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Citation of published version:
Jones, D., Quitmyer, I., Andrus, C. (2004): Seasonal Shell Growth and Longevity in Donax Variabilis from Northeastern Florida: Evidence from Oxygen Isotopes, *Journey of Shellfish Research*. 23(3). Direct Link: http://go.galegroup.com/ps/...

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Journal of Shellfish Research, Vol. 23, No. 3, 707–714, 2004.

SEASONAL SHELL GROWTH AND LONGEVITY IN *DONAX VARIABILIS* FROM NORTHEASTERN FLORIDA: EVIDENCE FROM OXYGEN ISOTOPES

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ABSTRACT The variable coquina clam, *Donax variabilis*, is one of the most common inhabitants of exposed sandy beach intertidal and shallow subtidal zones in the southeastern United States. Its exceptional burrowing and migratory behaviors are well documented, as are its biogeographic distribution and phylogenetic relationships. However, basic life history parameters such as season and rate of shell growth and longevity are poorly constrained for this species, usually estimated from size-frequency analyses of sample populations. High-resolution sampling of individual *D. variabilis* shells, and analysis of the oxygen isotopic variation in these samples, provides an alternate method of assessing shell growth and longevity in this species with a high degree of precision. Comparison of isotopic paleotemperature profiles with local seawater temperatures in the northeastern Florida study region indicates rapid shell growth (>4 mm/month) during a life span of 3 to 5 months, substantially shorter than most previous estimates. Detailed analysis of two modern shells indicates growth during spring and summer whereas four Archaic period archaeological shells revealed a summer-autumn growth record. In all cases the largest archaeological shells were substantially bigger than the largest modern shells, reflecting a greater longevity by about 2 months. Although recruitment can be fairly continuous throughout the year, size-frequency analyses of *D. variabilis* in separate years at the same locality reveal substantial interannual differences in population dynamics.

KEY WORDS: *Donax variabilis*, oxygen isotopes, shell growth, longevity, Florida

INTRODUCTION

The variable coquina clam, *Donax variabilis* Say, 1822, is one of the most common, recognizable bivalve mollusks from sandy beach habitats of the southeastern United States. It is found from Virginia to southern Florida and around the Gulf Coast to Texas (Ruppert & Fox 1988). Like other members of the Family Donacidae, *D. variabilis* is often the dominant macro-invertebrate inhabiting the high-energy environment of exposed sandy beaches where it often occurs in extremely high densities (Ansell 1983, Brown & McLachlan 1990, Pearse et al. 1942, Wilson 1999). In some cases *Donax* clams account for over 95% of the macrofaunal biomass on such beaches (McLachlan et al. 1981).

Donax clams are excellent burrowers, ideally suited to life in the surf zone (McLachlan & Young 1982, Trueman & Ansell 1969). The wedge-shaped outline of their shells facilitates penetration into the substrate. In addition to rapid burrowing, *D. variabilis* is also noted for its mobility, moving up and down the beach with the tides (Turner & Belding 1957), responding in a complex manner to wave action and especially to the acoustic shock of breaking waves (Ellers 1995a, Ellers 1995b). On longer time scales, Ruppert and Fox (1988) report a seasonal cycle of migration across the beach zone, down into the shallow sublittoral in fall, and returning onto the beach as juveniles in the late winter. This rather nomadic lifestyle, combined with its supreme ability as a rapid burrower, has enabled this species to colonize the sands of exposed beaches that otherwise are fairly devoid of macrofauna (Wilson 1999).

Despite its familiarity to scientists and shell collectors alike, the taxonomic status of *D. variabilis* has been debated for decades. Morrison (1971) envisioned 2 largely sympatric species, *D. variabilis* and *Donax parvula* Philippi, 1849, with the former further subdivided into a subspecies occurring in the southwestern portion of the range, *D. variabilis roemeri* Philippi, 1849. By contrast, Abbott (1974) and Dance (1990) considered *D. parvula* an ecomorph of *D. variabilis*. From studies of morphology, genetics and ecology, Nelson et al. (1993) concluded that *D. variabilis* and *D. parvula* were highly similar, but distinct species.

Using molecular techniques (RAPD DNA markers), Adamkewicz and Harasewych (1996) seem to have resolved the lingering systematics issues as well as simplified our understanding of the biogeography of *Donax* in eastern North America. They found no evidence for the existence of the subspecies *D. variabilis roemeri* and found *D. parvula* to be indistinguishable from the subtidal *Donax fossor* Say, 1822, with the latter synonym having taxonomic priority. Their biogeographic assessment has *D. variabilis* sharing both the Atlantic and Gulf coasts with a smaller, subtidal species, *D. fossor* on the Atlantic coast and *Donax texasianus* Philippi, 1847, in the Gulf of Mexico. The Florida peninsula separates the two subtidal species (Adamkewicz & Harasewych 1996).

The principal distinguishing feature between *D. variabilis* and *D. fossor*/*D. parvula* is the angle of the dorsal margins of the shell on either side of the umbo (Wilson 1999). Unfortunately, juvenile specimens often cannot be assigned to one species or the other (e.g., Bonsdorff & Nelson 1992) and ecophenotypic variation can further complicate specific determination, particularly in the field. Hence, we considered all small shells (≤3 mm) collected for this study to be *D. variabilis*, combining them with the larger specimens with which they were collected.

Despite its ecological importance, abundance and visibility on exposed sandy beaches, several key life history parameters of *D. variabilis* such as growth rate and longevity are known only to a first approximation with widely divergent estimates in the literature. This is particularly significant when *D. variabilis* is used as a model organism in ecological studies involving population dynamics and energy budgets on sandy beaches (Wilson 1999), or in investigations of the roles of biotic versus abiotic factors in determining spatial distribution and recruitment of beach fauna (Schoeman & Richardson 2002). Longevity estimates for *D. variabilis* range from less than 1 year (e.g., Bonsdorff & Nelson 1992) to higher than 3 years (e.g., Morrison 1971). At least part of the explanation for the lack of accurate data is the traditional method for assessing growth and longevity in this species—analysis of

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size-frequency diagrams—an approach with many inherent problems (Mikkelsen 1985). Other techniques such as mark-and-recapture studies are impractical because of the movements and high mortality of these clams (Mikkelsen 1985), and growth rings on the shell are indistinct, not useful for age determination (Wilson 1999). In this study we use oxygen isotopic variation in shell carbonate to produce high-resolution records of seasonal shell growth and longevity in *D. variabilis*.

