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INVESTIGATION OF DEAD OCEAN QUAHOGS (ARCTICA ISLANDICA) SHELLS ON THE MID-ATLANTIC BIGHT CONTINENTAL SHELF

by

Alyssa M. LeClaire

A Thesis
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and the School of Ocean Science and Engineering
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ABSTRACT

Ocean quahogs, *Arctica islandica*, are a long-lived, widely dispersed, biomass dominate in the Mid-Atlantic; therefore, quahog shells are valuable resources for studying climate change over time. Recently, dead ocean quahog shells were discovered south and inshore of the present biogeographic range of this animal. The presence of ocean quahog shells outside the current range is presumably a consequence of past regressions and transgressions of the Cold Pool, the bottom-trapped, cool body of water that allows boreal animals to live at lower latitudes. Dead ocean quahog shells were collected offshore of the DelMarVa Peninsula then radiocarbon-dated, evaluated for taphonomic condition, and aged to investigate spatial-temporal changes in growth. One hundred and twenty-one dead shell were dated with birth years ranging from 60-4,400 cal years BP, including ages contemporaneous with four major Holocene cold events. Shells with a longer time-since-death were discolored orange with no periostracum while shells with a shorter time-since-death had their original color, white, with some periostracum. The presence (or absence) of periostracum and discoloration followed a logistic process, with 50% of shells absent of periostracum and 50% discolored in about 1,000 years. This is the longest time series assessing taphonomic processes within the Holocene with the first reported logistic relationship between time-since-death and degradation. Changes in growth throughout time and space is evident when comparing growth curves fit with a Modified Tanaka model to contemporary populations for George's Bank, Long Island, and New Jersey.

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First, I want to thank my advisor, Dr. Powell, for his mentorship and the introduction into the world of Mid-Atlantic clam fisheries. I would also like to thank Dr. Mann who provided the use of the Molluscan Ecology Lab at the Virginia Institute of Marine Science as well as an extensive knowledge of bivalves.

I am thankful for crew of the *F/V Betty C* and *F/V Pursuit* for their assistance in collecting the samples and the use of their industry gear. As well, I am thankful for the National Marine Fisheries Service Northeast Fisheries Science Center (NEFSC) for making available the original datasets used in this study for site selection and we express particular appreciation of the efforts of the many individuals of the NEFSC survey branch that participated in survey data collection over the 1980-2011 time period that made this study possible.

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DEDICATION

This dissertation is dedicated to:

My parents, Amy and Grant

My siblings, Megan, Gabe, and Garrett

My partner, Austin

& the world's best dog, Nellie

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LIST OF ABBREVIATIONS

USM	The University of Southern Mississippi
SCEMFIS	Science Center for Marine Fisheries
GB	Georges Bank
LI	Long Island
MAB	Mid-Atlantic Bight
DMV	Delmarva Peninsula
NJ	New Jersey
MRA	Marine Reservoir Age
BP	Before Present
CE	Common Era
BCE	Before Common Era
MT	Modified Tanaka
RWP	Roman Warm Period
MWP	Medieval Warm Period
LIA	Little Ice Age

CHAPTER I INTRODUCTION

1.1 Background

Ocean quahogs, formally known as *Arctica islandica* (Linneaus, 1769), are among the longest lived non-colonial animals known to science (Merrill and Ropes, 1969; Dahlgren et al., 2000; Wanamaker et al. 2008; Ridgeway and Richardson, 2011) with the oldest individual (deemed Ming) aged at 507 years (Butler et al., 2013). These clams are a boreal, benthic species with a strict upper thermal limit at ~15℃, constraining the species to waters that do not exceed this tolerance. Hence, along the Northwest Atlantic continental shelf, ocean quahogs reside in the bottom-trapped, body of water known as the Cold Pool. The Cold Pool, a result of seasonal stratification, maintains temperatures well below 15℃ (Houghton et al., 1982; Bignami and Hopkins, 2003; Castelao et al., 2008; Lentz, 2017). However, the changing climate is warming the Mid-Atlantic faster than 90% of other oceans in the world, posing a threat to the duration of the Cold Pool and suitable habitat for the ocean quahog (Pershing et al., 2015; Saba et al., 2016; Lentz, 2017),

Conversely, the North Atlantic water temperature has continuously fluctuated throughout the current epoch, the Holocene. Consisting of the past 11.7 thousand years, the Holocene is characterized by various climate events including: the 4.2ka event, which defines the Northgrippian-Megalayan stage boundary (Helama and Oninonen, 2019), the Neoglacial (Jennings et al., 2002; Moossen et al., 2015), the Roman Warm Period(Wang et al., 2012), the Dark Ages Cold Period (Helama et al., 2017), the Medieval Warm Period (Graham et al., 2011; Moossen et al., 2015), and the Little Ice Age Ogilvie and Jonsson, 2001; Moossen et al., 2015; Moore et al., 2017). Subsequent to the Little Ice

Age, water temperatures in the Mid-Atlantic continue to cycle through warm and cool periods, a product of the Atlantic Multidecadal Oscillation (Moore et al., 2017; Cheng and Tang, 2018; Hou et al., 2019). These temperature regimes largely impact bottom water temperatures and the residing benthic species, including the ocean quahog.

Recently, Powell et al. (2020) found evidence that the oscillating climate may have impacted the biogeographic range of past ocean quahogs. Locations with only dead ocean quahog shells were mapped in relatively shallow water off shore of the Delaware-Maryland-Virginia Peninsula (Delmarva). This discovery is in stark contrast to the expected condition, where live clams co-occur with dead shells. These dead shell sites were mapped in locations both further south and inshore of the current range of *A. islandica*, suggesting that past environmental conditions sustained the clams outside of their present-range. Determining when these dead shells entered the death assemblage and consequently time-since-death would reveal the timing of these past occupations and concurrent climate events.

Presumably, spending more time in the death assemblage and the taphonomically-active zone (TAZ) would increase exposure of a shell to taphonomic processes such as discoloration and degradation, resulting in signatures that should indicate time-since-death (Butler et al., 2020). Death assemblages can provide information on the spatial and temporal changes in community composition caused by a changing climate (Kidwell, 2007; Negri et al., 2015; Bizjack et al., 2017; Arkle et al., 2018). Specifically, *Arctica islandica* are invaluable records of climate with a narrow, well-defined temperature tolerance, widespread distribution in the North Atlantic, and long lifespan (Dahlgren et al., 2000; Witbaard and Bergman, 2003; Wanamaker et al., 2011; Hemeon et al., 2021;)

These physiological traits make *A. islandica* useful for documenting the spatial and temporal influence of climate change in the Mid-Atlantic (Dahlgren et al., 2000; Witbaard and Bergman, 2003; Wanamaker et al., 2011; Hemeon et al., 2021;).

1.2 **Project Objectives**

This thesis expanded on the results of Powell et al., (2020a), investigating the collection of dead ocean quahog shells found and collected on the continental shelf off the Delmarva Peninsula. The first objective verified the timing of the shifting ocean quahog occupation indicated by the presence of dead shells via radiocarbon dating. Determining the timing of past occupations, revealed time-since-death that was obscured by the time-averaging within the death assemblage (Flessa and Kowalewski, 1994; Tomašovych et al., 2014; Dominguez et al., 2016) Taphonomic condition (discoloration and presence of periostracum) of shells was evaluated prior to extracting shell powder samples for radiocarbon dating to determine time-since-death. Hence, the second objective was comparing the taphonomic signatures to time-since-death to determine indicators related to age of dead shells, aiding in future shell selection to target specific time periods. Lastly, comparisons were made between regional and temporal changes in animal growth to assess the influence of spatio-temporal difference in growth rates. These data were evaluated as a tool for reconstruction of past range shifts and ocean quahog populations, and consequently support the potential for development of a predictive tools that can be utilized for future research with ocean quahogs.

