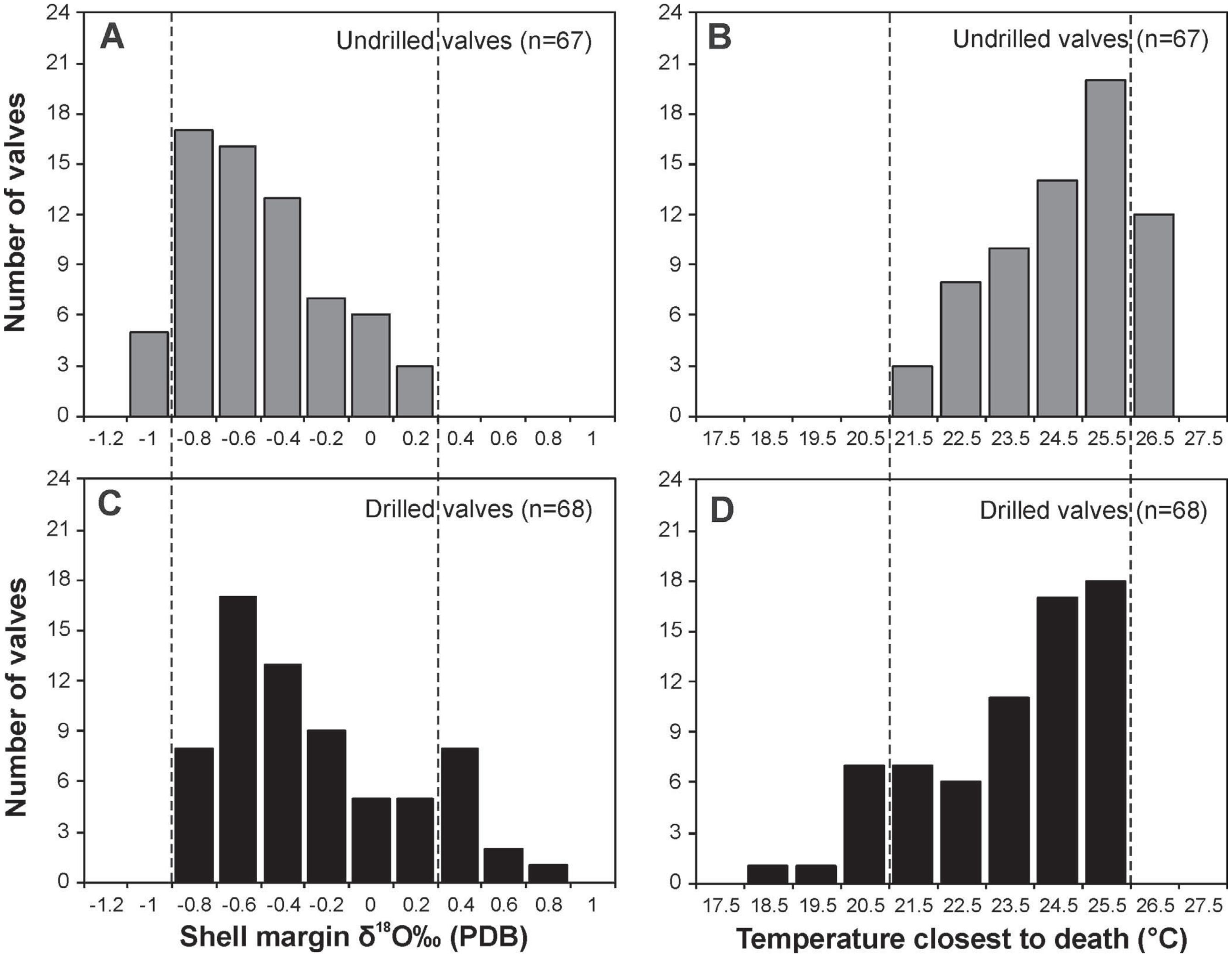

FIGURE 6—Frequency distribution of the oxygen isotope values and temperature estimates from the last growth event of *Lucina pensylvanica*. A) Shell margin $\delta^{18}O$ values of undrilled valves. B) Temperature estimates at the shell margin of undrilled valves. C) Shell margin $\delta^{18}O$ values of drilled valves. D) Temperature estimates at the shell margin of undrilled valves.