Florida coquina clams normally are not exploited as a food resource by humans today; however, archaeological sites in northeastern Florida attest to the fact that preColumbian people consumed vast quantities of coquina clams between the middle Archaic (ca. 5700 y BP) and St. Johns (ca. 400 y BP) periods (Milanich 1994). This study of growth and longevity in *D. variabilis* originated from an investigation of archaeological specimens recovered from coastal shell middens in northeastern Florida to determine if there was a seasonality to ancient shellfish harvest (Jones et al. 2003, Quitmyer et al. 2004). In addition to examining archaeological shells, year-round collections of living coquina clams were made to establish a modern analogue for comparative purposes. Oxygen isotopic profiles of both modern and archaeological shells document rapid seasonal growth and shorter life spans than previously acknowledged for this diminutive but important bivalve species.

MATERIALS AND METHODS

The earliest evidence for human use of marine resources in northeastern Florida comes from the many Archaic period coastal archaeological sites recognized from this region (Milanich 1994). Particularly abundant in these shell middens are specimens of *D. variabilis* that often dominate the zoo archaeological component of any particular site. Collections of *D. variabilis* have been made at many of the more prominent excavation sites by archaeologists and students from the University of Florida (Quitmyer et al. 2004). These are housed in the collections of the Environmental Archaeology Program at the Florida Museum of Natural History, University of Florida, Gainesville.

Four archaeological shells of *D. variabilis* were selected for oxygen isotopic analysis from among the largest specimens in the museum collections. Large specimens were chosen to increase the likelihood of measuring maximum longevity. Two well-preserved shells from the Preceramic Archaic were selected, one each from the Crescent Beach (4240 ± 80 corr. ^{14}C yr BP) and Spencer's Midden (5570 ± 80 corr. ^{14}C yr BP) sites (Fig. 1). The shell lengths of these specimens were 23.1 mm and 21.5 mm, respectively. In addition, two well-preserved specimens were selected from the Orange Period Archaic material, one shell (21.3 mm) from the Rollins Site (3760 ± 60 corr. ^{14}C yr BP) and another (20.5 mm) from the Guana Shell Ring (3600 ± 50 corr. ^{14}C yr BP).

To establish a modern analogue for comparison with the archaeological coquina shell material, *D. variabilis* specimens were live-collected at monthly intervals at Matanzas Beach between December 2001 to November 2002. The collection site on Anastasia Island is located just south of the beach access ramp from Fort Matanzas National Monument (N 29.7174°; W 81.2310°), north of the Matanzas Inlet, in the same vicinity and water depths where indigenous people could have harvested coquina clams thousands of years ago (see Fig. 1). Specimens were collected in the intertidal and shallow subtidal zones ($\leq$1.5-m depth) for a consistent 40-min interval each month. Live clams were water-sieved from bulk samples scooped from the sandy bottom using a 1.59 mm-gauge brass sediment sieve, identical to that used to sieve archaeological materials. The clams were bagged, stored in a cooler, and transported back to the museum where they were quickly frozen and stored. Soft tissues were removed by water maceration at a later date.

