

Life history patterns of modern and fossil *Mercenaria* spp. from warm vs. cold climates

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ABSTRACT

Recent work projects significant increases in sea surface temperature by the end of the 21st century. The biological consequences of such temperature increases are poorly understood. Study designs using a conservation paleobiology approach combined with sclerochronology methods can provide a powerful framework in which to assess these consequences. This study focuses on the ecological and economically important hard clam, *Mercenaria*, from modern and fossil settings that grew during climates that were warmer than or comparable to today. We compared lifespans and growth rates (von Bertalanffy k) of modern *Mercenaria* spp. populations to those from the Mid Pliocene Warm Period (MPWP) and early Pleistocene to better understand the influences of temperature on life history. We found that growth rates tend to increase with increasing temperature both through space and time. However, the relationship between lifespan and climate state is not as clear. Further, we observe that mid-to high-latitude individuals seem to be more impacted by changes in climate state than low latitude individuals. We suggest in response to increased seawater temperatures, mid- and high-latitude individuals might experience significant shifts towards faster growth rates whereas low latitude individuals might not see as much change. These findings provide insight to how growth rates and lifespans of *Mercenaria* might shift in response to future increases in seawater temperature. Understanding such impacts are critical for the development of management strategies and policies for future environmental change.

1. Introduction

Future warming projected by the Intergovernmental Panel on Climate Change (IPCC) estimates a 0.3–4.8 °C increase in global mean surface temperature by the end of the 21st century (Collins et al., 2013). Such changes pose significant socioeconomic stresses given potential extreme weather events, rising sea-level, and migrating ecosystems and resources (Robinson et al., 2008). One way to understand the impacts of climate change on marine ecosystems, in particular, is through conservation paleobiology. This field of research uses geohistorical analysis to understand species response to changing climate (Dowsett et al., 2009; Dietl and Flessa, 2011; Smith et al., 2020). Such knowledge is critical in acquiring a long-term perspective on modern ecosystems and to develop more effective tools for conserving and restoring biodiversity and ecosystems in the face of an uncertain future (Dowsett et al., 2009; Dietl and Flessa, 2011; Dietl et al., 2015).

Sclerochronology, the study of periodic growth structures in the skeletal portions of organisms that grow by accretion (Buddemeier et al.,

1974; Jones, 1988), is a powerful tool used in conservation paleobiology. Bivalves are one of the major groups in a wide range of organisms studied using sclerochronology (Surge and Schöne, 2015). Like tree rings, growth increments in bivalves act as skeletal diaries preserving life history patterns and records of environmental change. As some of the longest-lived non-colonial organisms on the planet today (e.g., Schöne et al., 2005; Ridgway and Richardson, 2011; Butler et al., 2013), bivalves are ideal targets for paleoclimate and sclerochronology research. In addition to their exceptional longevity, modern bivalve species exhibit a latitudinal pattern relative to their life history. Individuals from low latitudes tend to have faster growth rates and shorter lifespans compared to those from mid-high latitudes, suggesting environmental conditions (e.g., food availability, water temperature, etc.) influence longevity (Moss et al., 2016, 2017; Saulsbury et al., 2019). Under the premise that water temperature is an important factor in determining life history, here, we ask how lifespans and growth rates of bivalves change during warm and cold climate conditions?

We compare mid-Pliocene, early Pleistocene, and modern *Mercenaria*

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spp. shells from the Mid-Atlantic Coastal Plain (MACP) and Gulf Coastal Plain (GCP) of the United States to establish the relationship between lifespan and growth rate across spatial and temporal scales from different climate states. We test the following hypotheses: (1) latitudinal life history gradients exist in fossil and modern *Mercenaria* spp. irrespective of climatic setting, and (2) warmer climates (mid-Pliocene) will have faster growth rates and shorter lifespans compared to those from colder climates (early Pleistocene). Establishing the relationship between lifespan and growth rate during climate conditions warmer than today will provide us with a deeper understanding of marine bivalves' potential response to future environmental change. Understanding these responses will provide insight for future management of the marine ecosystems which bivalves inhabit.

2. Geologic context and material

2.1. Collection sites

Fossil *Mercenaria* spp. shells were collected from MPWP (Duplin Formation, NC; Lower Pinecrest Beds, FL), early Pleistocene (Lower Waccamaw Formation, NC; Caloosahatchee, FL), and modern localities in North Carolina and Florida (Fig. 1A) to investigate life history patterns through space and time (see Supplemental Material Table S1 for latitude and longitude). North Carolina fossil collection sites were selected based on similar paleoenvironments (i.e., depth and salinity) using indicator taxa (e.g., *Conus* sp. and *Cypraea* sp.) and facies relations (e.g., highstand system tracts to ensure maximal depth, prevent erosional mixing, and minimize time averaging biases). To minimize time averaging biases, we targeted within-habitat time-averaged (i.e., time averaging over a period of environmental stability) assemblages (Kidwell, 1997).

Duplin Formation shells were collected from the Robeson Farm locality southwest of the Cape Fear River, approximately 2 km east-southeast of Tar Heel, North Carolina. As described by Britt et al. (1992), this locality includes a ravine exposure, a smaller overlying slump exposure, and a gully exposure. These exposures contain several meters of mid-Pliocene clastic open-marine to nearshore sediments. Shells from the Lower Waccamaw Formation were collected from the Register Quarry locality in Columbus County, North Carolina. This exposure consists of mollusc-rich, fine to coarse sand. Bivalves are generally in life position with some rough bedding orientation, and some bivalves are still articulated (Ward et al., 1991). Shells from modern North Carolina were collected alive in approximately 1 m water depth from the University of North Carolina at Wilmington's (UNCW) marine sanctuary, Wilmington, North Carolina. Florida fossil localities used for this study are former quarry localities that are now submerged under water and no longer accessible. Given these challenges, the Florida Museum of Natural History provided shells from the Lower Pinecrest, Caloosahatchee, and modern setting in Florida (see Supplemental Material S1 for locality details).

2.2. Stratigraphy

Previous studies extensively describe the Plio-Pleistocene stratigraphy within the MACP and GCP (Gardner, 1943; Ward, 1980; Ward and Blackwelder, 1987; Krantz, 1991). Within these sequences, the early Pleistocene Lower Waccamaw and Caloosahatchee Formations unconformably overlie the mid-Pliocene Duplin Formation and Lower Pinecrest Beds Member of the Tamiami Formation in North Carolina and Florida, respectively (Fig. 1B) (Hazel, 1977; Ward and Blackwelder, 1980, 1987; Cronin, 1988; Jones et al., 1991; Willard et al., 1993). These deposits are known for their abundant and pristine preservation of marine fauna, including the bivalve genus *Mercenaria*.

The Lower Pinecrest Beds are stratigraphically equivalent to the Duplin Formation (Olsson and Petit, 1964; Hazel, 1977; Gibson, 1983, 1987; Cronin, 1988; Jones et al., 1991; Krantz, 1991; Allmon, 1993).

Faunal assemblages indicate the Lower Pinecrest Beds (~3.5–2.5 Ma) and the Duplin Formation (~3.5–2.4 Ma) were deposited in a transgression event during the MPWP (Hazel, 1977; Gibson, 1983, 1987; Cronin, 1988; Jones et al., 1991; Allmon, 1993; Willard et al., 1993; Missimer, 2001). Deposition of the Lower Pinecrest Beds and Duplin Formations occurred over a period of approximately one million years (Hazel, 1977; Gibson, 1983, 1987; Cronin, 1988; Jones et al., 1991; Allmon, 1993; Willard et al., 1993; Missimer, 2001). Ostracod and foraminifer records of the Lower Pinecrest Beds indicate warm-temperature conditions deposited in offshore, mid-shelf, normal marine conditions (Willard et al., 1993; Jones and Allmon, 1995). Molluscan fauna analysis of the Duplin Formation is also indicative of warm-temperate conditions deposited in shallow, warm marine, inner to middle shelf conditions (Richards, 1967; Ottens et al., 2012).