days of the summer months (Fig. 5B). Taylor et al. (2004) observed that *L. pensylvanica* from Florida Keys grows rapidly and uninterruptedly to a length of ~18 mm. Since most shells studied here (111 out of 135) are smaller than ~17 mm in valve length, we assume that growth was relatively continuous, but with restrictions during the summer (Table 2; Figs. 4–5A), when breeding may be enhanced (Bigatti et al., 2004). Yet, a higher-resolution intrashell $\delta^{18}O$ study is necessary to evaluate variations in shell growth rates of *Lucina* from Bahamas at submonthly resolution. The latest shell material deposited may not necessarily correspond to the exact time of death because shell growth may have ceased some time prior to the organism's death. Nevertheless, our intrashell results suggest that carbonate precipitation is not drastically interrupted seasonally (Fig. 5). Indeed, shell margin recorded both fall–winter (~18.1–24.0 °C; n = 70) and spring (~24.1–26.4 °C; n = 65) temperatures (Table 1; Figs. 6B, D). Accordingly, as noted also above, the oxygen isotopic composition extracted from the shell margin of *L. pensylvanica* from the Bahamas likely approximates (or at worst, for summer months, predates) plausibly well the time of the organism's death. Finally, the degree of time averaging associated with variable amounts of carbonate milled out from larger against smaller specimens (i.e., samples from smaller specimens would require a larger amount of carbonate, and therefore, may average a longer time interval than samples from larger specimens), may have introduced some noise into the observed patterns. Older specimens tend to grow slower, however, so variable amounts of carbonates milled from younger and older specimens may be comparable in terms of time averaging.

Taphonomic Hypothesis.—This hypothesis is supported by multiple lines of evidence. Drilled valves represent more than 50% of all valves for most temperature bins (Figs. 6B, D), suggesting that differential transport biased the data. Note here that mortality from drilling predation cannot exceed 100%, so accumulations with >50% drilled valves must have been transported or winnowed preferentially. Previous field observations suggest that drilled valves tend to be sorted differentially by water currents (e.g., Lever et al., 1961; Harper et al., 1998; Kaplan and Baumiller, 2000) and experimental studies suggest that the current entrainment velocity needed for lifting a drilled valve is lower than the current velocity needed for an undrilled valve (e.g., Lever et al., 1961). The fact that drilled valves were significantly smaller (Mann-Whitney U test; U = 1439, $p < 0.001$) than undrilled valves (Figs. 2A–B) is also consistent with the taphonomic hypothesis, as size sorting of drilled against undrilled valves implies a different response to water movement. While we cannot rule out completely that predation frequency and growth rates varied seasonally, the aforementioned lines of evidence suggest that taphonomic bias is likely to have played an important role in the studied setting. The seasonal changes may reflect either (1) an increase in the strength of sorting process, mostly related to seasonal variation in the hydrodynamic

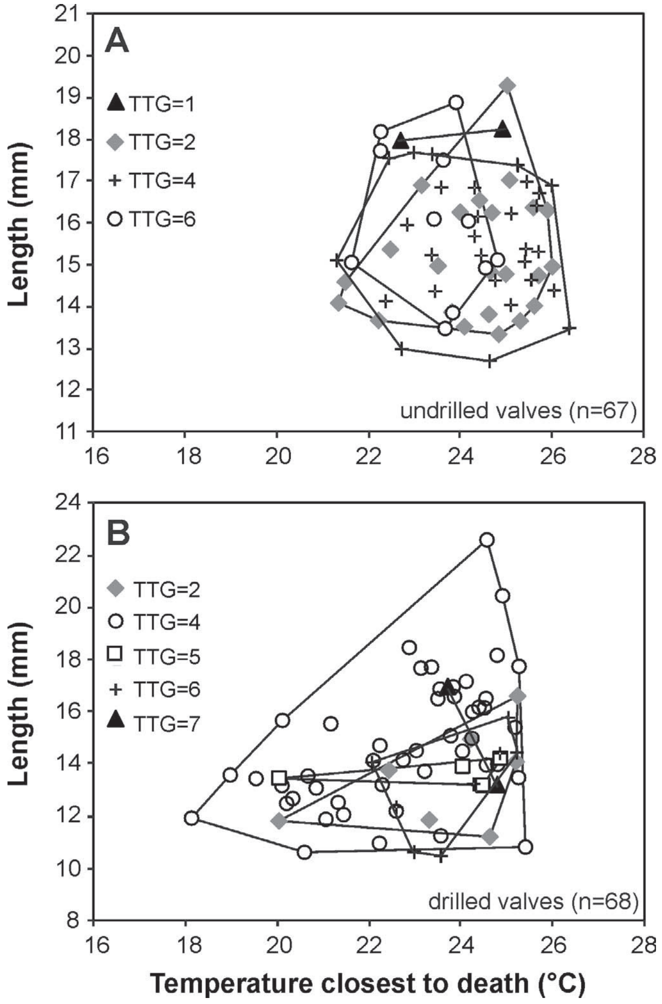

FIGURE 7—Valve length and temperature estimates from the $\delta^{18}O$ values at the shell margin grouped by Total Taphonomic Grade (TTG). A) Undrilled valves. B) Drilled valves.