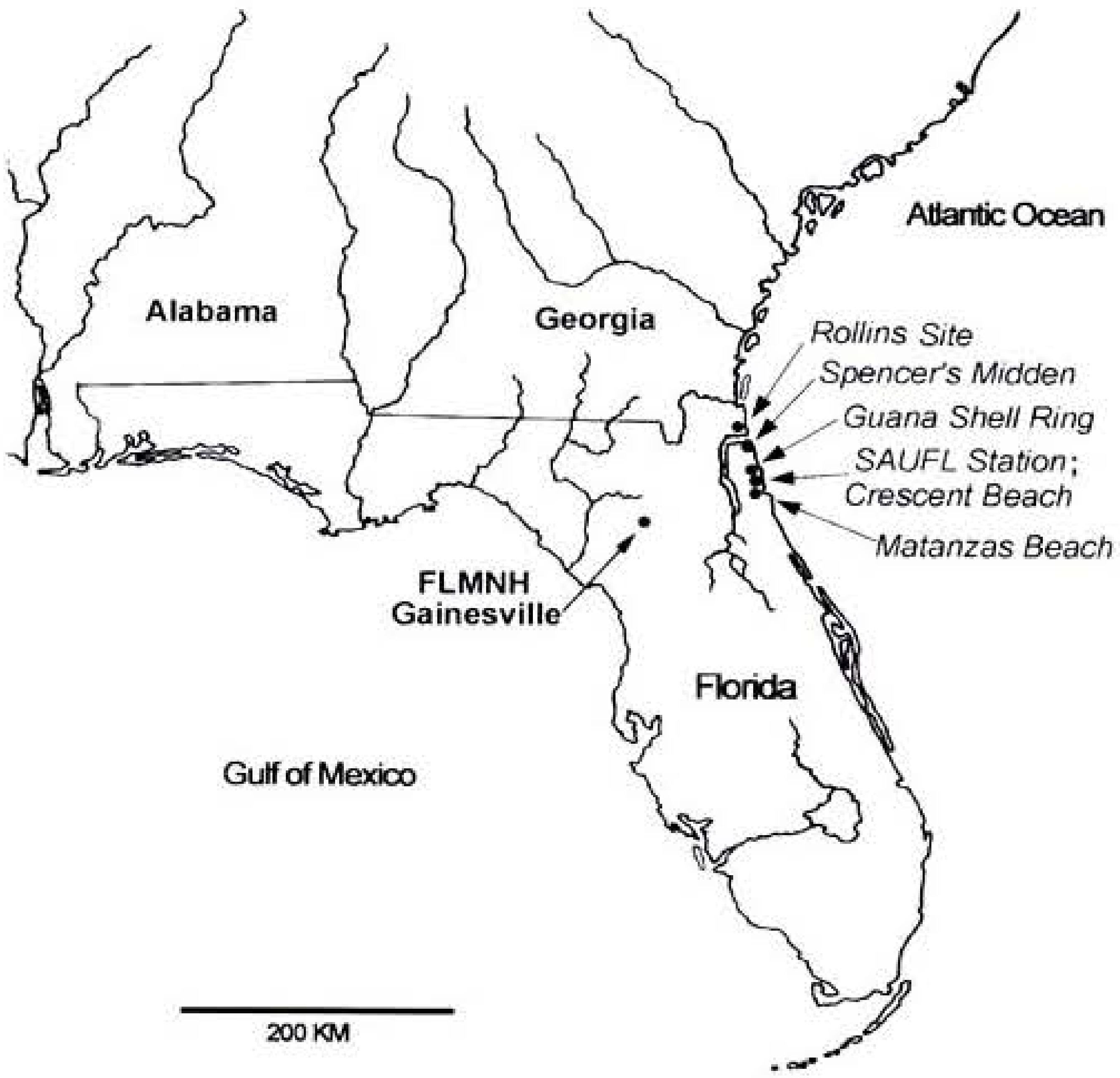

Figure 1. Location map showing archaeological midden sites along the northeastern coast of Florida, including site of modern *D. variabilis* collection at Matanzas Beach and SAUFL station at Crescent Beach.

A comparable assemblage of *D. variabilis* shells, live-collected at monthly intervals between January to December 1988 at the same locality, was also available at the museum. These shells were collected by Dr. Michael Russo during the course of research in the Department of Anthropology at the University of Florida (Quitmyer et al. 2004).

The maximum shell length, anterior to posterior, was measured for each shell in every monthly collection from both data sets using a dial caliper. The monthly shell length frequencies were calculated and plotted in 1-mm increments to facilitate the temporal comparison of shell size variation in the populations. Similar size-frequency data were constructed by Quitmyer et al. (2004) for archaeological coquina clam shells excavated from middens in northeastern Florida. Two of the largest modern shells were selected for stable isotopic analysis (13.1 mm, 13.2 mm). These specimens were collected by Russo in July 1988.

When carefully sampled in ontogenetic sequence from the umbo to the ventral shell margin (Fig. 2), the pattern of oxygen isotopic variation across a bivalve shell can provide a wealth of information about seasonal growth, shell growth rates, longevity, and season of death (Jones & Quitmyer 1996, Jones et al. 1983, Wefer & Berger 1991). To assess these parameters in *D. variabilis*, and to look at possible changes through time, sequential samples of shell carbonate were recovered from the two modern and four archaeological shells.

Prior to sampling each valve was cleaned following Andrus and Crowe (2002), with a wire brush under distilled water and then treated with a 30% solution of H_2O_2. After rinsing in distilled water and drying in a vacuum oven, the samples were mounted

Figure 2. Archaeological *D. variabilis* shell from Guana Shell Ring site showing sampling grooves from milling procedure to collect powders for oxygen isotopic analyses. Scale bar divisions = 2 mm.

onto glass slides with epoxy and fixed to the sample stage of a Merchantek EO Micromill at the Savannah River Ecology Laboratory. Carbonate samples were milled from the outer surface of the valve in shallow, 25 μm-deep grooves parallel to the growth lines. Each sampling groove was approximately 100-μm wide. The spacing between adjacent grooves averaged 200 μm with grooves near the ventral margin slightly more closely spaced than those near the umbo, reflecting the slowing of shell growth with age (see Fig. 2).

The isotopic analyses were conducted in the Light Stable Isotope Mass Spectrometry Laboratory, Department of Geological Sciences, University of Florida. The powdered $CaCO_3$ samples were analyzed according to standard techniques (Jones & Quitmyer 1996) which involved an initial reaction *in vacuo* with 100% orthophosphoric acid at 90°C for 0.25 h. An on-line automated carbonate-preparation system facilitated the production and purification of the evolved CO_2 gas. The isotopic differences between the derived CO_2 gas and the VPDB standard were determined with a VG Isogas PRISM Series I mass spectrometer equipped with triple collectors and mico-inlet system. All values are reported in standard δ notation where:

$$\delta^{18}O = [(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard} - 1] \times 10^3 \text{ per mil } (‰)$$

The weight of the individual microsamples was so low that replicates of unknowns could not be run and often required that adjacent samples be combined. However, replicated standards run before and after sample strings varied by less than ±0.1‰.

The $\delta^{18}O$ value of seawater from the Matanzas Beach collection site was measured via CO_2 equilibration following Socki et al. (1992) at the University of Georgia, Geology Stable Isotope Laboratory. Five monthly samples were analyzed (December to March & August), providing a measure of seasonal $\delta^{18}O$ range. Precision was estimated based on analysis of the laboratory working standard of Athens tap water to be ±0.05 (1σ). The $\delta^{18}O$ values of seawater at the Matanzas Beach collection site were very consistent (Dec. 1.0‰; Jan. 1.2‰; Feb. 1.0‰; Mar. 1.1‰; Aug. 1.1‰), averaging 1.08‰ SMOW (±0.08‰, 1σ: maximum range = 0.2‰).

We calculated the temperature of the water in which the shell carbonate formed using the paleotemperature equation of Grossman and Ku (1986) for the temperature-dependent fractionation of aragonite in mollusks relative to seawater:

$$T(°C) = 21.8 - 4.69\,[\text{shell } \delta^{18}O_{VPDB} - (\text{seawater } \delta^{18}O_{SMOW} - 0.2‰)].$$

The paleotemperature data from the coquina shells are presented in ontogenetic sequence and graphed to the mean weekly seawater temperature curve based on historical measurements made in 1988 at the nearby St. Augustine National Data Buoy Center station, SAUFL (http://www.ndbc.noaa.gov/Maps/Florida.shtml).

RESULTS

At Matanzas Beach, 2,493 specimens of *D. variabilis* were collected in 1988 by Russo and measured as part of this study. Another 2,545 specimens were measured from the collection made in 2001 to 2002. This latter number represents the total of all specimens collected each month except April 2002 when 28,372 specimens were collected during the usual 40-min regimen. A subset of shells (344 specimens) equal in weight to the previous month's sample (March) was selected from the April 2002 sample for measurement. The monthly length-frequency relationships for each of these samples are illustrated in Figures 3 and 4.