The Caloosahatchee and Lower Waccamaw Formations are stratigraphically equivalent units deposited in a transgressive event during the Gelasian Stage of the early Pleistocene (Olsson and Petit, 1964; Gibson, 1983, 1987; Cronin, 1988; Jones et al., 1991; Krantz, 1991; Allmon, 1993). Biostratigraphy provides age constraints for the Caloosahatchee (~1.8–2.5 Ma) and the Lower Waccamaw (~1.8–2.1 Ma) Formations, both representing less than one million years of deposition (Bender, 1973; Hazel, 1977; Ward and Blackwelder, 1980, 1987; Cronin, 1988; Jones et al., 1991; Willard et al., 1993). Molluscan assemblages of the Caloosahatchee Formation suggest warm-temperate conditions (Lloyd, 1969; Willard et al., 1993; Missimer, 2001). Several researchers assigned a warm-temperate designation to the Lower Waccamaw Formation (Blackwelder, 1981; Gibson, 1983, 1987; Krantz, 1990). However, winter temperatures estimates based on isotopic data fall below 12 °C (Krantz, 1990) indicative of cold-temperate conditions as defined by Briggs (1995) and Briggs and Bowen (2012). Thus, we redefine the Lower Waccamaw Formation as cold temperate. Both the Caloosahatchee and Duplin Formations generally represent shallow, marine conditions (Lloyd, 1969; Blackwelder, 1981; Krantz, 1991; Willard et al., 1993; Missimer, 2001).

2.3. Paleoclimate context

Paleoclimate reconstructions of the MPWP and the Gelasian stage of the early Pleistocene are based on proxy data and general circulation models (e.g., Raymo et al., 1996; Sloan et al., 1996; Lisiecki and Raymo, 2005; Dowsett, 2007; Robinson et al., 2008; Scherer et al., 2008; Dowsett et al., 2009; Chan et al., 2011; Winkelstern et al., 2013; Zhang et al., 2013; Johnson et al., 2017). Reduced global ice volume and increased global warmth characterize the MPWP (Dowsett and Cronin, 1990; Krantz, 1990). Previous studies link the MPWP along the MACP and GCP with increases in meridional heat transport as a result of the shoaling and closure of the Isthmus of Panama (Keigwin, 1978, 1982; Maier-Reimer et al., 1990; Missimer, 2001; Brierley et al., 2009; Dowsett and Robinson, 2009). Paleoclimate reconstructions based on faunal analysis suggests annual temperature ranges of 13–24 °C and 15–25 °C for the MPWP Duplin Formation and Lower Pinecrest Beds, respectively, during the time of deposition (Dowsett and Cronin, 1990; Cronin, 1991; Willard et al., 1993; Cronin and Dowsett, 1996). Winkelstern et al. (2013) reconstructed shallow seawater temperature using oxygen isotope ratios of fossil *Mercenaria* spp. from the Rushmere Member of the Yorktown Formation in Virginia, which is equivalent to the Duplin Formation and Lower Pinecrest Beds. Their study reports mid-latitude sea surface temperature during the winter months was 17 ± 2 °C and the summer temperature was 25 ± 2 °C.

Following mid-Pliocene warming, subsequent global cooling trends dominated the early Pleistocene Gelasian stage (Lisiecki and Raymo, 2005). Alternations of glacial and interglacial cycles controlled by obliquity oscillations characterize this time interval (Ruddiman et al., 1986; Raymo et al., 1989; Lisiecki and Raymo, 2005). Individual interglacial periods of the Gelasian stage correspond to climate conditions comparable to or warmer than today (Mercer, 1978; Krantz, 1990;

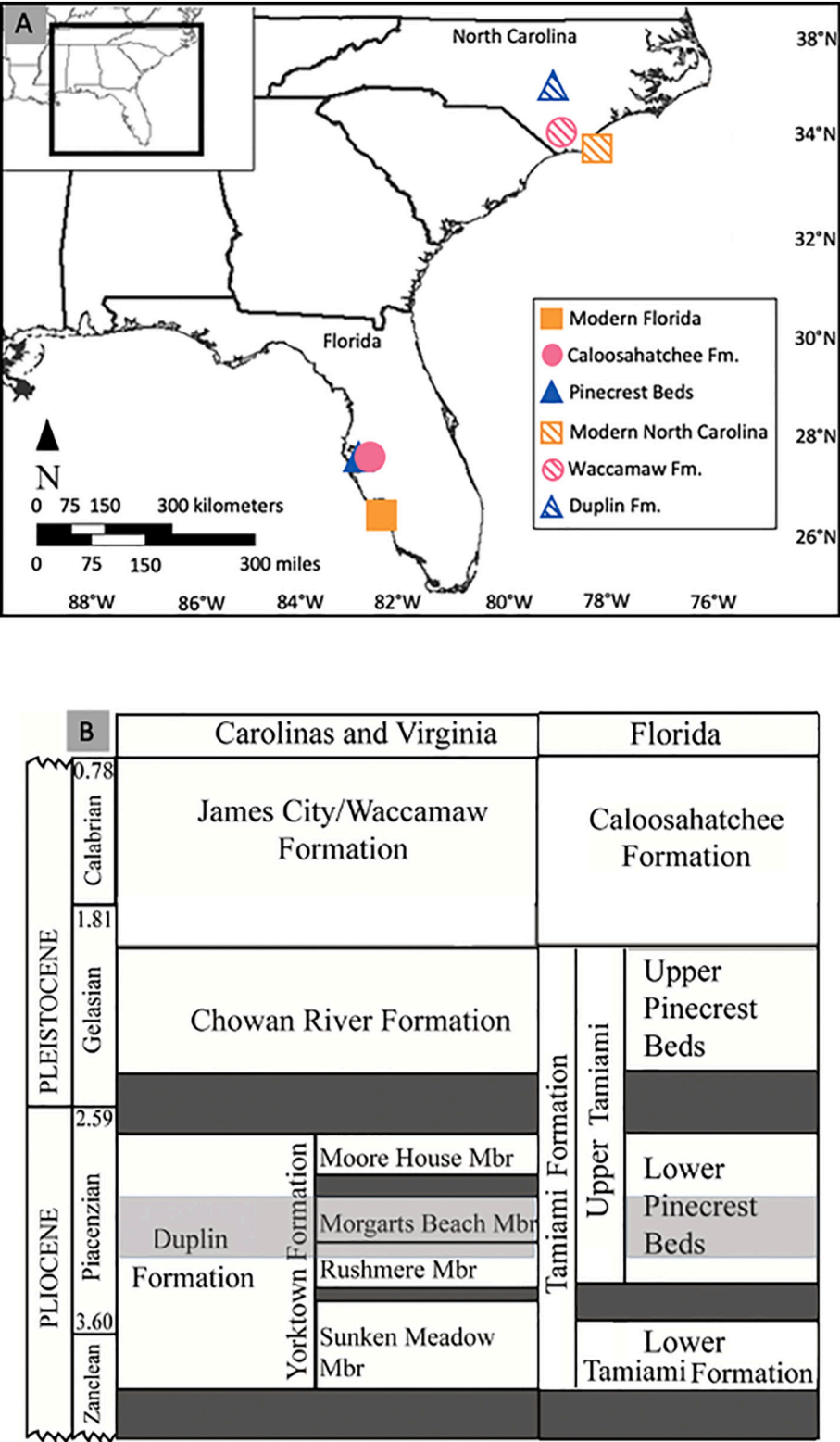


Fig. 1. A) Collection sites along the Mid-Atlantic and Gulf Coastal Plains. Triangles = MPWP, circles = early Pleistocene, and squares = modern localities. B) Plio-Pleistocene stratigraphy of the MACP and GCP. Gray box indicates the MPWP. See table S1 in the Supplemental Material for locality details.