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CHAPTER II HISTORICAL BIOGEOGRAPHIC RANGE SHIFTS AND THE INFLUENCE OF CLIMATE CHANGE DURING THE HOLOCENE ON OCEAN QUAHOGS (ARCTICA ISLANDICA) IN THE MID-ATLANTIC BIGHT

Modified from:

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2.1 Introduction

Key climate events in the North Atlantic during the middle to late Holocene include the Neoglacial Period (Jennings et al., 2002; Moossen et al., 2015), the Roman Warm Period (RWP) (Wang et al., 2012), the Dark Ages Cold Period (DACP) (Helama et al., 2017), the Medieval Warm Period (MWP = Medieval Climate Anomaly) (Graham et al., 2011; Moossen et al., 2015), and the Little Ice Age (LIA; Ogilvie and Jonsson, 2001; Moossen et al., 2015; Moore et al., 2017). Since the end of the LIA the waters of the U.S. northeastern continental shelf have been in a cycle of warming and cooling periods, a consequence of the Atlantic Multidecadal Oscillation (AMO; Moore et al., 2017; Cheng and Tang, 2018; Hou et al., 2019), superimposed on a persistent warming trend (Hanna et al., 2004; Wallace et al., 2018) well documented in the meteorology of the region (Augut et al., 2019). Recently, the Western North Atlantic has been warming at a rate faster than >90% of oceans around the world (Pershing et al., 2015; Saba et al., 2016; Lentz, 2017), likely due to a northward shift of the Gulf Stream (Sachs 2007; Neto et al., 2021). Warming water alters bottom conditions, affecting the survival and distribution of benthic species on the US continental shelf (Scavia et al., 2002; Friedland and Hare, 2007; Lucey and Nye, 2010; Hofmann et al., 2018).

The boreal, benthic clams known as ocean quahogs, *Arctica islandica* (Linneaus, 1769), have supported a major fishery on the U.S. Mid-Atlantic continental shelf since 1967 (Merrill and Ropes, 1969; Dahlgren et al., 2000; Hennen, 2015), with most landings post-1980 (NEFSC, 2017b). As a boreal species, these clams are constrained to water less than or equal to 15℃; hence, ocean quahogs are found exclusively within the Cold Pool on the MAB continental shelf. The Cold Pool, a seasonal finger of cold water located on the outer continental shelf, maintained by thermal stratification during the summer, rarely rises above 15°C (Houghton et al., 1982; Bignami and Hopkins, 2003; Castelao et al., 2008; Lentz, 2017). The inshore boundary of the Cold Pool and surrounding coastal water form an ecotone sensitive to climate change. This sensitivity is exemplified by the progradation of Atlantic surfclams (*Spisula solidissima*) across the continental shelf in response to rising temperatures that are causing the inshore boundary of the Cold Pool to recede (Weinberg, 2005; Kavanaugh et al., 2017; Hofmann et al., 2018; Friedland et al., 2020). The latitudinal extent of this boundary presents a chance to evaluate conditions that prompt range shifts of thermally-sensitive species, like the ocean quahog.

The National Marine Fisheries Service – Northeast Fisheries Science Center (NMFS-NEFSC) has surveyed ocean quahogs on the MAB continental shelf from 1982 to present day (NEFSC, 2017b). Before 2012, the NEFSC survey collected data not only on live animals but also estimated the abundance of dead shells. Using these data, Powell et al. (2020) were able to map locations where live clams and dead shells co-occurred (the expected condition), and localities where only dead shells were found. Powell et al.

(2020) discovered an abundance of sites where only dead ocean quahog shells were found extending farther inshore and covering a larger range than the contemporary ocean quahog population. This inshore distribution of shells was most apparent in the southern portion of the MAB (Powell et al., 2020). The ocean quahog fishery began off the Delmarva Peninsula and then moved north to its present focus off Long Island, but landings have never been recorded in the target region for this study, the inshore waters off Delmarva (NEFSC, 2017b); thus, dead shells found outside of the present range do not originate from modern fishing activities, but suggest that past environmental conditions sustained living ocean quahogs closer to shore in the past.

The NEFSC survey only encompasses the last 40 years of the present warming period beginning in the 1800s (Pace et al., 2017a, 2017b). Regional population age frequencies suggest *A. islandica* existed in relatively low abundance over its present biogeographic range during the late LIA, followed by a rapid population expansion in the late 1800s throughout the MAB (Pace et al., 2017b, Hemeon et al., in press) with high population abundance continuing through today. During the LIA and through the 1800s, colder water presumably extended closer inshore, supporting the inshore range of ocean quahogs documented by the distribution of dead shells.

The distribution of shells described by Powell et al. (2020) suggests that the inshore range boundary for ocean quahogs has shifted offshore across the continental shelf, driven by the changes in bottom water temperatures. Records of sea surface temperatures in this region extend to the mid-1800s. However, few oceanographic records of sea bottom temperature exist before 1950. Consequently, historical temperature records do not capture Cold Pool water as it is a bottom-tending phenomenon (Hulme and Jones, 1994; Hanna et al., 2004). Evidence of bottom water temperature shifts is limited to documentation of events such as the well-known tilefish mass mortality of 1882, an event commonly attributed to an extreme cold deviation from average conditions (Fisher et al., 2014). In addition, very limited temperature data extend back to the late 1700s and early 1800s, and what records exist are all atmospheric. For this region of the continental shelf, only temperature proxies support inferences that it was colder than today (Pace et al., 2018; see also Moore et al., 2017). This inadequate database of past surface and bottom water temperatures limits the reconstruction of MAB bottom water temperatures by hydrodynamic models (Kang and Curchitser, 2013).

Arctica islandica shells have proven to be effective as paleothermometers used to inform on bottom water temperatures over extended time periods (Weidman et al., 1994, Schöne et al., 2005; Butler et al., 2013; Holland et al., 2014, Mette et al., 2016; Reynolds et al., 2016, Reynolds et al., 2017 Wanamaker et al., 2011; Butler et al., 2013, von Leesen et al., 2017, Crippa et al., 2019). Typically, modern applications of the death assemblage focus on the study of historical conditions and anthropogenic-induced shifts in community structure. Limited attention has been given to the death assemblage as a recorder of geographic climate change (Scourse et al., 2006, Kidwell, 2007, Kidwell, 2008 Wanamaker et al., 2008, Kosnik et al., 2009, Wanamaker et al., 2011, Meadows et al., 2019, Powell et al., 2020) Negri et al., 2015; Bizjack et al., 2017). Ocean quahogs are unique in their potential to contribute to long-term chronologies with a lifespan exceeding 500 years (Butler et al., 2013). In the MAB, animals of 250+ years have been collected live (Pace et al., 2017b). The discovery of dead shells inshore of the present-day distribution presents an opportunity to improve the understanding of bottom water temperature history in the Mid-Atlantic Bight as well as evaluate the distributional dynamics of this species during periods of climate change.

This report tests the hypothesis of Powell et al. (2020) that the presence of ocean quahogs inshore of the present-day range boundary provides a record of historical climate change in the MAB and long-term variability in the Cold Pool. To test this hypothesis, dead shells were collected inshore of their present southern range boundary in August 2019 and the approximate birth date estimated with radiocarbon dating. The history of past inshore occupations and range shifts can be reconstructed from these samples and evaluated to support the development of a predictive tool for future range shifts on the MAB continental shelf.