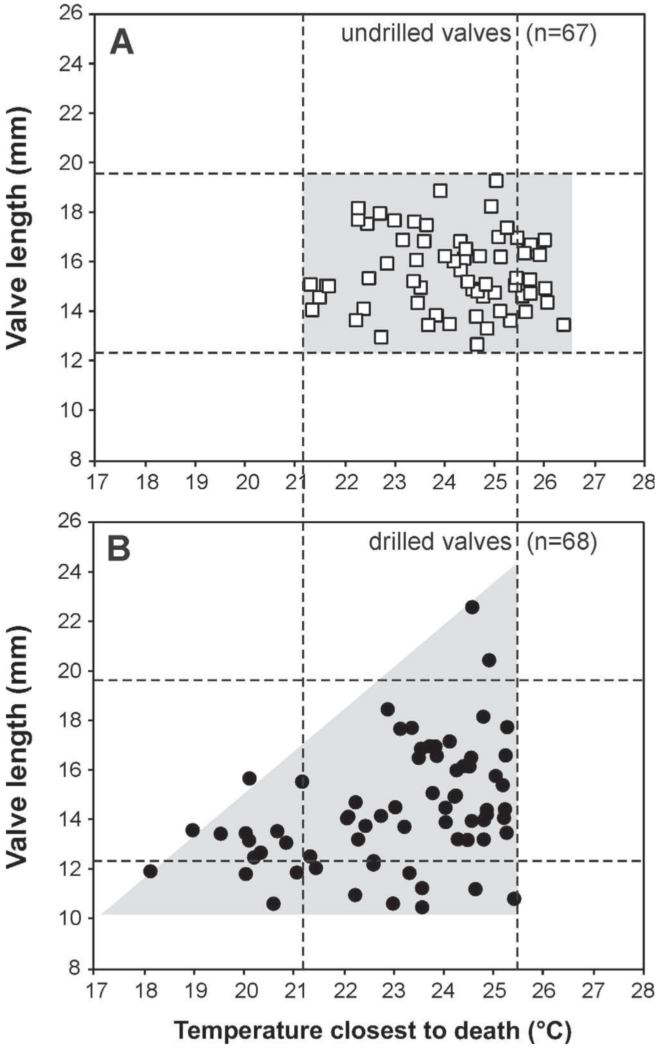

FIGURE 8—Relationship between temperatures at the last bivalve growth event against valve length. A) Comparison between valve length of drilled individuals and the estimated temperature closest to death. B) Comparison between valve length of undrilled specimens and the estimated temperature closest to death.

conditions, (2) a seasonal variation in predation intensity, secondarily biased by sorting that does not vary through seasons, (3) a seasonal (temperature) preference for growth (i.e., fall–winter–spring over summer), followed by postmortem bias, or (4) a combination of the three processes where all predation intensity, growth rates, and taphonomic bias vary seasonally. The collected material represents shoreface material that is unlikely to be preserved in the fossil record. Thus, the postulated taphonomic filter (i.e., selective removal of drilled shells from subtidal shell assemblages that are more likely to be preserved) is likely to produce the paleoecological record that is biased against detecting drilling predation. Such differential transport of valves to the shoreface (i.e., an effective removal of those valves from the future fossil record) may also vary seasonally and thus, the severity of this taphonomic bias may be climate-dependent.

CONCLUSIONS

Shell assemblages embrace complex but often interpretable insights into paleoenvironmental conditions, taphonomic processes and predation intensity. The oxygen isotopic composition of the shell margin of bivalves may represent the sea surface temperature prevailing near the time of the organism's death. This is true as long as specimens do not grow intermittently throughout the year. In tropical settings, sea surface temperatures are high enough ($>\sim 18$ °C) so that organisms do not need to stop growing during winter as much as they do at higher (colder) latitudes. Intrashell oxygen isotope values of several specimens of *L. pensylvanica* from Grand Bahama Island suggest that individuals deposited shell throughout most seasons, excluding the hottest (summer) months, with growth arrested, most likely, due to breeding or heat stress. Hence, the $\delta^{18}O$ value at the shell margin was assumed to approximate or at worst (for summer months) predate the temperature closest to the time of the individual's death. Multiple drilled and undrilled valves measured for $\delta^{18}O$ values at the shell margin suggest that most specimens died throughout the year, matching with intrashell isotope profiles and most observed SST. The assemblage was clearly biased by seasonal postmortem transport and shell sorting, however, because only drilled (=lighter and more taphonomically altered) valves recorded the coldest temperatures at the last growth episode, whereas merely undrilled (=heavier and less taphonomically altered) valves tracked the hottest temperatures at the shell margin. Although seasonal variations in ecological processes and growth rates may have affected the results to some extent, differing responses of drilled against undrilled valves to seasonal variations in hydrodynamic conditions explain, either partly or entirely, the observed patterns. This study highlights both the potential interpretative value as well as substantial challenges involved in combining isotope geochemistry, taphonomy, morphometrics and predation traces to reconstruct seasonal context of ecological and taphonomic processes recorded in subfossil and fossil shell assemblages.

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