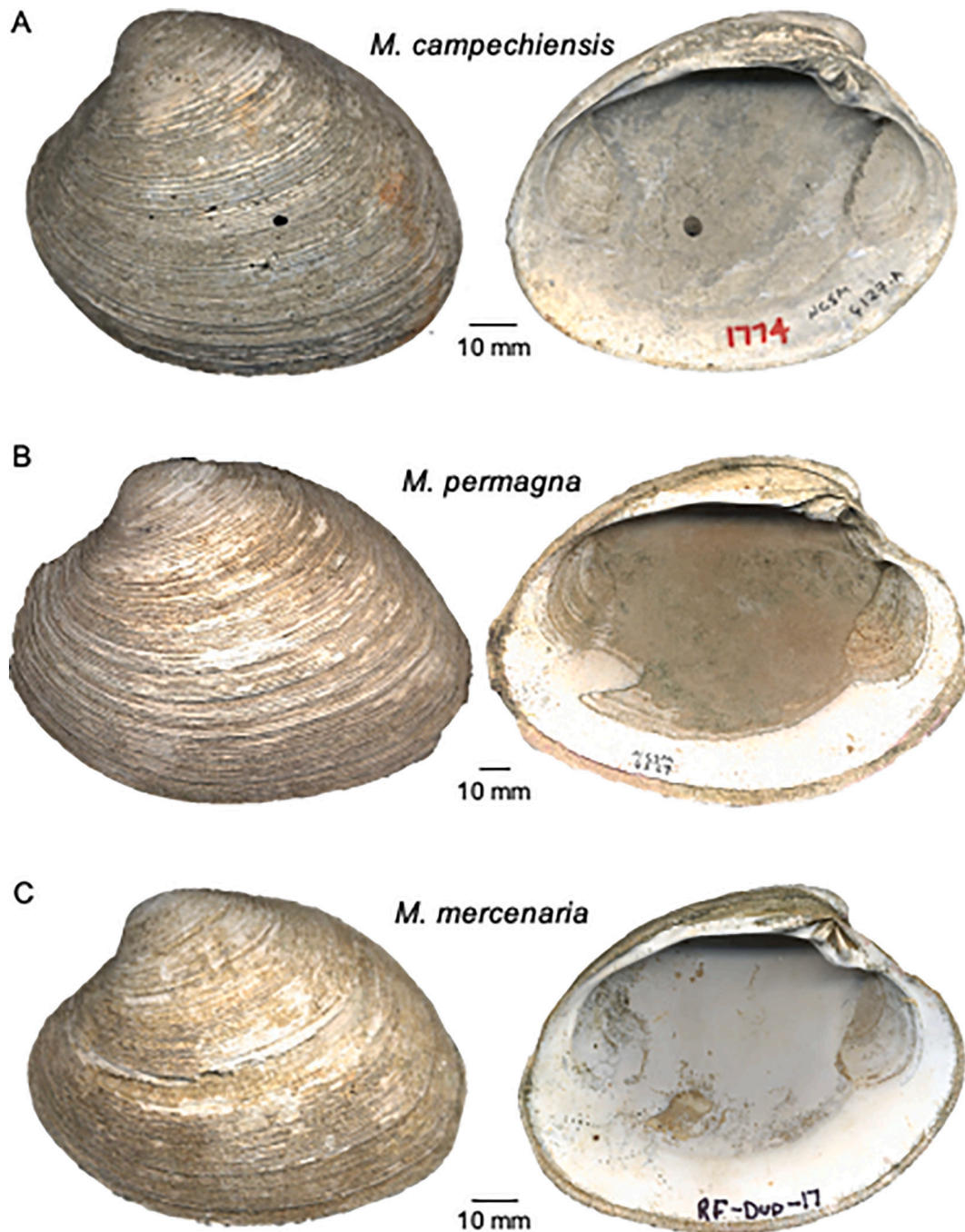


Fig. 2. Interior and exterior images of (A) *M. campechiensis* (NCSM 6127), (B) *M. permagna* (NCSM 6527), and (C) *M. mercenaria* from the Duplin Formation.

Lisiecki and Raymo, 2005). Paleoclimate reconstructions based on isotopic and faunal analysis suggest annual temperature ranges of 16–25 °C and 6–21 °C for the Caloosahatchee and Lower Waccamaw Formations, respectively (Krantz, 1990; Willard et al., 1993; Cronin and Dowsett, 1996; Tao, 2012). Winkelstern et al. (2013) report coldest winter temperatures (12 ± 2 °C) and warmest summer temperatures (21 ± 2 °C) from the early Pleistocene Chowan River Formation in Virginia, equivalent in depositional timing to the Lower Waccamaw and Caloosahatchee Formations.

3. Biogeography and ecology of *Mercenaria*

Mercenaria species are infaunal suspension feeders commonly found within estuaries, tidal flats, and offshore environments (Jorgensen,

1975; Peterson et al., 1984; Grizzle et al., 2001). They are shallow burrowers, burrowing approximately 4 cm beneath the surface (Ansell, 1962). *Mercenaria* can survive in mean annual water temperatures between 9 and 31 °C (Ansell, 1968). The most rapid growth of *Mercenaria* occurs in salinities between 20 and 30 and temperatures between 15 and 25 °C (Ansell, 1968). Spawning takes place in favorable temperature ranges unique to their biogeographic region. For example, in Core Sound, NC spawning is typically when water temperatures are between 27 and 30 °C (Peterson and Fegley, 1986), whereas in Alligator Harbor, FL, it is between 16 and 20 °C (Hesselman et al., 1988). They reach sexual maturity at a minimum shell length of 20–35 mm (Belding, 1930; Loosanoff, 1937; Hesselman et al., 1988; Walker and Heffernan, 1995). The age of sexual maturity varies with biogeographic region. For example, *M. mercenaria* from the Gulf of St. Lawrence and Massachusetts

take up to three years to reach sexual maturity (Belding, 1930; Loo-sanoff, 1937), whereas in Georgia and Florida it takes as little as one year (Hesselman et al., 1988; Walker and Heffernan, 1995).

The genus *Mercenaria* first appears in the fossil record during the Oligocene in deposits along the Gulf and Atlantic Coastal Plains of the United States (Stenzel, 1955; Harte, 2001). Today, two extant species of *Mercenaria* exist within the MACP and GCP: *M. mercenaria* (northern hard clam) and *M. campechiensis* (southern hard clam). Modern *M. mercenaria* ranges from Canada to central Florida, whereas *M. campechiensis* ranges from North Carolina to Florida and are more commonly found offshore in their northern limits (Dillon and Manzi, 1989; Carriker, 2001; Harte, 2001). While both species are abundant, fisheries primarily target *M. mercenaria* for human consumption because of their longer shelf life (MacKenzie et al., 2001; Arnold et al., 2009).