Each of the monthly graphs for 1988 (see Fig. 3) reveals a concentration of specimens at the smaller sizes. During winter (December to February) most of the shells in the population ranged between 2–6 mm, reflecting a preponderance of new recruits entering the population. A small percentage of larger shells were observed, up to 12 mm. In the spring (March to May) clams were more abundant than during any other season. Most shell lengths ranged between 2–10 mm with peaks at 3, 5, and 7 mm, indicative of shell growth and continued recruitment. A few specimens in the May sample reached 14 mm. The summer quarter (June to August) was marked by a very strong peak at 3 mm indicating that recruitment remained vigorous. Shell lengths ranged between 2–13 mm. Although individuals were scarce compared with other seasons, the greatest proportion of large shells was encountered in summer (see Fig. 3). By autumn (September to November) the average shell length of the population had declined with a major influx of juvenile shells in the 2–5 mm range and a decrease in the percentage of large shells.

The monthly graphs for 2001 to 2002 (see Fig. 4) show similarities and significant differences from those of 1988. The winter months were characterized by specimens in the range of 1–11 mm. Peaks at 2, 4, and 5 mm in successive months reflect an influx of new recruits in December followed by individual shell growth and a concomitant increase in the average shell length throughout the winter. The continuation of this pattern during spring resulted in peaks at 3, 7, and 10 mm. Except for June 2002, the sample sizes in July and August were very small, insufficient for a robust interpretation of patterns. The autumn samples show a very strong peak at 3 mm and also some of the largest shells recovered in either year of collecting, up to 15 mm. Heavy recruitment is indicated as well as individual shell growth by older specimens.

High-resolution milling of the *D. variabilis* shells resulted in powdered $CaCO_3$ samples whose weights were toward the lower limits of those typically analyzed. Therefore, successive samples were combined to insure a sufficient sample size. With respect to the modern shells, this resulted in 8 unique samples for specimen

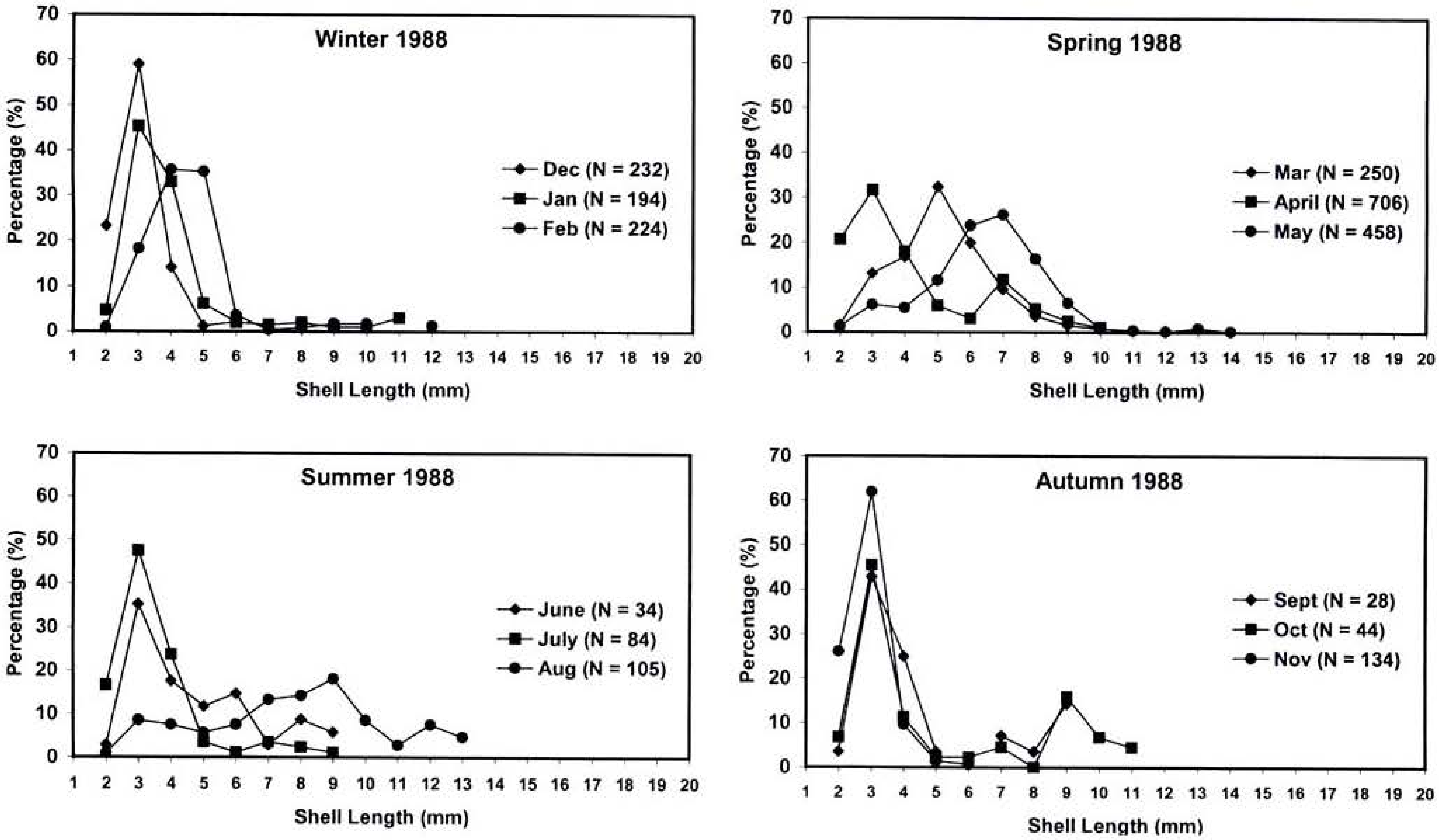

Figure 3. Shell length-frequency diagrams for *D. variabilis* collected at monthly intervals during 1988 from Matanzas Beach, FL.