2.2 Materials and Methods

2.2.1 Sample Collection

To investigate the timing of range shifts, dead ocean quahog shells were collected inshore of the species' present-day southern inshore range boundary. A hydraulic dredge with a dredge width of 2.54 m was used to collect dead shells during an August 2019 research cruise aboard the F/V Betty C, a typical commercial clam boat (Parker 1971; Meyer et al., 1981). The dredge was lined with 1-inch square wire on the bottom and knife shelf, and 1x2-inch rectangular wire on the sides, back, and door. The wire lining retained clams ~≥40 mm. Tows had a swept area of approximately 118 m^2 with tow distance limited to prevent overfilling of the dredge. Ocean quahogs shells were manually selected from the dredge haul material passed along a central belt. Sample stations extend along the continental shelf off the Delmarva peninsula (Fig. 1, Table 1). Of the 27 stations sampled, 22 stations were also NEFSC federal survey stations for ocean quahogs and Atlantic surfclams sampled during 1982-2011 (NEFSC, 2017b) and identified by Powell et al. (2020). Five additional stations were added to this study from Powell et al. (2017).

2.2.2 Radiocarbon dating

Valves selected for dating were cut using a Kobalt wet tile saw. The valves were ground using 240 grit silicon carbide abrasive paper to remove any contaminants along the edge. Shell powder samples were extracted from half of the cut valve using a Dremel tool to grind the cut edge of the shell near the hinge and umbo to collect carbonate from the portion of the shell with early ontogenetic growth; that is, shell deposited during the first few years of life. Shell powder was collected and the resulting >10-mg sample was sent to the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine for analysis. Radiocarbon ages of samples will be referred to hereafter as birth years to clarify that the ages represent the time near the beginning of the lifespan which often exceeds 200 years for ocean quahogs.

Radiocarbon ages (±15-25 years depending on sample) were corrected for marine reservoir age (MRA) using Marine13 (400 years) (Reimer et al., 2013). MRA differs both temporally and spatially as a consequence of spatio-temporal variations in ocean mixing (Alves et al., 2018; Heaton et al., 2020). Ocean quahogs live in the Cold Pool, which derives water in varying proportions from Arctic and North Atlantic sources depending on the year (Wang et al., 2019; Chen and Curchitser, 2020; Chen et al., 2021; Miles et al., 2021), providing some uncertainty in this correction factor. In addition, the majority of earlier estimations for the North Atlantic come from the eastern Atlantic, greater depths, or higher latitudes, with mixes of water sources divergent from the composition of the

Cold Pool (Eiriksson et al., 2004; Sherwood et al., 2008; Ascough et al., 2007; Tisnérat-Laborde et al., 2010; Heaton et al., 2020). Given the absence of a regional MRA in the MAB offshore of the Delmarva Peninsula, a series of live *A. islandica* were obtained from sites off New Jersey, Long Island, and Georges Bank as described by Hemeon et al., (2022) and Sower et al., (unpublished data). Shells from live animals were processed and radiocarbon dated using the same method followed for dead shells.

[Insert Figure 2.] A comparison of the birth year obtained by directly aging the shells of these live-caught bivalves to the radiocarbon ages obtained for their shells demonstrated a good fit to the Marine13 MRA correction factor of 400 yr (Fig. 2). The median residual when compared to the Marine13 MRA obtained from this comparison was -5 year, a mean of -7 year, and a standard deviation of ±38.67 year. Nevertheless, to constrain the potential error when calibrating marine carbon dates in this region, further research is needed to determine the regional variability in MRA in the Cold Pool. Given the presently available database shown in Figure 2, birth dates in this contribution were corrected under the assumption that bottom water conditions present at the time the dated shells were alive were consistent with the Marine13 MRA.

Ocean quahogs alive after 1950 were exposed to bomb carbon from the detonation of the atomic bombs in the late 1950s and 1960s. Exposure to ‘bomb carbon’ resulted in a spike of 14C in the shell. The reference time series of Δ14C (‰ deviation of the sample from the radiocarbon standard defined by Stuiver and Polach, 1977) determined by Kilada et al. (2007) was applied to radiocarbon values from ocean quahog shells to estimate birth years post-1950 (Scourse et al., 2012).

2.3 Results

A total of 121 *Arctica islandica* shells were radiocarbon-dated. Of these, 116 dead shells were born pre-bomb and 5 shells were born post-bomb. Radiocarbon ages ranged from 4,392 cal BP to 61 cal BP (Table 1). Of the 121 shells dated, 60 were alive in the 1800-1900s (Fig. 3, Fig. 4). Most of these shells were alive between 1805 and 1865, within and just after the final years of the Little Ice Age (Mann et al., 2009; Cronin et al., 2010). Because of the uncertainty surrounding the exact end of the LIA, the ending of the LIA bas been set arbitrarily to 1819 to split the radiocarbon dates obtained from this time period into two relatively equivalent groups. Radiocarbon dates for six more shells were between 4.3 and 4.1 cal ka BP, contemporaneous with the Northgrippian-Megpalayan boundary of the Holocene circa 4.2 cal ka BP (Fig. 3a; Helama and Oninonen, 2019). Twenty-three *A. islandica* were born between 3.8-3.0 cal ka and 2.4 cal ka BP, coinciding with the time referred to as the Neoglacial Period (Fig. 3a; Jennings et al., 2002; Larsen et al., 2012; Wang et al., 2012; Moossen et al., 2015). One dead shell lived in 2.0 cal ka BP which coincides with the Roman Warm Period (Wang et al., 2012). Twelve animals lived during the Dark Ages Cold Period (Fig. 3b; Buntgenet al., 2011; Larsen et al., 2012; Moossen et al., 2015; Helama et al., 2017). Two shells were born in 0.8 cal ka BP toward the end of the Medieval Warm Period. The eighteen shells recruited between 1500-1800 cal CE were alive during the Little Ice Age (Fig. 3b; Larsen et al., 2012; Cronin et al., 2019).

Shells collected from nine stations lived during the first half of the Neoglacial, around the 4.2 cal ka event (Fig.1). Two of the seven stations with shells dated during the Neoglacial also had shells dated during the 4.2 cal ka event (Fig. 5). Shells at two collection sites were born during the Dark Ages Cold Period (Fig. 6). Shells at eleven stations lived during the Little Ice Age, and shells at five of these stations also lived during previous cold periods (Figs. 1, 5). Shells at fifteen stations lived between 1819-1965; at seven of these stations, shells lived during the Little Ice Age (Fig. 7), and shells at three stations also lived during the Neoglacial periods (Figs. 1, 5, 7).

The distribution of shell dates among stations showed that samples often included shells with dates from more than one previous cold period. Seven of 25 stations provided shells from more than one cold period, with 3 of these stations providing shells with dates from 3 cold periods. In addition, dead shells collected from 9 stations were alive in 1820 or later and during the LIA (defined arbitrarily to end in 1819). Thus, the sampled stations were routinely occupied by ocean quahogs during earlier cold times and these multiply-occupied sites were also distributed throughout the sampled region.

2.4 Discussion

2.4.1 Understanding the Death Assemblage

Finding solely dead shells can indicate the spatial or temporal under-sampling of the community or allochthonous redistribution of shells (Staff and Powell, 1988; Kidwell, 2002). Although the possibility of allochthonous input cannot be ignored, the rarity of fishing vessel routes in the area suggests that ocean quahogs found offshore of Delmarva were not discarded shells from fishing vessels (e.g., NEFSC, 2017a, 2017b; see also Ropes, 1972, 1982). The geographic extent of the federal survey assures adequate sampling of the region and validates the absence of live animals at sampled stations and throughout the adjacent region. Moreover, the life span of the species minimizes the possibility of failing to capture live animals due to seasonal or interannual variations in abundance, a consideration for shorter-lived species (e.g., Staff and Powell, 1988, 1990; Kidwell, 2008). Finally, water depth limits any shoreward transport of shells by storms (Miles et al., 2015). The shells represent the remains of animals originally living at these sites and the birth years fall after the period of rapid sea-level rise in the early years of the Holocene, meaning that the MAB continental shelf depths were similar to today (Engelhart et al., 2011).