4. *Mercenaria* species identification

The two extant species of *Mercenaria* along the MACP and GCP, *M. mercenaria* and *M. campechiensis*, are traditionally identified by morphological and genetic analyses. The morphologic characteristics that distinguish the two species include interior shell color, shell thickness, shell shape, lunule shape, and concentric ridges on the outside of the shell (Dillon and Manzi, 1989; Harte, 2001). *Mercenaria mercenaria* are known to have purplish coloring along the posterior end of the shell that *M. campechiensis* lacks (Harte, 2001). Compared to *M. mercenaria*, *M. campechiensis* are thicker, rounder, larger, and have a shorter lunule length (Dillon and Manzi, 1989; Harte, 2001). Further, *M. mercenaria* have thin shell ridges that easily erode, whereas *M. campechiensis* have thicker shell ridges that generally do not entirely erode (Dillon and Manzi, 1989). In addition to the difference in morphology, isozyme frequencies differ significantly between the two species (Dillon and Manzi, 1989; Jones and Allmon, 1995). Given such isozyme differences, genetic analysis can identify the two species (e.g., Dillon and Manzi, 1989; Bert et al., 1993; Quitmyer et al., 1997; Arnold et al., 1998; Surge et al., 2008). Though past studies relied on morphological and genetic analyses to identify the two species (e.g., Dillon and Manzi, 1989; Bert et al., 1993; Quitmyer et al., 1997; Arnold et al., 1998; Surge et al., 2008), these analyses are not always diagnostic.

The general morphology of *M. campechiensis* closely resembles *M. mercenaria* and have been considered a conspecific with *M. mercenaria* in the past (Arnold et al., 1998; Harte, 2001). Juvenile *M. campechiensis* shells are known to resemble *M. mercenaria* more than adult *M. campechiensis*, making identification of juvenile *Mercenaria* species complicated (Harte, 2001). Further, shell morphology alone is not an accurate delimiting characteristic of the two species given the dependence of shell morphology on environmental conditions such as nutrient availability, substrate, temperature, and salinity (Kondo, 1987; Stanley, 1988; Harte, 2001). Identifying these two species becomes more problematic due to their tendency to hybridize (Dillon and Manzi, 1992; Bert et al., 1993; Powell, 2000), which is common in regions where they co-occur. For example, in the Indian Lagoon River on the Atlantic coast of Florida, Dillon and Manzi (1992) report that approximately 87.5% of the individuals are hybrids. They also report individuals that morphologically identify as *M. mercenaria* contained alleles of *M. campechiensis* and vice versa. Given these challenges, distinguishing between *M. mercenaria* and *M. campechiensis* is not always straight forward, especially in the fossil record.

5. Methods

5.1. North Carolina fossil *Mercenaria* identification

Identification of modern *Mercenaria* is sometimes challenging and becomes more problematic in the fossil record. The necessary tissue for genetic analysis of *M. mercenaria* and *M. campechiensis* is not preserved in the fossil record, and therefore, genetic analysis is not possible with

fossil specimens. Thus, species identification of fossil *Mercenaria* shells primarily relies on morphological characteristics (Jones and Allmon, 1995; Winkelstern et al., 2013). Preservation can pose challenges when using morphological characters. For example, pigmentation and exterior shell ridges and lunule lengths, useful in distinguishing modern species, are not often preserved or have been modified by transportation and deposition such that they are no longer useful.

To determine if species of *Mercenaria* have disparate life history traits and how uncertainty in identification of our fossil specimens might influence our results, we compared the life history of six identified fossil *Mercenaria* specimens, *M. permagna* ($n = 3$), and *M. campechiensis* ($n = 3$), to our *Mercenaria* spp. from the Duplin Formation. *M. permagna* and *M. campechiensis* samples were provided by the North Carolina Museum of Natural Sciences. We chose *M. permagna* for this comparison because their more elongated and less inflated shell is easy to distinguish from that of *M. mercenaria* and *M. campechiensis*. (Tuomey and Holmes, 1857; Bush et al., 1999; Dillon and Manzi, 1989; Harte, 2001) (Fig. 2).

5.2. Sample selection and preparation

We selected approximately 25 fossil and modern shells from each study site ($n = 188$) for life history analysis. When possible, we selected only the right valves for analysis to avoid potentially counting growth increments in the same individual more than once. Shells were selected based on preservation and taphonomic grade. Specimens with poor preservation in the hinge region, due to biological activities (i.e., boring), were discarded. Individuals were first labeled and scanned with

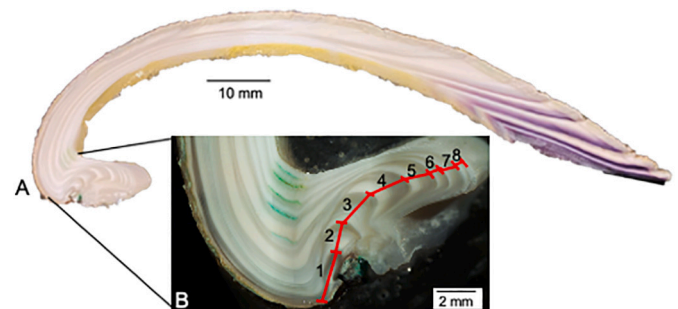


Fig. 3. A) *Mercenaria* sp. thick section from North Carolina cut along the axis of maximum growth. B) Couplets of light and dark increments in the hinge region under reflected light representing annual growth, and numbers represent ontogenetic growth years.

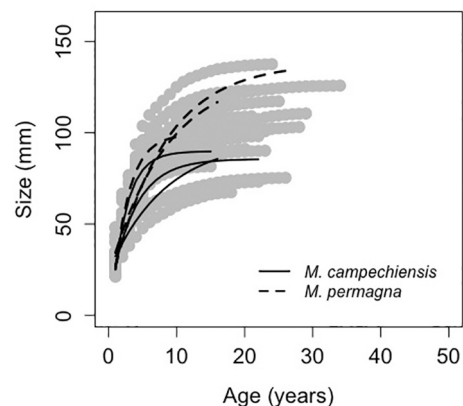


Fig. 4. Growth curves for identified specimens of *M. campechiensis* (solid black line) and *M. permagna* (dashed black line) from collections at the North Carolina Museum of Natural history compared to our *Mercenaria* spp. (gray lines) from the same locality.