#1 (13.1 mm) and 13 unique samples for specimen #2 (13.2 mm). Oxygen isotopic analyses of these samples produced values that ranged from 1.91‰ to 0.03‰ for specimen #1 and from 1.61‰ to 0.83‰ for specimen #2.

Figure 5 shows the mean weekly sea surface temperature variation at Matanzas Beach for 1988 based on historical measurements made at the nearby St. Augustine National Data Center Buoy station, SAUFL. The oxygen isotopic data from two shells col-

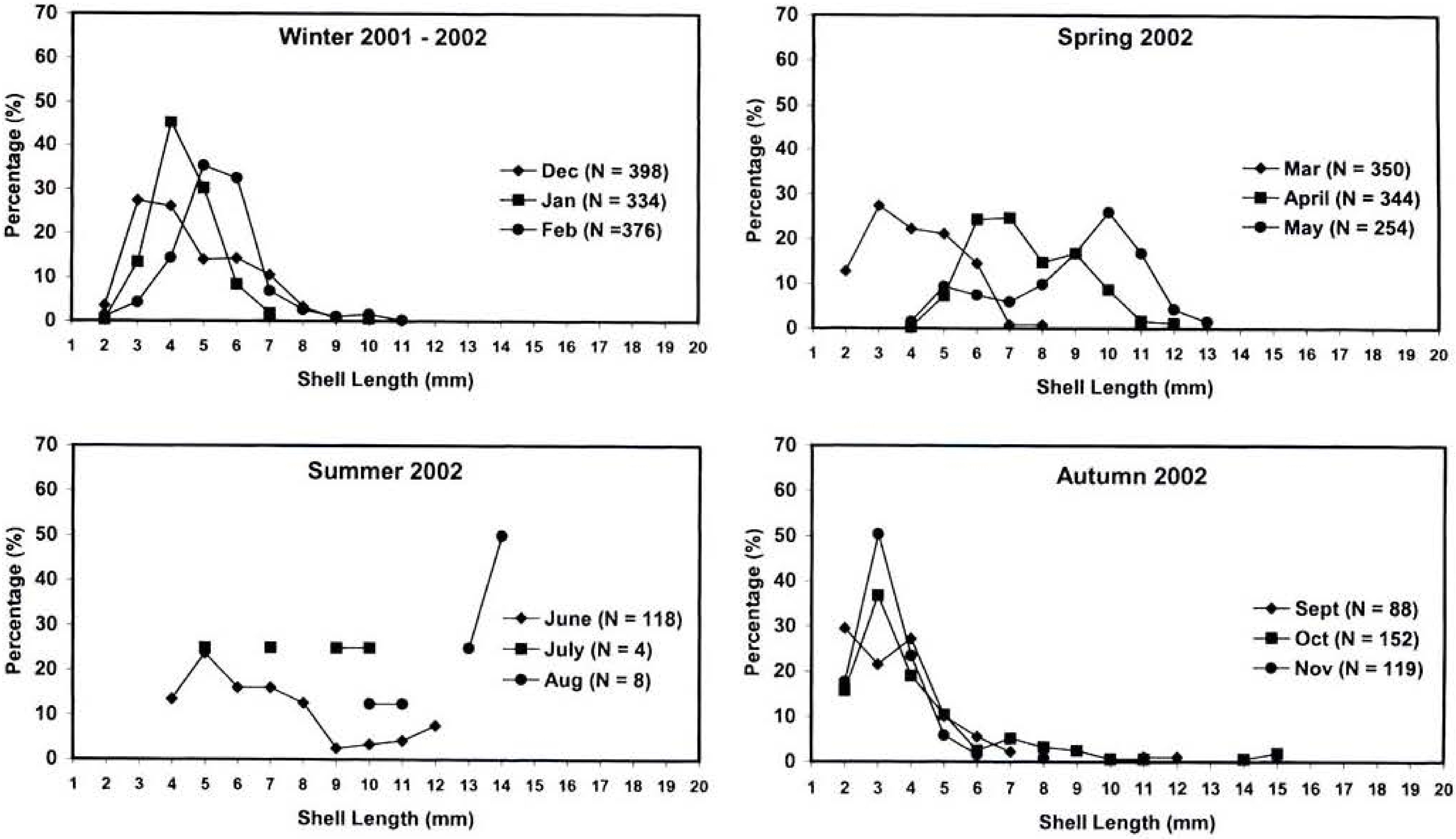

Figure 4. Shell length-frequency diagrams for *D. variabilis* collected at monthly intervals from December 2001 to November 2002 at Matanzas Beach, FL.