The number of the shells dated during a given time interval is not an indication of the relative abundance of the shells in situ, as no effort was made to age shells in proportion to the numbers retrieved by the dredge. The shells retrieved were present in the top ~8 cm of the sediment column, as hydraulic dredges are not designed to dig deep into the sediment. Only a small vertical section of the death assemblage was accessed; however, these dredges are efficient collectors of material in this surficial horizon (Poussard et al., 2021).

The time periods recorded by these shells in the death assemblage are a function of preservation processes, including limited burial rates, and shell degradation (Powell, 1992; Smith and Nelson, 2003; Olszewski, 2004; Tomašových, 2004). Ocean quahogs shells degrade slowly and as a result persist in the death assemblage (Powell et al., 2008, 2011a, 2011b). Hence, age distributions observed support the inference that gaps in the distribution are likely to record times when living animals were not present, rather than a failure to be preserved. Large numbers of shells recorded from the 19th century relative to earlier times support the hypothesis of exponential loss in time-averaged assemblages proposed by Tomašových et al. (2014), Dexter et al. (2014), and Kosnik et al. (2009).

Thus, the majority of birth dates being after 1800 CE does not indicate a lesser population abundance prior to those times.

2.4.2 **Generality of findings**

The distribution of birth dates among stations reveals that samples at the same station often included shells from more than one previous cold period. Stations were routinely occupied by ocean quahogs during multiple cold events and were distributed throughout the study region. Station samples containing shells from multiple climate events within the entire study region of approximately 1.5 degrees of latitude suggests that the study does not include the entire geographic extent of past ocean quahog occupations, but rather suggests that further study would reveal a much more widespread occupation in the studied region for each of the cold periods identified.

2.4.3 **Distribution and range shifts**

The locations sampled harboring only dead clams are geographically distinct from the species present-day range (Fig. 1-4); therefore, the death assemblage preserves a record of past occupation and the historical shifting range of this species (Powell et al., 2020). Utilizing these data, the death assemblage in these areas can further the understanding of past, ongoing, and future range shifts consequent of changes in bottom water temperatures (Powell et al., 2020).

Sea bottom temperatures (SBTs) in the MAB directly affect the distribution of *A. islandica* (Dahlgren et al., 2000), as seen in the connection between the 15°C isotherm and the inshore range of these boreal clams (Mann, 1982; Harding et al., 2008). Although *A.islandica* grow shell at temperatures as low as 0-1°C (Witbaard et al., 1997, Schöne et al., 2004, Wanamaker et al., 2008, Wanamaker et al., 2011), in the MAB region, the minimum bottom temperature in the Cold Pool ranges between 4-5°C (Chen & Curchitser, 2020) and the presence of clear growth increments confirms limited growth at these winter temperatures in MAB populations. Therefore, inferring a practical thermal range for adult ocean quahogs in the MAB to be between 4-16°C (Harding et al., 2008), the presence of these shells suggests that bottom temperatures during their lifetimes were within the same thermal range (Powell et al., 2020). Currently, the SBTs in the sampled region (Fig. 1) are too warm to support ocean quahogs and even too warm to continuously support Atlantic surfclams (Hofmann et al., 2018), which have a higher thermal maximum (Munroe et al., 2013; NEFSC, 2017a). During the late Holocene, however, the distribution of *A. islandica* was both farther inshore and farther south than the present ocean quahog range (Figs. 1, 5-7).

Shells containing radiocarbon from certain time periods indicate animals were alive when optimum environmental conditions prevailed for a boreal species. Over half of the radiocarbon dates indicate that animals were alive in the late 1700s to 1800s at these shallower inshore depths, years that are contemporaneous with the recruitment of the modern living population farther offshore in southern New Jersey (Pace et al., 2017b). This connection signifies that rising temperatures over the past 200 years are the likely cause of the disappearance of ocean quahogs from these inshore habitats. The remaining radiocarbon dates substantively predate the late 1700s-1800s. The majority of these years align with known cooling events in the late Holocene (Mayewski et al., 2004; Wanner et al., 2011). Wanner et al. (2011) determined that the post-glacial climate was interrupted by 6 cold periods during the Holocene. Two periods occurred before the earliest birth of any sampled shells, indicating conditions were outside the optimal thermal range probably because lower sea level produced depths too shallow for habitation in the sampled region during these times. However, the other four cooling periods described by Wanner et al. (2011) correspond with *A. islandica* recovered from the MAB death assemblage. Negative temperature anomalies in North America reveal cooling events in 4.3-3.8 cal ka BP, 3.3-2.5 cal ka BP, 1.75-1.35 cal ka BP, and 0.7-0.15 cal ka BP (Mayewski et al., 2004; Wanner et al., 2001). These times align with known past climate events including the Neoglacial, Dark Ages Cold Period, and Little Ice Age (Jennings et al., 2002; Larsen et al., 2012; Wang et al., 2012; Moossen et al., 2015; Helama and Oninonen, 2019) and are represented by ocean quahog shells dated in this study.

The exact timing and extent of the Neoglacial is uncertain, but estimates range between 6-2 cal ka BP (Jennings et al., 2002; Weidick et al., 2012; Moossen et al., 2015; Weiser et al., 2021). Shells dated between 4.4- 3.8 cal ka BP, 3.5-3.0 cal ka BP and 2.4 cal ka BP are contemporaneous with this time interval as well as specific cold events within it. The oldest shells coincide with the Northgrippian-Meghalayan boundary of the Holocene, an event marked by colder climate and a long megadrought that lasted from 4.2 to 3.9 cal ka BP as well as increased ice cap size in 4.2 cal ka BP and 3.0 cal ka BP (Larsen et al., 2012; Walker et al., 2018; Helama and Oninonen, 2019). Anderson et al. (2004) also inferred cooling events in 4.7, 4.3, and 2.8 cal ka BP from fossil diatoms found in the North Atlantic; these times align with the birth dates of the ocean quahogs.

Radiocarbon from one *A. islandica* sequestered during 2.0 cal ka BP, indicated a birth date within the RWP, the warming period that last from 2.3-1.6 cal ka BP. Despite evidence of a warming period in North America, during this time conditions were not above the temperature tolerance in the MAB for *A. islandica* at the sample station.

Helama et al. (2017) reviewed the Dark Ages Cold Period (DACP) literature finding a more detailed chronology of DACP indicated an average start and end date of 450 cal CE and 800 cal CE, with a North Atlantic event of ice-rafted debris in the middle, about 1.4 cal ka BP, as well as support for a negative NAO phase. Additionally, another cooling phase within the DACP from 540-660 cal CE, identified as the ‘Late Antique Little Ice Age’ (LALIA) can be seen within tree ring data (Büntgen et al., 2016; Helama et al., 2017). Six dead shells were alive at the end of these cooling events before the start of the MWP.

One shell collected was born at the tail end of the MWP and the start of the LIA and may indicate a prelude to the start of the LIA. Several shells date from the middle of the LIA, 462-222 cal BP. The majority of the radiocarbon dates in and after the LIA fall towards the end of the LIA in the early 19th century (Grove et al., 2004, Wanner et al., 2008), during the coldest portion of the LIA, and subsequently through the late 1800s cal CE. Sixteen dead shells had radiocarbon dates coinciding with this major cold event, indicating that the animals were alive in the 1840-1865 cal CE timeframe. Pace et al. (2017b) found an increase in ocean quahog recruitment before 1860 cal CE in a site just offshore and north of the region sampled in this study. Pace et al. (2017a) proposed that the increased recruitment may be related to the end of the LIA and the decline in shells with radiocarbon dates post-1865 cal CE might be interpreted as the initiation of increased mortality on the inshore edge of the range as temperatures continued to warm in the last half of the 19th century.