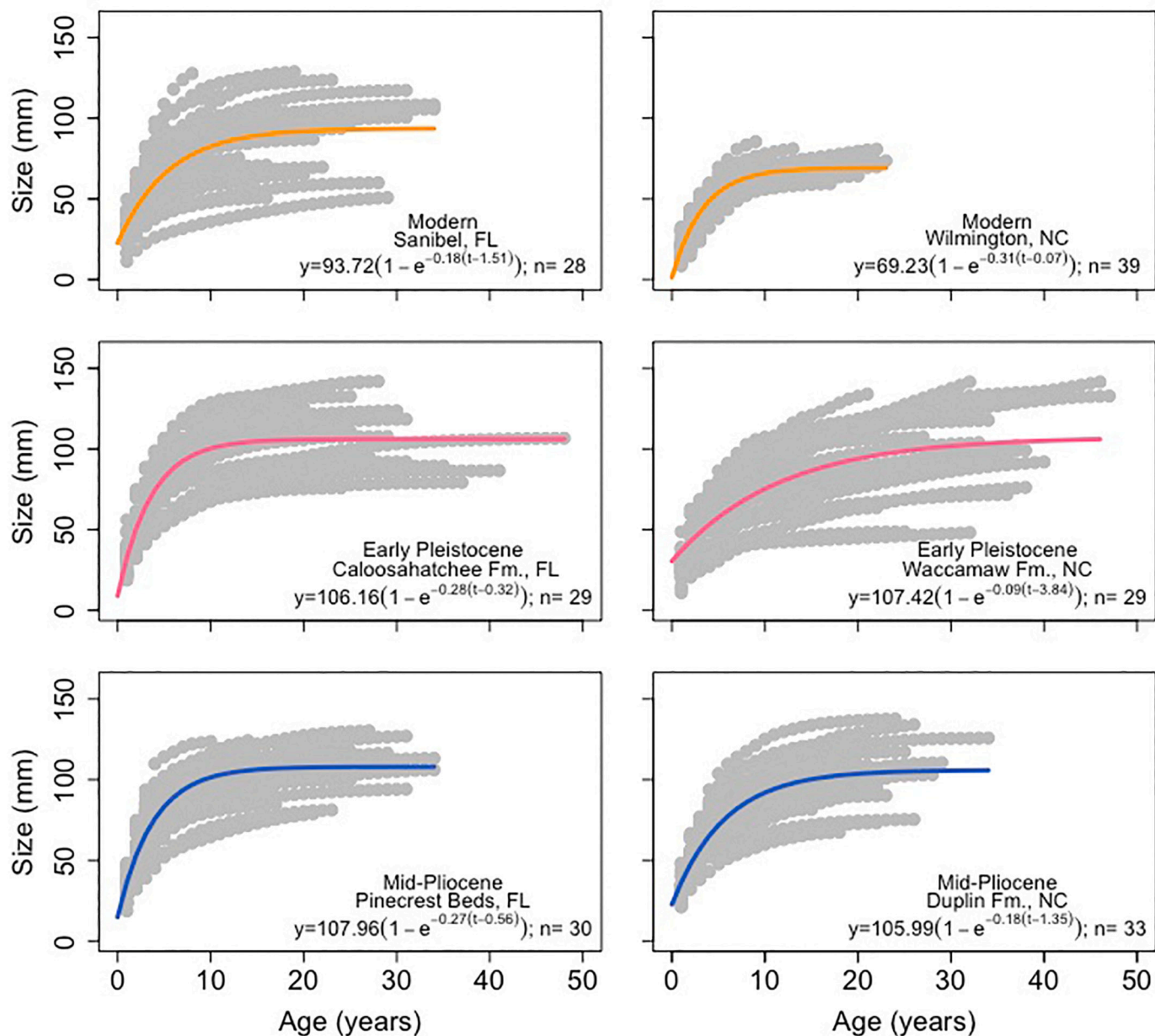


Fig. 5. von Bertalanffy growth curves fit to modern and fossil *Mercenaria* spp. size-at-age data. Gray circles = size-at-age data from each individual; solid color lines = best fit population von Bertalanffy curve.

an accompanying scale using an Epson GT-15000 Professional Scanner to preserve their two-dimensional measurements. Shell length (anterior to posterior) and maximum height (dorsal to ventral) were measured using digital calipers to the nearest 0.01 mm for each specimen. Previous work has shown *Mercenaria* species to form annual growth increments in the hinge region (e.g., Jones et al., 1989; Jones et al., 1990; Quitmyer et al., 1997; Ridgway et al., 2011; Winkelstern et al., 2013), and we presume growth increments in our specimens are annual as well (Fig. 3). To prevent loss of shell material when serially cutting specimens along the maximum axis of growth, we coated each shell with a layer of epoxy resin (Gorilla Glue Clear Epoxy) and allowed them to cure in a fume hood for at least 24 h. Shells were cut using a Lortone Lapidary Trim Saw model FS6. Thick sections were made using a Buehler Isomet low-speed saw. Each thick section was polished using a Buehler MetaServ 2000 variable speed grinder/polisher with a 600 grit silicon carbide disc and finished with diamond suspension solutions of 1 and 6 μ m. Polished

Table 1

Calculated von Bertalanffy growth parameters for populations. DUP = Duplin Formation; WAC = Lower Waccamaw Formation; SANC = Modern North Carolina; PINE = Lower Pinecrest Beds; CAL = Caloosahatchee formation; and SFL = Modern Florida.

Population	n _{shells}	MLSP	k	L _∞	t ₀
<i>Modern</i>					
SANC, NC	39	35	0.31	69.23	−0.07
SFL, FL	28	23	0.18	93.72	−1.51
<i>Early Pleistocene</i>					
WAC, NC	29	48	0.09	107.42	−3.84
CAL, FL	29	47	0.28	106.16	−0.32
<i>Mid-Pliocene</i>					
DUP, NC	33	34	0.18	105.99	−1.35
PINE, FL	30	34	0.27	107.96	−0.56

cross-sections were imaged using an Olympus DP71 12.5-megapixel digital camera attached to an Olympus SZX7 stereomicroscope. Annual growth increments in the hinge region were counted and measured using Olympus Stream Essentials version 2.2 imaging software. Hinge increments were then scaled to whole shell length using a ratio between shell length and hinge plate length to give us size-at-age data.

5.3. Life history analysis

To understand how life history parameters relate to climate state, we use the von Bertalanffy growth (VBG) equation (Bertalanffy, 1938):

$$L_t = L_{\infty} (1 - e^{(k(t-t_0))}) \quad (1)$$

where L_t is shell length at time t , L_{∞} is the asymptotic size, k is the rate at which L_{∞} is approached, and t_0 is the time at which L_t equals zero. We fit the VBG equation to the pooled size-at-age data using the non-linear least squares (<https://www.rdocumentation.org/packages/stats/versions/3.6.2/topics/nls>) procedure in the open-source R language (cran.r-project.org). The parameter k acts as a proxy, though not a direct measure of growth rate. Individuals with higher k values typically approach L_{∞} quicker than those with lower k values. We use R to perform Tukey's Honestly Significant Difference test (<https://www.rdocumentation.org/packages/stats/versions/3.6.2/topics/TukeyHSD>) to understand differences in mean lifespan between populations.

6. Results

6.1. Life history of *M. campechiensis* and *M. permagna*

By comparing the life history of fossil *M. campechiensis* and *M. permagna* to our samples from the Duplin Formation, we evaluated whether uncertainty in species identification would influence our results. The growth curves of *M. campechiensis* and *M. permagna* from museum collections fall within the range of our pooled population of *Mercenaria* spp. (Fig. 4). Though the curves visually appear different, VBG k values for all individuals show a similar range of 0.13–0.46. In addition, the lifespans of *M. campechiensis* (15–22 years) and *M. permagna* (10–26 years) also fall within the range of the lifespans of

our *Mercenaria* spp. individuals (7–34 years). The overlap in life history parameters gives us confidence that distinguishing between morphologically similar species in our fossil populations will not significantly influence our conclusions.

6.2. Population-level lifespan and growth rate

Well-preserved annual growth increments in *Mercenaria* spp. allow us to compare population life history parameters through space and time (Fig. 5; Table 1). VBG k values vary both spatially and temporally and are distinguishable by non-overlapping 95% confidence intervals (Fig. 6). During the MPWP, VBG k is higher in the Lower Pinecrest Beds (0.27) from Florida than in the Duplin Formation (0.18) from North Carolina. A similar pattern is present in the early Pleistocene where the southernmost population k value from the Caloosahatchee Formation (0.28) is higher than the northernmost population k value from the Lower Waccamaw Formation (0.09). Our modern populations do not follow this trend. The population k value of modern shells from Florida (0.18) is lower than shells from North Carolina (0.31). Temporally, VBG k values do not change significantly from the Pliocene (0.27) to the Pleistocene (0.28) in Florida. However, we see a decrease in VBG k in our North Carolina populations over the same time interval.

Maximum reported lifespans (MLSP) are the same during the MPWP (Lower Pinecrest Beds = 34 years; Duplin = 34 years) and similar during the early Pleistocene (Caloosahatchee = 47 years; Lower Waccamaw = 48 years). However, our modern Florida population is longer lived (35 years) than North Carolina (23 years). It is important to note that modern shells were collected alive, so we assume they could have lived longer; thus, their lifespans and perhaps von Bertalanffy k values might be different than that from a natural death assemblage.