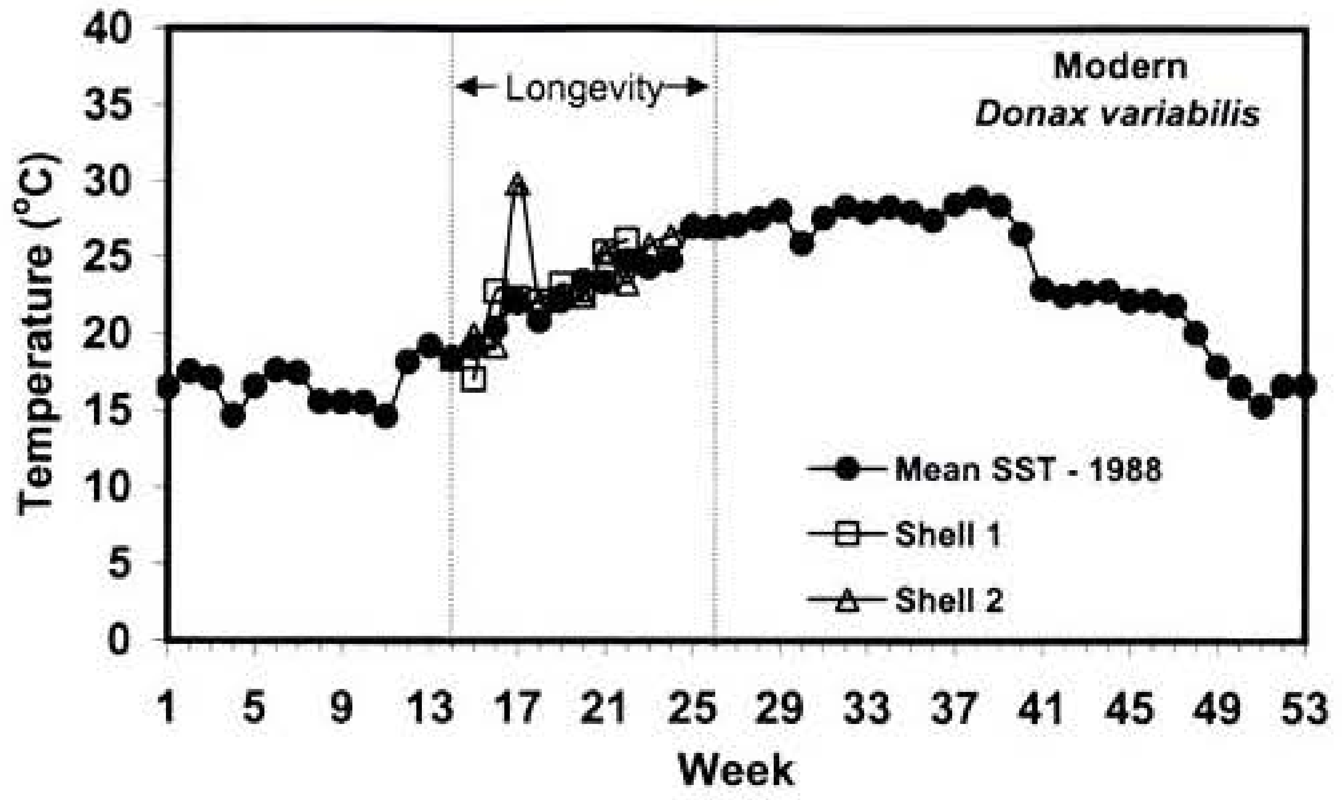

Figure 5. Weekly mean sea surface temperature data (black circles) from the SAUFL station for 1988 with isotopic paleotemperature profiles from two modern specimens of *D. variabilis* plotted in open symbols. Longevity of specimens corresponds to the length of the isotopic records, approximately 13 wk (14–26).

lected in July 1988 were converted to paleotemperatures and overlain in ontogenetic sequence onto the portion of the temperature curve that provided the best fit.

With the exception of only one data point, the isotopic paleotemperature data exhibit an excellent fit to the segment of the curve corresponding to spring and early summer. The exceptionally close match confirms the absence of vital effects influencing shell $\delta^{18}O$ values in *D. variabilis*, as in most mollusks (Wefer & Berger 1991). The shell-edge paleotemperature values correspond nicely with the water temperature at the time of collection in early July 1988. The isotopic records indicate that shell growth in both specimens occurred over a 13-week interval, approximately corresponding to weeks 14 to 26 of the year (mid April to early July).

In a similar manner, the four larger archaeological shells were sampled and analyzed for oxygen isotopic ratios. A total of 18 samples was analyzed from the Crescent Beach specimen. The $\delta^{18}O$ values ranged from 0.29‰ to 1.55‰. From the Spencer's Midden shell a total of 20 samples was analyzed whose $\delta^{18}O$ values ranged between 1.16‰ and 1.37‰. A total of 20 samples from the Rollins Site shell yielded $\delta^{18}O$ values that ranged between 1.26‰ and 1.96‰. From the Guana Shell Ring specimen, 13 samples were analyzed. These produced $\delta^{18}O$ values that ranged from 0.88‰ to 1.49‰.

The oxygen isotopic data were converted to paleotemperatures and these were overlain onto the seawater temperature curve (Fig. 6). The results are comparable with those achieved for the modern shells with a few important differences. The paleotemperature profiles for the two Preceramic Archaic shells from the Crescent Beach and Spencer's Midden sites show the closest correspondence with weeks 25 to 45 of the annual temperature curve. This pattern suggests shell growth occurred for about 21 weeks, from late June into mid-November. The paleotemperature profiles for the two younger shells from the Orange Period Archaic sites (Rollins and Guana Shell Ring) reveal a similar pattern. Shell growth over a period of about 20 weeks is indicated, corresponding to weeks 24 to 43 of the year, mid-June to late October.

All four archaeological shells were larger in size than any of the modern shells collected as part of this study. The results indicate that the ancient clams achieved their larger size by growing for a longer period of time (i.e., 8–9 wk longer) than their modern counterparts. Whereas maximum longevity among the modern shells was approximately 3 months, the archaeological specimens lived for up to 5 months. The paleotemperature records indicate that each of the four archaeological shells was harvested in autumn. Although the seasonal pattern of paleotemperature change recorded by the oxygen isotopes in the archaeological shells mirrors that of modern seawater at this site, the values reveal a consistent negative offset from modern conditions. The paleotemperature values from both archaeological periods reflect ocean water conditions in this region that were warmer than modern temperatures by about 3.5°C.