Although one cannot prove that the distribution of ages observed in this study is comprehensive of the time periods when ocean quahogs lived farther inshore than present-day, the near absence of shells born during the warm periods, RWP and MWP, strongly suggests that the distribution of birth dates observed identifies cold-period biogeographic range shifts inshore rather than the uncertain chance of collection. Powell et al. (2020) identified locations inshore and farther south of the present area of sampling from which there were reports of dead ocean quahog shells. Thus, this survey does not constrain either the inshore extent or southern extent of ocean quahog habitation during earlier cold times.

2.4.4 **Summary**

The death assemblage provides a view of the long-term geographic distributions of species prior to modern survey and monitoring programs. In particular, the death assemblage can provide a new view of the history of community response to climate change on the continental shelf over long time periods. In this study, shells of *Arctica islandica* were sampled on the Mid-Atlantic Bight (MAB) continental shelf at locations where living animals were not observed over the time of the 20th century federal survey time series. These shells identify habitable regions in the past that are not presently habitable by this species and in particular past times colder than today. Collection sites further inshore and south of the present range of the ocean quahog were once colder and thus suitable habitat for ocean quahogs. Examining the aggregation of radiocarbon date frequencies, the inshore range of ocean quahogs has transgressed and regressed at least 4 times over the last 4,500 years. The largest aggregation of radiocarbon dates reveals a recent ocean quahog transgression and regression inshore, with the regression likely beginning post-1865. Moreover, all of these dates coincide with historical times of cooling found in the Holocene climate literature. The radiocarbon dates obtained do not designate birth years randomly distributed over the time span of dated individuals. Very few shells date from times of warming, also well-documented in the Holocene climate literature, supporting the interpretation of range shifts onshore and offshore across the continental shelf as a consequence of climate warming and cooling phases with bottom water temperatures sufficient to permit and preclude the occupation of these long-lived bivalves.

The presence of these clams indicates that SBTs would need to be within the range of thermal tolerance for *A. islandica*, between ~5-15 °C, during these cold phases. These comparisons can be used as predictive tools to determine future range shifts for ocean quahogs as climate change continues to increase bottom water temperatures in the MAB. The record provided by *A. islandica* may provide an important constraint on the modeling of the history of the Cold Pool which today determines the community structure of the continental shelf from Virginia to Georges Bank. Future work expanding the geographic footprint of dated *A. islandica* shells would be most valuable in this regard.

2.5 Tables

Table 2.1 Coordinates, depths, number of samples aged, and approximate birth dates of radiocarbon dated shells for stations shown in Figures 1 and 5-7. Radiocarbon ages are the number of calendar years from 2021.

Station Number	Latitude (degrees N)	Longitude (degrees W)	Depth (M)	Radiocarbon ages (cal yr BP) (Birth Dates)	Climate Events
2	38.0398	-74.7433	21.95	192, 207	Modern, Little Ice Age
3	37.9833	-74.7500	33.83	3427, 3452, 3462, 3467	Neoglacial
5	38.0333	-74.8450	24.99	237	Little Ice Age
7	38.1060	-74.3995	38.10	272, 2643, 2843, 2888, 3093, 3468, 3542, 3817	Little Ice Age, Neoglacial, Meghalayan Boundary
8	37.9666	-74.9166	23.77	61, 62, 62, 63	Modern
9	37.7652	-74.8140	34.44	243, 263,302, 2813, 3083, 3418, 4182	Little Ice Age, Neoglacial, Meghalayan Boundary
10	37.7258	-74.8507	31.70	3032, 3047, 3057	Neoglacial
13	37.6833	-74.9833	30.18	3472	Neoglacial
15a	38.0680	-74.6020	33.53	172, 177, 177, 177, 182, 182, 198, 262, 4302	Modern, Little Ice Age, Meghalayan Boundary
15b	37.5833	-74.9166	35.05	57, 132, 128, 158, 172, 212, 4392	Modern, Little Ice Age, Meghalayan Boundary
16	38.1127	-74.6000	33.83	137, 142, 157, 157, 177, 182, 182,182, 188, 193, 197, 198, 203, 212, 222, 3517, 4102	Modern, Little Ice Age, Neoglacial, Meghalayan Boundary
17	38.1525	-74.5986	39.93	167, 172, 177, 177	Modern
25	37.4333	-75.0500	28.04	157, 162, 167, 197, 2447	Modern, Roman Warm Period
26	37.4167	-74.9833	34.44	182, 858, 1168, 1183, 1187, 1187, 1187, 1188, 1208, 1212, 1223	Modern, Medieval Warm Period, Dark Ages
27	37.3950	-75.0117	33.53	72, 157, 162, 1167, 1207, 1223, 2578	Modern, Dark Ages, Neoglacial
28	37.3551	-75.0118	37.19	65, 197, 232, 242, 462	Modern, Little Ice Age
29	37.3000	-75.0333	36.88	177, 182, 197, 237	Modern, Little Ice Age
30	37.2285	-75.0858	32.00	2017, 3512, 3512, 3532	Roman Warm Period, Neoglacial
31	37.2299	-75.1469	29.57	162, 172, 187, 207, 877	Modern, Little Ice Age, Medieval Warm Period
32	38.2335	-74.5800	37.19	3437, 3447, 3472, 3502, 3527	Neoglacial
33	38.2685	-74.6090	39.32	212	Little Ice Age
34	38.3160	-74.6005	35.66	117, 137, 147	Modern
35	38.3537	-74.5118	33.22	157, 157, 192	Modern
38	38.4762	-74.5475	36.58	142, 202, 202	Modern
40	38.4378	-74.5790	32.61	4172, 4182	Meghalayan Boundary