6.3. Individual shell lifespan

To better understand variation in lifespans through space and time, we used Tukey's Honestly Significant Difference (Fig. 7; Table 2 and Table 3) to test for differences in mean lifespans between each population. Spatially, during the MPWP, we found no significant difference ($p > 0.05$) in mean lifespans between the Lower Pinecrest Formation ($\mu = 20.13$ years; $\sigma = 7.39$) and the Duplin Formation ($\mu = 19.33$, $\sigma = 6.10$).

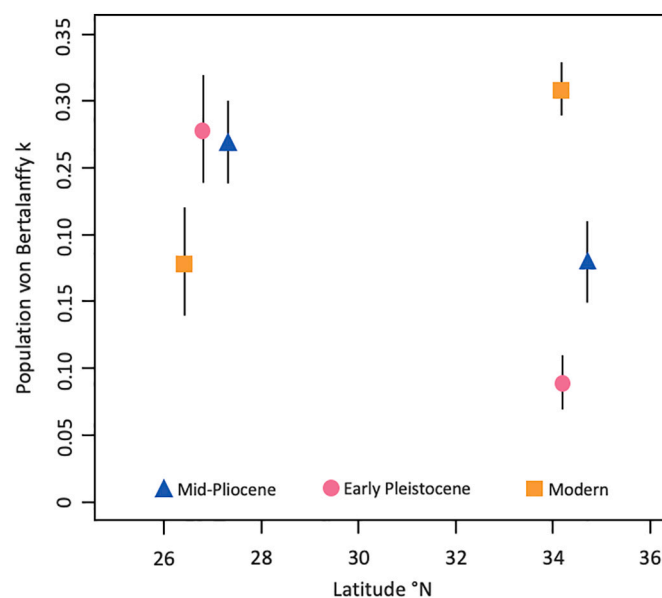


Fig. 6. Population VBG k values with 95% confidence intervals. Blue triangles = mid-Pliocene. Pink circles = early Pleistocene. Orange squares = modern. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

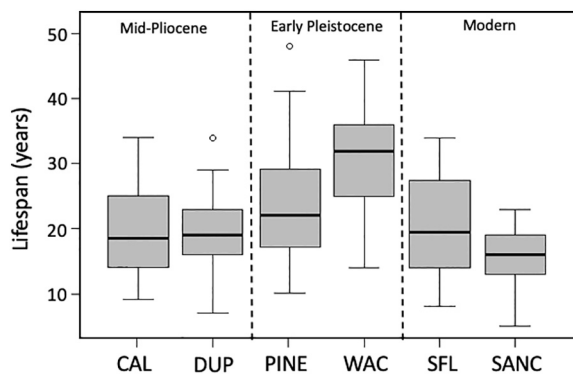


Fig. 7. Box plot of lifespans for each population. CAL = Caloosahatchee Formation; DUP = Duplin Formation; PINE = Lower Pinecrest Beds; WAC = Lower Waccamaw Formation; SFL = Modern Florida; and SANC = Modern North Carolina.

Table 2

Summary of lifespan statistics for fossil and modern *Mercenaria* spp. populations: mean lifespan (LSP), standard deviation (σ), maximum (MAX), and minimum (MIN) values. DUP = Duplin Formation; WAC = Lower Waccamaw Formation; SANC = Modern North Carolina; PINE = Lower Pinecrest Beds; CAL = Caloosahatchee Formation; and SFL = Modern Florida.

Population	n _{shells}	LSP	σ	MIN	MAX
<i>Modern</i>					
SANC, NC	39	15.56	4.59	5	23
SFL, FL	28	20.25	7.93	8	34
<i>Early Pleistocene</i>					
WAC, NC	29	30.21	7.91	14	46
CAL, FL	29	23.93	9.13	10	48
<i>Mid-Pliocene</i>					
DUP, NC	33	19.33	6.10	7	34
PINE, FL	30	20.13	7.39	9	34

Table 3

Tukey Honestly Significant Difference test results for mean lifespan comparisons. PINE = Florida, Mid Pliocene Warm Period; CAL = Florida, early Pleistocene; SFL = Florida, Modern; DUP = North Carolina, Mid Pliocene Warm Period; WAC = North Carolina, early Pleistocene; SANC = North Carolina, modern. $p < 0.05$ = significant difference in lifespan.

	PINE	CAL	SFL	DUP	WAC
CAL	0.33				
SFL	0.99	0.38			
DUP	0.99	0.12	0.99		
WAC	<0.05	<0.05	<0.05	<0.05	
SANC	0.10	<0.05	0.09	0.23	<0.05

However, during early Pleistocene individuals from the Waccamaw formation in North Carolina ($\mu = 30.21$, $\sigma = 7.91$) were significantly different ($p < 0.05$) than those from the Caloosahatchee Formation ($\mu = 23.93$, $\sigma = 9.13$). We observe no significant difference between our modern populations ($p > 0.05$). Temporally, we found no significant difference ($p > 0.05$) between individuals from Florida through time – mean lifespans do not change in our southern-most populations regardless of climate state. However, we did find a significant difference ($p < 0.05$) between our higher latitude populations from North Carolina through time. Mean lifespan of the early Pleistocene Lower Waccamaw Formation is higher than the MPWP Duplin Formation and modern North Carolina specimens.

7. Discussion

7.1. Fossil *Mercenaria* life history: space and time

To interpret changes of life history in our ancient populations spatially and temporally, it is important to understand what influences these parameters in modern settings. Previous work has established that both within specific groups, and across the Bivalvia as a whole, growth rates are faster in the tropics than at the poles. Low-latitude bivalves typically grow faster and die younger than their high-latitude counterparts (Moss et al., 2016). Strong relationships with latitude suggest some sort of environmental control on life history. Longer lifespans seem to be promoted across a range of groups by lower metabolic rates (e.g., Van Voorhies, 2001). Metabolic rates of ectoderms are in part a function of body size and temperature (Gillooly et al., 2001); they are faster at higher temperatures and larger body sizes. In addition to temperature, metabolic rates are also regulated by food availability. In high-latitude settings, where food can be extremely seasonal because of polar light regimes, metabolic rates of bivalves can be quite low for significant periods of time (Peck and Conway, 2000; Brockington and Clarke, 2001; Clarke et al., 2004; Norkko et al., 2005; Sato-Okoshi and Okoshi, 2008). Thus, the modern pattern of increasing lifespan and decreasing growth rate towards the poles in bivalves is likely driven by some combination of cool temperatures and low and seasonal food availability, though a recent analysis suggests that temperature might be more important (Saulsbury et al., 2019).

Our data from the MPWP and early Pleistocene lend support to the idea that temperature is an important control on life history. Population von Bertalanffy k values from Florida sites are higher than those from sites in North Carolina during both the MPWP and the early Pleistocene. Florida k values show little change from the mid-Pliocene to the early Pleistocene (0.28 to 0.27), whereas k values from North Carolina populations show a much more dramatic change (0.18 to 0.09). Latitudinal climate gradients in the MACP and GCP were likely much steeper in the early Pleistocene than in the mid-Pliocene (Cronin and Dowsett, 1990; Krantz, 1990; Cronin, 1991; Willard et al., 1993). Thus, the steepening of our von Bertalanffy k gradients in the early Pleistocene might be closely related to decreasing temperatures at mid-latitudes, especially during the winter.