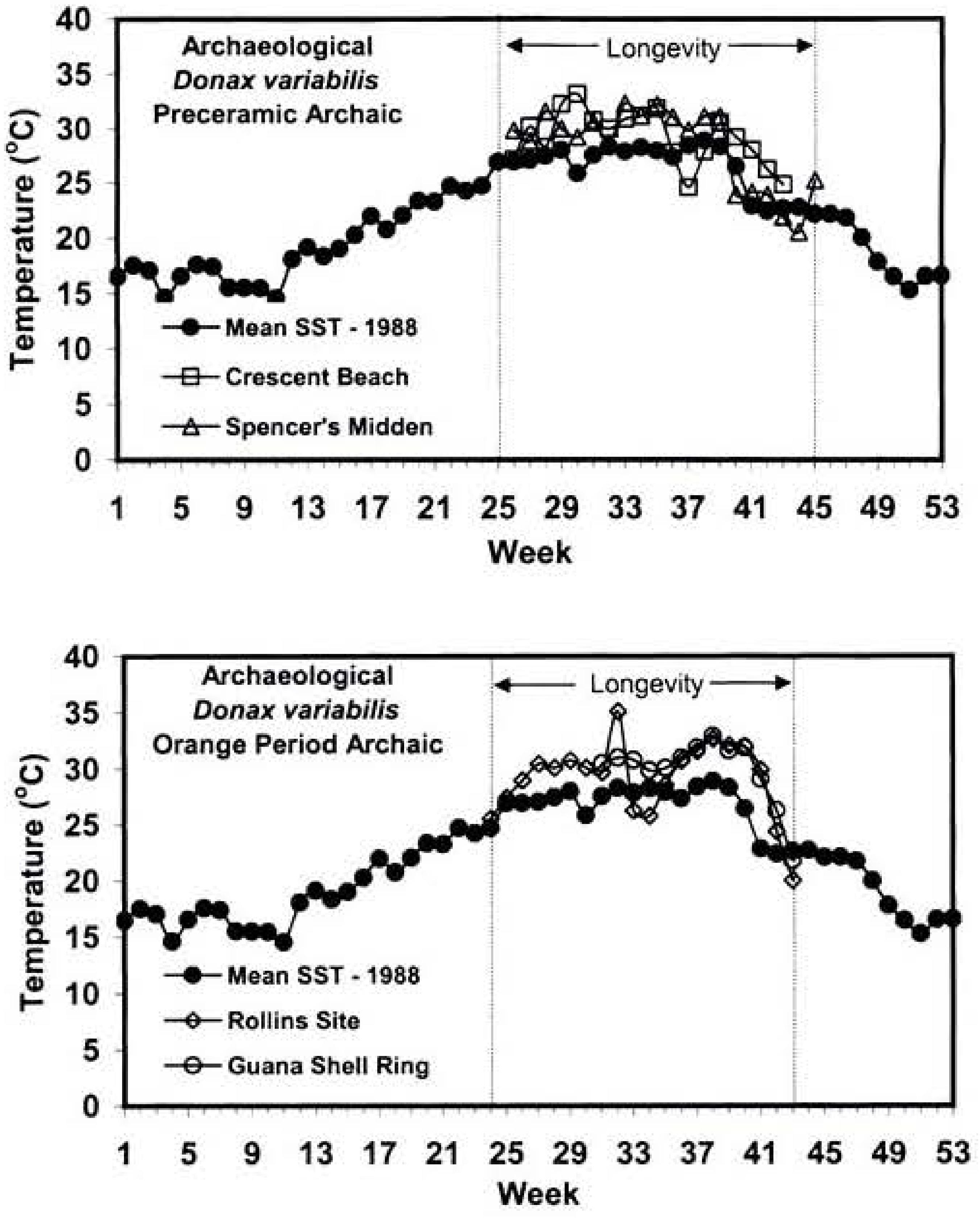

Figure 6. Weekly mean sea surface temperature data (black circles) from the SAUFL station for 1988 with isotopic paleotemperature profiles from two Preceramic Archaic shells (upper) and two Orange Period Archaic shells (lower) of *D. variabilis* plotted in open symbols. Longevity estimates for ancient shells correspond to the lengths of the isotopic records, approximately 21 wk (25–45, upper) and 20 wk (24–43, lower).

DISCUSSION

Despite its abundance and familiarity to scientists and shell collectors, key life history parameters such as growth rate and longevity are poorly constrained for *D. variabilis*. As this short-lived but abundant bivalve finds increasing use in ecological modeling of exposed beach ecosystems, it is essential that basic life history parameters are determined more precisely.

The oxygen isotopic evidence from modern and archaeological shells of *D. variabilis* provides the most accurate assessment of seasonal shell growth and longevity in this species to date. These data serve to refine previous estimates that were based largely on size-frequency analyses that required critical assumptions to be made about the seasonal timing of recruitment and migrations, assumptions that may or may not be warranted. Inherent problems in the interpretation of life-history information from size-frequency data are acknowledged by several authors including Mikkelsen (1985, p. 310) who states, "... repeated sampling of the population to construct length-frequency graphs was used, although problems exist with its use."

In his overview of the biology of the genus *Donax*, Ansell (1983) reported that most species are short-lived with life spans of 1–2 y, rapid growth to maximum size, and early maturity. Morrison (1971) suggested that *D. variabilis* has a 2-year life span, and that in some cases individuals may survive a third year. Ansell (1983) reported a 1- to 2-year life cycle for *D. variabilis*. Mikkelsen (1985) estimated that *D. variabilis* in Florida grew at a rate of 3.0–3.7 mm/month in the summer months and that, "the majority of individuals probably live for approximately 1 year, with a few entering a second year" (Mikkelsen 1985, p. 310). This conclusion generally agrees with Loesch (1957) and Pearse et al. (1942) who also used length-frequency graphs to examine growth and longevity in this species.

"Bonsdorff and Nelson (1992) estimated a maximum growth rate of 3.43 mm/month for a Florida population of *D. variabilis*, at which rate the animals would grow to maturity in just 2 months" (Wilson 1999, p. 78). The oxygen isotope results achieved in this study support such rapid growth rate estimates and reduced longevity (i.e., months, not years). In fact, the growth rates calculated from our isotopic data are even higher, 4.3–4.4 mm/month for the modern specimens and 4.1–4.6 mm/month for the archaeological shells.

The isotopic data also call into question whether any of these clams actually survive for 1 full year as the modern and archaeological shell isotope records indicated life spans of 3 to 5 months, respectively. Admittedly both the modern and archaeological specimens were live-collected by humans and therefore it could be argued that they still had the potential to grow larger and live longer. However, both sets of shells were among the largest specimens out of the thousands recovered in either the modern or zooarchaeological collections, thereby minimizing this possibility. Our results cast serious doubt on previous longevity estimates for this species that hypothesize growth and survival into a second or even a third year of life.

In a study involving *D. variabilis* from the South Carolina coast, Wilson (1999, p. 69) states: "Survival of *Donax* beyond a shell length of 10–11 mm, which length it can attain in less than 1 year, was poor and these large individuals only rarely contributed more than 1% to 2% of the population." He goes on to lament that growth rings on the shell were indistinct and it was not possible to verify the age of specimens by this method. Furthermore, constant movement of beach sands and contained clams, as well as the migratory ability of *Donax variabilis*, prevented the use of a "mark-and-recapture" technique for growth measurement. These same observations hold true regarding the populations in northeastern Florida and reinforce the value of the oxygen isotopic technique for growth rate and age determination.