2.6 Figures

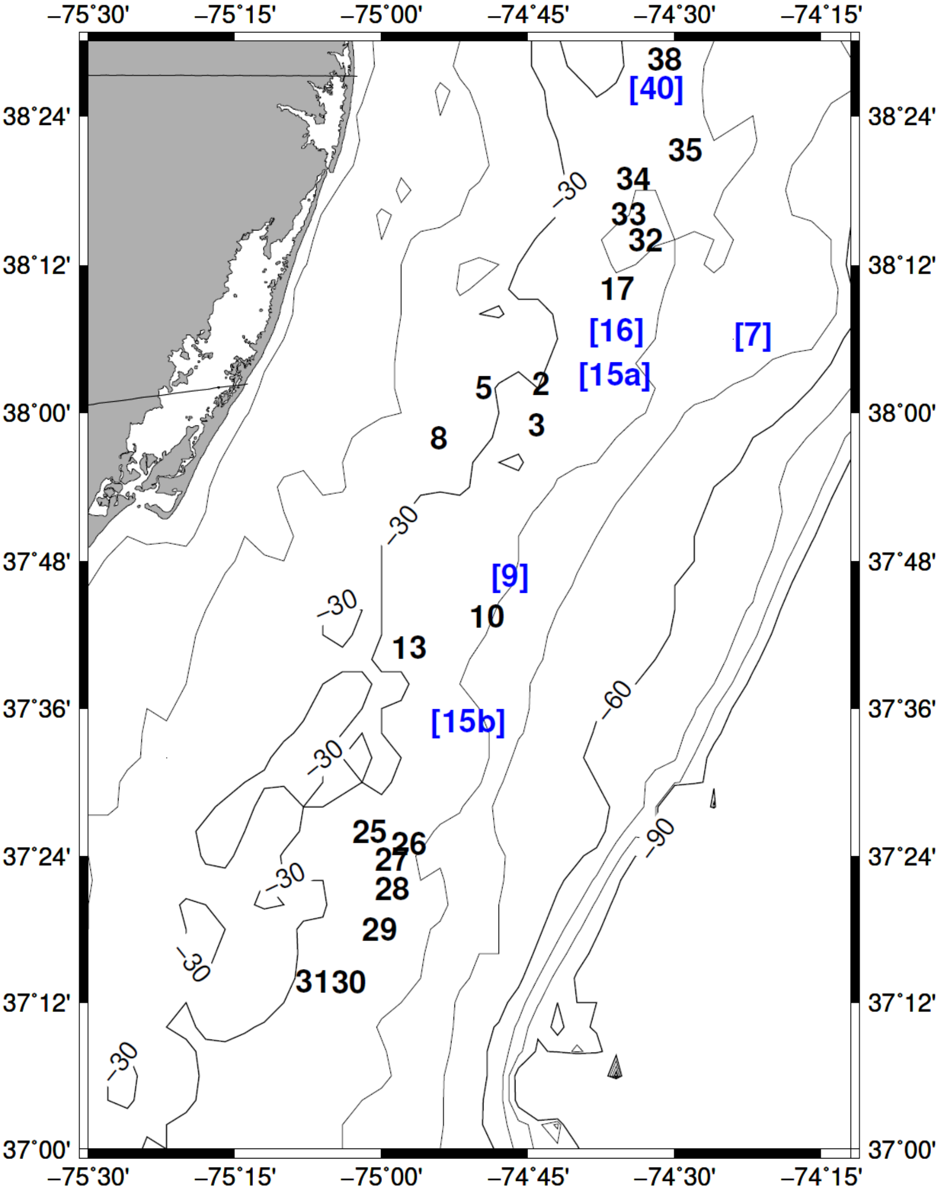

Figure 2.1 Map of sample stations as numbered during the survey. Bathymetric contour depths in meters. Bracket numbers in blue represent the station location where shells were dated during the first half of the Neoglacial period, approximately at the time of the Northgrippian-Megpalayan boundary of the Holocene. For a map of the present-day distribution of *Arctica islandica*, see Powell et al. (2020) and NEFSC (2017b).

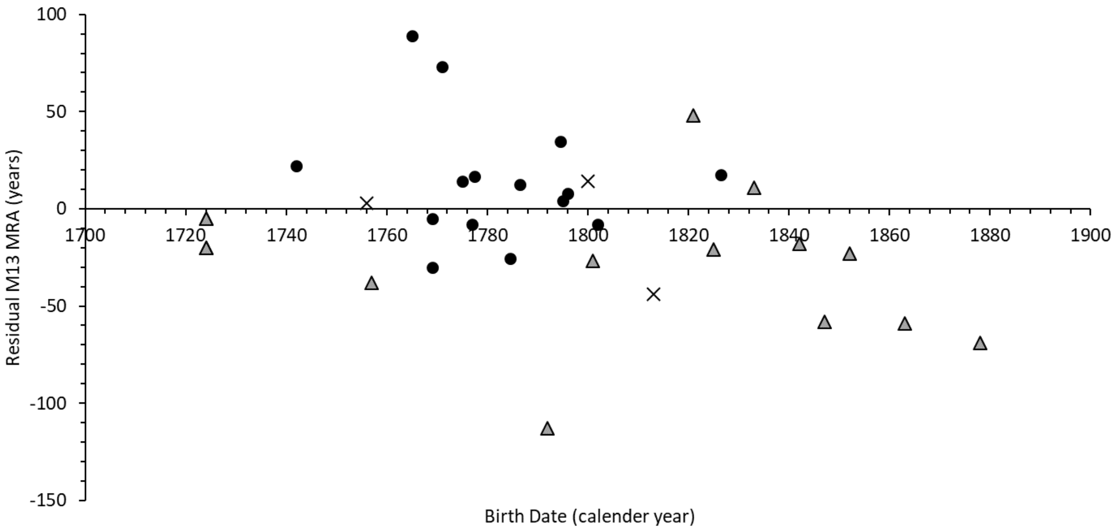

Figure 2.2 Marine reservoir age residuals obtained by comparing the global marine reservoir age of 400 year from Marine13 (Reimer et al., 2013) with the birth dates determined by visual aging from a sample of live-caught radiocarbon-dated *Arctica islandica* obtained from Georges Bank (40.72767°N 67.79850°W, 72.5 m; Hemeon et al., in press), Long Island (40.09658°N 73.01057 W, 47.5 m; Pace et al., 2017b), and northern New Jersey (39.33°N 73.12 W, 62.5 m).

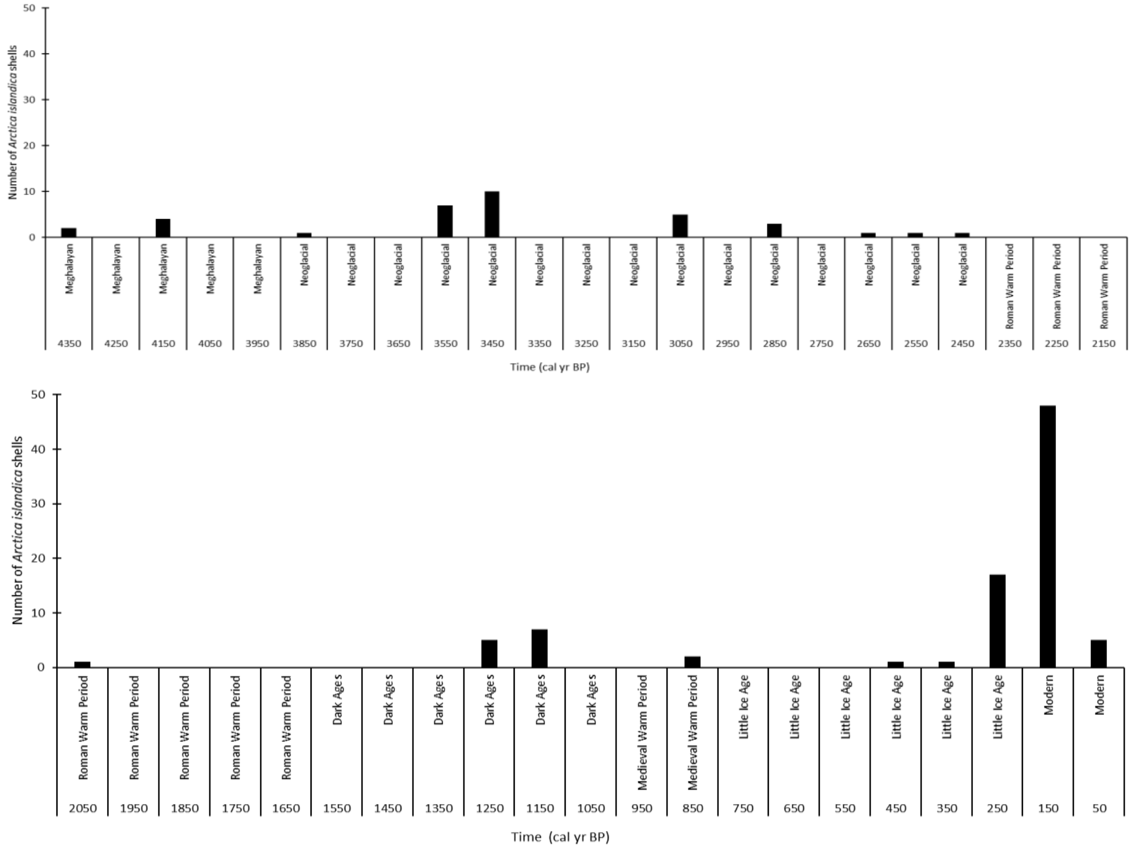

Figure 2.3 Panel A shows the frequency of Arctica islandica births in years before present (BP) and the simultaneous climate events: Northgrippian-Meghalayan Boundary (Helama and Oinonen, 2019). Neoglacial (Jennings et al., 2002), and Roman Warm Period (Wang et al., 2012; Moosen et al., 2015). Panel B shows the frequency of birthdates in years before present and the simultaneous climate events: Roman Warm Period (Wang et al., 2012; Moosen et al., 2015), Dark Ages Cold Period (Buntgenet al., 2011; Larsen et al., 2012), Medieval Warm Period (Graham et al., 2011; Geirsdotter et al., 2013), Little Ice Age (Ogilvie and Jonsson, 2001), and post-Little Ice Age (Modern).