The relationship between lifespan and latitude seems to depend on climate state. During the MPWP, a greenhouse period, there is no significant difference between lifespans of *Mercenaria* spp. from Florida and North Carolina. In contrast, during the early Pleistocene, which is marked by a transition to cooler temperatures, the population from North Carolina is significantly longer-lived than the population from Florida. These trends are not necessarily borne out by maximum lifespans as during each interval they are nearly identical. This pattern is not unsurprising as maxima of any trait are inherently tricky to estimate as increased sampling would likely result in finding an older individual. It is interesting that in both populations during the early Pleistocene there is an increase in MLSP by over 10 years though sample sizes are very similar.

Cooler temperatures in the early Pleistocene, especially at our mid-latitude sites in North Carolina, seem to be promoting slow growth (lower k values) and longer lifespan. In contrast, life history traits of our low latitude sites seem to be less impacted by climate state than those at mid-latitudes (Fig. 8). Even though the early Pleistocene was a cooler time globally, low latitude temperatures did not change significantly (Dowsett and Cronin, 1990; Cronin, 1991; Willard et al., 1993; Tao, 2012) and neither did life history parameters. This might have significant evolutionary implications. Today, metabolic rates of bivalves are faster at lower latitudes (Vladimirova et al., 2003), where von Bertalanffy k values are highest. During both the MPWP and the early Pleistocene, *Mercenaria* k values are higher in the tropics than they are at mid-latitudes, which might suggest metabolic rates are higher too. Lower latitudes might thus facilitate higher metabolic rates and von

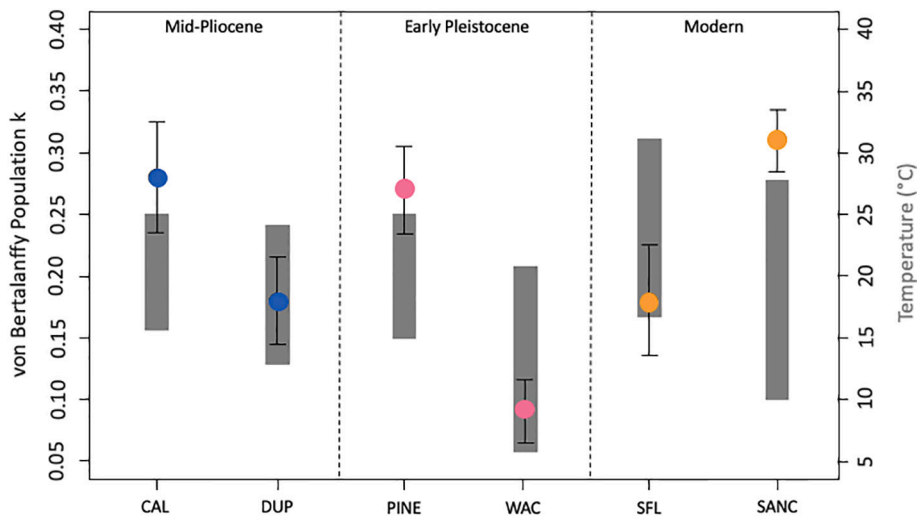


Fig. 8. Relationship between von Bertalanffy k and annual temperature range. Solid color circles = population k values with upper and lower confidence intervals. Gray boxes = annual temperature ranges. CAL = mid-Pliocene, Caloosahatchee Formation (Dowsett and Cronin, 1990; Cronin, 1991; Willard et al., 1993); DUP = mid-Pliocene, Duplin Formation (Dowsett and Cronin, 1990; Cronin, 1991); PINE = early Pleistocene, Lower Pinecrest Beds (Willard et al., 1993; Tao, 2012); WAC = early Pleistocene, Lower Waccamaw Formation (Krantz, 1990); SFL = Modern Florida (https://my.sfwmd.gov/dbhydropl/sql/show_dbkey_info.main_menu); and SANC = Modern North Carolina (<https://cdmo.baruch.sc.edu/dges/>).

Bertalanffy k values through time regardless of global climate state. If this hypothesis is correct, and growth is always faster in the tropics, this might be related to latitudinal diversity gradients through time (e.g., Mannion et al., 2014).

7.2. Life history of modern *Mercenaria*

Our life history data for modern *Mercenaria* do not show the expected trend of increasing lifespan and decreasing growth rate with latitude. Individuals from our Florida population grow slower ($k = 0.18$) and tend to live longer (LSP = 20.25, $\sigma = 7.93$) than those from North Carolina ($k = 0.31$, LSP = 15.56, $\sigma = 4.59$). While this would seem to raise questions to the patterns we observe in the fossil record, a number of factors could be influencing our modern data set, which we discuss below.

Habitat-specific conditions such as depth, sediment type, and salinity influence the growth of *Mercenaria*. For example, salinities below 15 and above 32 can inhibit *Mercenaria* growth and long-term survival (Channley, 1957; Castagna, 1973; Winkle et al., 1976). Studies have also shown variation in growth rates of *Mercenaria* in response to sediment types. For example, *Mercenaria* from substrates with higher sand content tend to have faster growth rates compared to those from muddy bottoms (Grizzle and Morin, 1989). Similarly, *Mercenaria* tend to have faster growth rates on vegetated compared to unvegetated seafloors (Arnold et al., 1991; Slattey et al., 1991). Finally, *Mercenaria* living at deeper depths tend to grow slower than those at shallower depths because of a decrease in seasonal food availability and interference in filtering by resuspended bottom sediments (Arnold et al., 1991).

Habitat specific differences in environmental conditions are unlikely to influence our modern samples. Shells were collected from the bay sides of Sanibel and Masonboro Islands in Florida and North Carolina, respectively. These localities all have sandy to muddy bottoms absent of high vegetation, and shells were collected at depths of approximately 1 m. However, the most significant difference in environmental conditions is in the salinity variations at each site. Our North Carolina locality has restricted access to the open ocean through the Masonboro inlet and limited freshwater inflow occurs primarily through the Hewletts and Whisky Creeks. The salinity of this locality ranges from 11.8–37.1 (<https://cdmo.baruch.sc.edu/dges/>). In comparison, Florida localities receive significant freshwater inflow from the Caloosahatchee River. However, these localities are also exposed to the open ocean through the opening between Sanibel Island and Punta Rassa and multiple inlets along Sanibel Island. Salinity within this region range 22.6–34.7 (https://my.sfwmd.gov/dbhydropl/sql/show_dbkey_info.main_menu). Both sites then, typically fall within the normal range of salinity for *Mercenaria*, and we do not suspect these differences are influencing life

history significantly.

Sampling procedures likely played a role in the life history patterns we see in modern North Carolina *Mercenaria*. Our samples were all collected alive from the same small area within UNCW's marine sanctuary, which is a protected marine habitat. When we examine their age distribution, we found that they have not only the shortest reported maximum lifespan, but also smallest mean lifespan (16 years, $\sigma = 4.59$) of any of our populations sampled, modern or fossil. This finding likely means that we have sampled what might be a few cohorts or groups of individuals that represent only a few spat falls. It is possible that this population was collected too early, and undoubtedly had we left them alone, they would have lived longer. It is difficult to compare the life history of our modern North Carolina shells because they are probably not a true representation of modern populations. Our Florida samples on the other hand were obtained from museums which were collected from various localities over a span of approximately 25 years, and they might be more representative of a modern population and perhaps more comparable to a fossil population given an artificially introduced degree of time mixing.