The length-frequency graphs (see Figs. 3, 4) from the monthly collections of 1988 and 2001 to 2002 also reinforce Wilson's observation concerning the rarity of large individuals. The maximum SL in the modern Florida samples was 15 mm and such large shells were very rare. In contrast, the *D. variabilis* shells recovered from the archaeological shell midden sites ranged up to 25 mm and specimens in the 10–22 mm range were most common (Quitmyer et al. 2004). It seems clear from the zooarchaeological analyses that ancient harvesting strategies involved selection for larger shell sizes, but it is not clear why the coquina shells from the ancient past exceed the size of modern shells from the same vicinity.

The presence of small clams in the population virtually year-round suggests that recruitment to the population may take place throughout the year. This was especially noticeable in the 1988 samples (see Fig. 3) and has been mentioned as a possibility by previous authors (e.g., Bonsdorff & Nelson 1992). The pattern in 2001 to 2002 (see Fig. 4) was somewhat different with continuous recruitment indicated during September to March and weak or negligible recruitment over the spring and summer months. Leber (1982) recorded juvenile recruitment to a North Carolina population occurring in February and November. The February settlement was indicative of a winter spawning. At the lower latitude of Florida, it seems reasonable that such winter spawnings could occur with greater regularity. The differences in the monthly shell size distributions between the 2 years sampled here suggest considerable year-to-year variability in the population dynamics at this northern Florida locality.

The population structure observed by Wilson (1999) at Waites Island, South Carolina, suggested an annual cycle of settlement and growth, with reproduction and death in spring, although questions of a second, lesser spawning in autumn remain. A similar pattern was evident in the Florida population of *D. variabilis* discussed by Bonsdorff and Nelson (1992). Two spawnings per year have been reported for *D. sordidus* (McLachlan & van der Horst 1979) and for *D. semistratus* (Neuberger-Cywiak et al. 1990), although a single spawning per year is the default condition reported or assumed for most other species of *Donax*, even the short-lived, tropical species. However, the evidence is somewhat equivocal as Ansell et al. (1972) suggest that individuals of species like *D. incarnatus* may be in spawning condition at all times. Wilson (1999) acknowledges that the same might be said for the Waites Island *D. variabilis* population, although he believed the majority of individuals were semelparous.

The size-frequency data collected as part of this study support the emerging realization that spawning and recruitment can vary considerably from 1 year to the next in *D. variabilis* and need not conform to the pattern of one major seasonal spawning per annum. Such an interpretation agrees with Ansell's (1983) observation that the typical spawning pattern for *Donax* consists of repeated spawnings by individuals over an extended spawning season. Following maturity, Ansell (1983) reports that reproduction is potentially continuous with repeated partial spawnings, but growth, reproduction, and settlement may all show seasonal responses to environmental change. Certainly our data from 1988 argue against the statement by Sastre (1984) that *Donax denticulatus* from Puerto Rico is the only known species of *Donax* with continuous recruitment.

Whereas the size-frequency analyses of the monthly samples provide important insights into the population dynamics of *D. variabilis* along the northeastern Florida coast, there are better methods available to investigate specific life history parameters such as age and growth rate. One such technique is the high-resolution sampling and analysis of oxygen isotopic variation in shell carbonate used here. This approach has yielded the most detailed records of seasonal shell growth and longevity available to date for this species. It is also applicable to archaeological and fossil shells. The excellent correspondence between paleotemperatures derived from oxygen isotopes and the measured seasonal variation in water temperature at the site made it possible to reconstruct the timing and duration of shell growth to a weekly level of resolution. Life spans that proved to be appreciably shorter than generally acknowledged in the literature, 3 to 5 months in duration, represent an unanticipated outcome of this study. Whereas budget constraints limited the number of shells analyzed isotopically in this study, it would be highly desirable to expand the size and geographic breadth of the sampling to broaden the scope of this investigation.

Several important differences were observed between the modern and archaeological *D. variabilis* shells. These are intriguing and warrant additional study as well. The questions arising from these observations can be grouped into 3 broad categories: archaeological, biologic, and climatic. With respect to the first, all four archaeological shell records, from distinct Archaic Period time horizons, indicated shellfish harvest in the autumn. This suggests a clear seasonal pattern of behavior by indigenous peoples that needs to be verified through the analysis of additional shells from other sites and time periods (Quitmyer et al. 2004).

The biologic differences include greater maximum size and longevity for the archaeological shells, an extended growing season, and a shift in the growing season from spring-early summer to mid summer-autumn. Isotopic analyses of additional modern and archaeological shells will be necessary to document the extent of these differences and gauge their changes through time. The possibility of size reduction from over-fishing, observed in many marine species (Jackson et al. 2001) and in other bivalves such as *Mercenaria* spp. from Florida midden sites (Quitmyer & Jones 2000), must be considered. Finally, the warmer water temperatures recorded by the archaeological shell isotopes (ca. 3.5°C) may reflect the midHolocene climatic maximum in this region (Jones et al. 2003). By attempting additional oxygen isotopic analyses of *D. variabilis* shells from older as well as younger archaeological time periods, it should be possible to chart the history of water temperature change in this region since the last glacial episode.

ACKNOWLEDGMENTS

The authors thank Dr. Michael Russo, National Park Service, Southeastern Center, Tallahassee, for sharing unpublished data in the support of this research. Jenna Chojnowsk, Catherine Liu, Nick Moskowitz, Kate Quitmyer, Erin Thornton, and Brian Worthington assisted with fieldwork, sample preparation, data acquisition, and curation. We acknowledge the Invertebrate Paleontology and Environmental Archaeology Laboratories, Florida Museum of Natural History, for supplying essential resources. US Department of Energy grant #DE-FC09-96SR18546 (CFTA) provided partial support of this research. We appreciate the analytical assistance given by Dr. Jason Curtis of the Light Stable Isotope Mass Spectrometry Laboratory, Department of Geological Sciences, University of Florida.

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