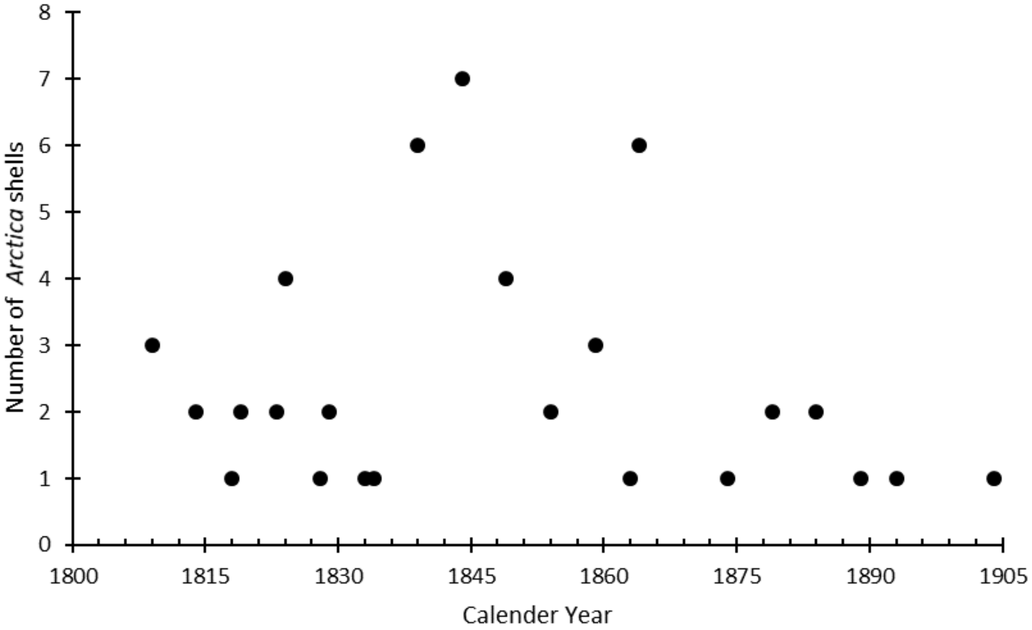

Figure 2.4 Shorter timeline focusing on the frequency of Arctica islandica birth years during the 19th century.

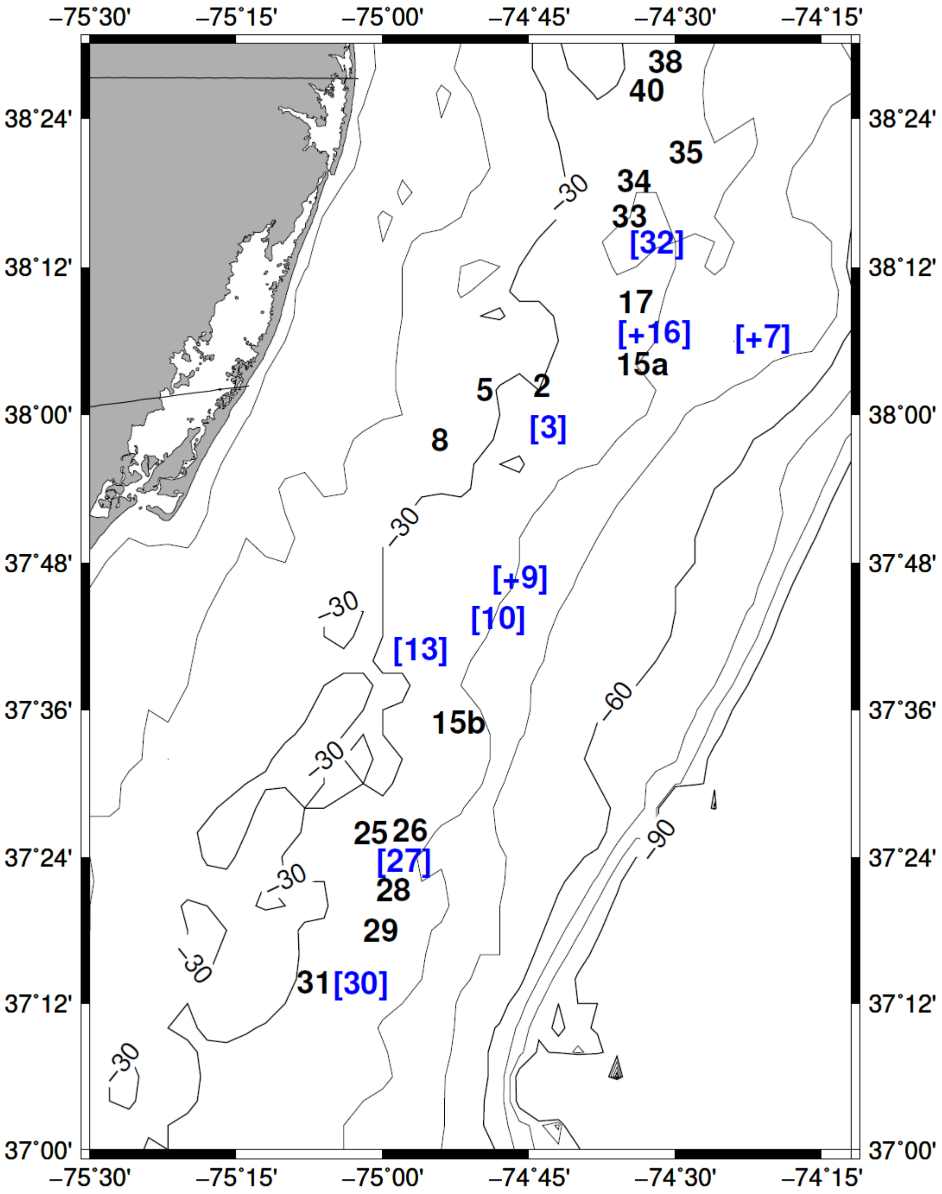

Figure 2.5 Map of sample stations as numbered during the survey. Bathymetric contour depths in meters. Bracket numbers in blue represent the station locations where shells were dated during the second half of the Neoglacial period. Station numbers with a plus represent stations with samples dated to multiple cold periods (Fig. 1).