Finally, our inability to recapture a modern latitudinal life history trend in *Mercenaria* might be due to the noisy nature of life history data themselves. The modern latitudinal life history gradient not only shows inverse trends in lifespan and von Bertalanffy k , but also demonstrates that variance in these traits is not equal across latitude. In fact, variance in von Bertalanffy k decreases with increasing latitude, whereas variance in lifespan increases with increasing latitude. Thus, at any given latitude, we should expect to see some range in life history parameters. Growth rates and lifespans of modern *Mercenaria* populations are well studied throughout their biogeographic range (Hopkins, 1930; Saloman and Taylor, 1969; Peterson et al., 1983; Walker and Tenore, 1984; Peterson, 1986; Jones et al., 1990; Arnold et al., 1991; Slattey et al., 1991; Eversole et al., 2000; Surge and Walker, 2006), and when we incorporate data from other studies (Fig. 9), latitudinal trends in life history of modern *Mercenaria* from Florida to North Carolina become more apparent. Our von Bertalanffy k value for Florida falls towards the lower range of what was expected, and our maximum lifespan appears to be a record for that latitude. Published data from North Carolina are more sparse ($k = 0.14$ – 0.18), and our von Bertalanffy k value ($k = 0.31$) falls outside the reported range. In addition, data from other studies (Hopkins, 1930; Saloman and Taylor, 1969; Peterson et al., 1983; Walker and Tenore, 1984; Peterson, 1986; Jones et al., 1990; Arnold et al., 1991; Eversole et al., 2000; Surge and Walker, 2006) suggest that at that latitude much older individuals exist that we may not have sampled. This possibility is likely influencing our VBG k values and with more and perhaps better targeted sampling we would likely find much

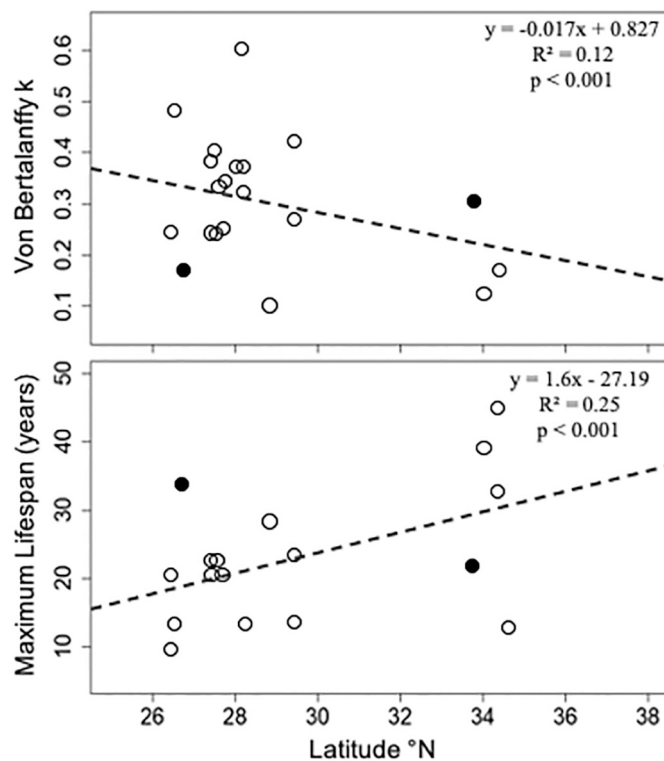


Fig. 9. Top: Relationship between latitude and k value of modern *Mercenaria* spp. Bottom: Relationship between latitude and lifespan of modern *Mercenaria* spp. Solid circles = our study. Empty circles = k and lifespan values from the following publications: Hopkins (1930), Saloman and Taylor (1969), Peterson et al. (1983), Walker and Tenore (1984), Peterson (1986), Jones et al. (1990), Arnold et al. (1991), Slattery et al. (1991), Eversole et al. (2000), and Surge and Walker (2006).

older individuals. In addition, though we were able to incorporate some data from previous studies, the size-at-age data required to obtain VBG k values and lifespans are not reported consistently or readily available. Some of these studies only report single population life history parameters. For example, Peterson et al. (1983) reports the relationship between length and total annual increments but does not specify length at specific ages. Peterson (1986) reports the age when specimens were collected but not the size of the shells. Slattery et al. (1991) report maximum size and maximum age of *Mercenaria* but they do not specify the size at every age for the shells. As the study of life histories becomes more common, especially in fossil bivalves, we should be aware of these issues and report all size-at-age data so they can be used by future researchers.

7.3. Implications for conservation paleobiology

Bivalve shellfishing contributes over \$800,000,000 annually to the US marine fisheries industry (<https://www.fisheries.noaa.gov/national/sustainable-fisheries/commercial-fisheries-landings>), yet the impact of climate and environmental change on shellfisheries are only now starting to be understood. Recent studies on growth of the long-lived *Arctica islandica*, a primary source in the U.S. of clams for chowder, have found significant impacts of rising global temperatures over the past century and a half. Off the coast of the eastern U.S., living *A. islandica* now reach 80 mm, the size at which they are selected by commercial dredges, in approximately 30 years, compared to about 60 years in the early 1800s (Pace et al., 2018). In the Atlantic Surfclam, *Spisula solidissima*, populations have been pushed further offshore and into deeper water off Long Island. This shift has caused increased starvation mortality as decreased food availability at deeper depths is not

sufficient to maintain respiration rates in older, larger individuals (Narváez et al., 2015; Munroe et al., 2016). Both of these changes in life history strategy took place over an approximately 1 °C increase in seawater temperature.

How will life histories of modern marine bivalves change if the highest estimates of the 2013 IPCC report (4.8 °C) by 2100 are reached? Much like in modern bivalves, our fossil data show a strong relationship between temperature and growth rate: as temperature increases growth rates increase at our mid-latitude site. In the cooler early Pleistocene, *Mercenaria* spp. from North Carolina took approximately 20 years to reach 100 mm, whereas in the mid-Pliocene, this size was attained in only 10 years. However, growth and lifespan does not change much at the lower latitude sites, perhaps because temperatures in tropical regions are more stable even between climate states. These observations suggest that in response to increasing seawater temperatures, life history patterns in low-latitude *Mercenaria* may not change appreciably, but those from mid-latitudes may shift to faster growth rates. Thus, mid-latitude populations may reach a harvestable size and sexual maturity quicker. Faster growth would be predicted to come with shorter lifespans as the two are inversely related. What either might mean for the future of *Mercenaria* harvestability at mid-latitudes remains somewhat unclear as the relationship between lifespan and fecundity has not been seriously addressed. Either way, it could have serious impacts on population management and accounting for such responses will be critical when constructing management plans, harvesting seasonings, and even catch allowances. Given the reliance of shellfisheries on this species, it is important to understand these potential responses to properly prepare for what future shellfisheries might face with projected environmental change.

8. Conclusions

The potential response of marine organisms to rising seawater temperatures remains uncertain. This uncertainty is in large part due to the time scale over which these processes happen. Fortunately, the fossil record provides us an opportunity to explore how species have responded to environmental change in the past. Here, we turn to the fossil record to give us insight on how the economically and ecologically important bivalve genus, *Mercenaria*, might respond to projected increases in seawater temperature. We accomplished this by analyzing life history parameters of fossil *Mercenaria* spp. from climate intervals warmer than or comparable to today. Further, we examined how temperature influences these life history parameters by comparing growth rates and lifespans in fossil populations from the warm MPWP and subsequent cooling of the early Pleistocene. We found that growth rates vary with temperature. In general, specimens from warmer climates have faster growth rates compared to those from cooler climates. However, the relationship between lifespan and climate state is not as clear. Further, we observe that individuals from low latitudes seem to be less impacted by climate state than those at mid latitudes. Given these findings, we suggest mid-high latitude individuals might experience shifts in growth rates, whereas low-latitude individuals might not experience such impacts. These findings provide useful data for conservation biology and restoration ecology that can be used to set policy or develop management plans in the face of projected future warming.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2021.110227>.

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