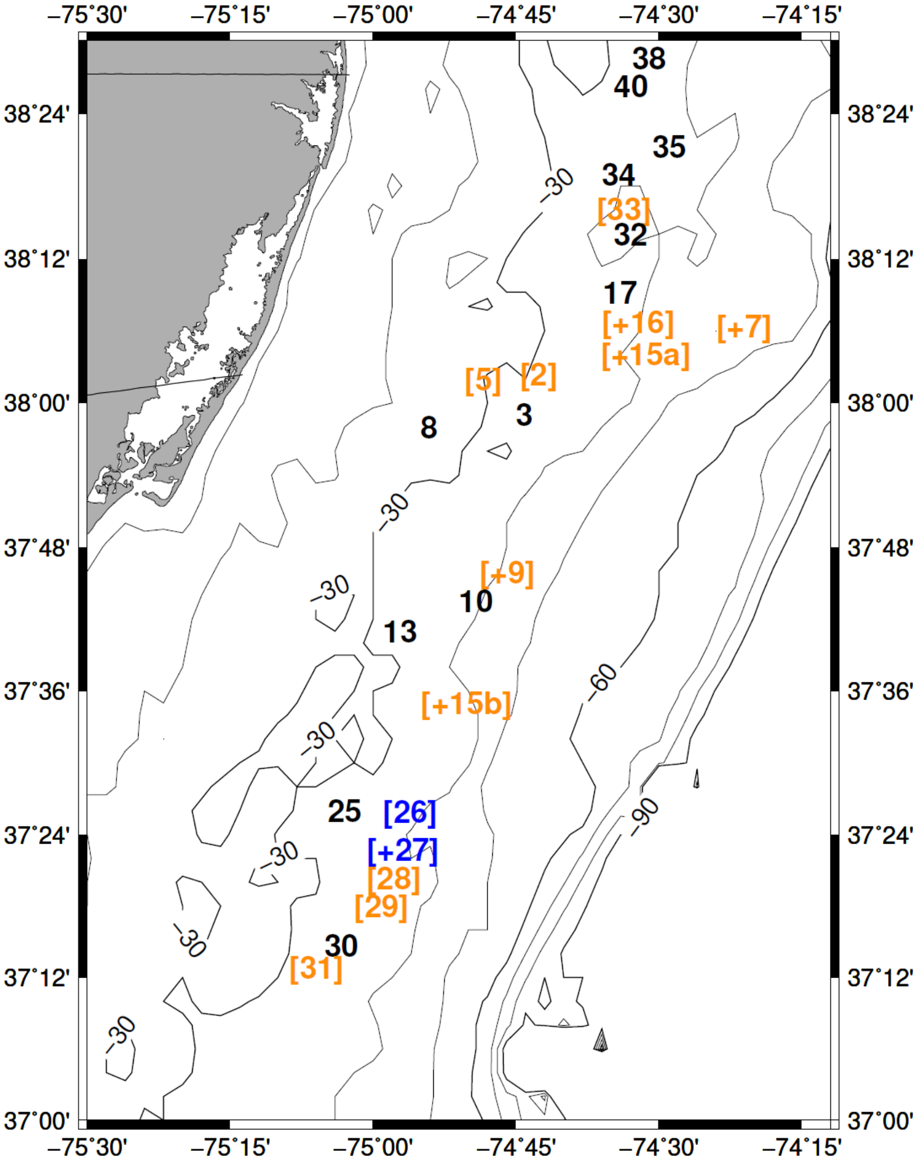

Figure 2.6 Map of sample stations as numbered during the survey. Bathymetric contour depths in meters. Bracket numbers in blue represent the station locations where shells were dated during the Dark Ages Cold Period. Orange bracketed numbers represent shells dated during the Little Ice Age through 1819. Station numbers with a plus represent stations with samples dated to multiple cold periods (Figs. 1, 5).

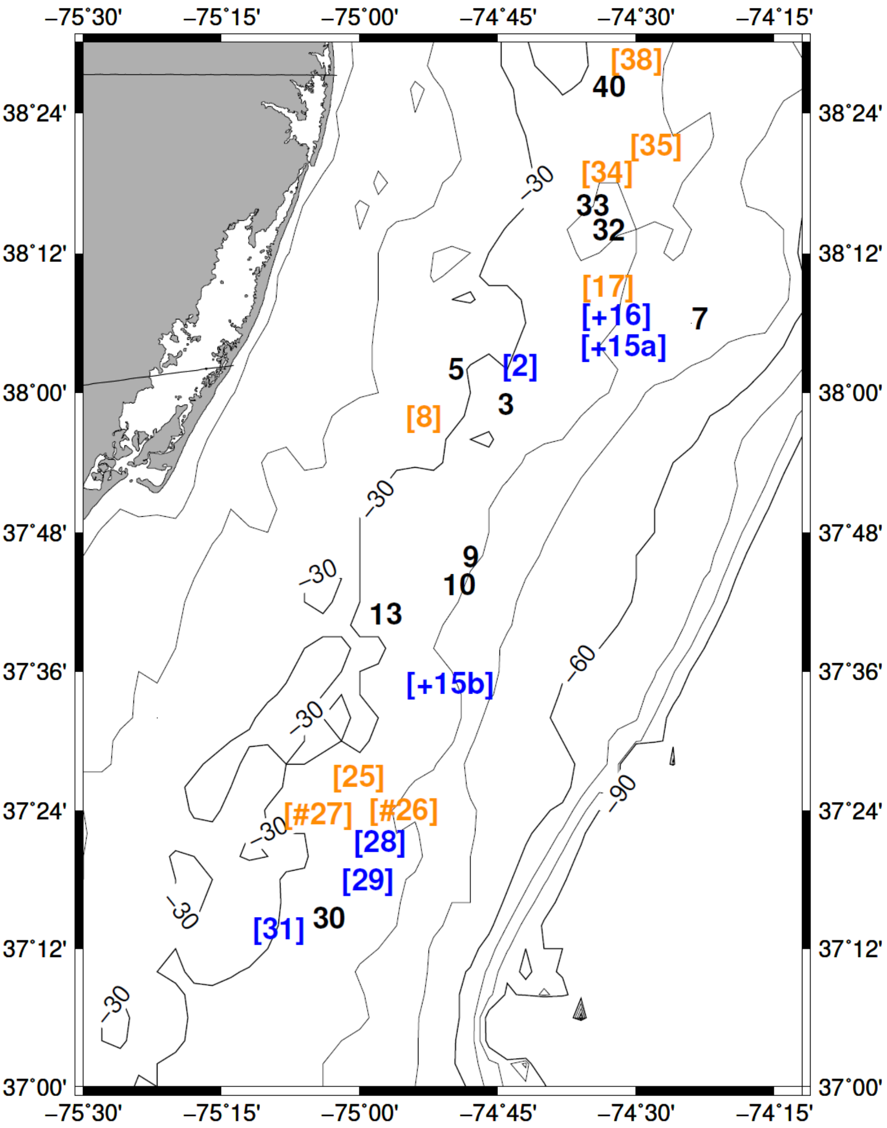

Figure 2.7 Map of sample stations as numbered during the survey. Bathymetric contour depths in meters. Bracketed numbers in blue represent stations where shells were dated during the Little Ice Age (Fig. 6) and between 1819-1965. Station numbers with a plus show stations that yielded shells dating to the Neoglacial periods (Figs. 1, 5). Station numbers with a hashtag show stations that yielded shells dating to the Dark Ages Cold Period (Fig. 6). Bracketed orange numbers show stations yielding shells that dated between 1819-1965, but not during the Little Ice Age.

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CHAPTER III TAPHONOMIC INDICATORS OF DEAD OCEAN QUAHOG (ARCTICA ISLANDICA) SHELL AGE IN THE DEATH ASSEMBLAGE OF THE MID-ATLANTIC BIGHT CONTINENTAL SHELF

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3.1 Introduction

Death assemblages are composed of skeletal remains representing the remnants of living communities spanning multiple years, a phenomenon known as time averaging (Flessa et al., 1993; Kowalewski, 1996; Kidwell, 1998, 2013; Butler et al., 2020). Exposure to the elements of the surrounding environment alters these skeletal remains, increasingly degrading them with time-since-death (Powell and Davies, 1990; Walker 2001; Powell et al., 2011a). Presumably, with more time spent in the taphonomically-active zone (TAZ), thereby increasingly exposing the skeletal elements to taphonomic processes such as dissolution, abrasion, discoloration, and fragmentation, the accumulating taphonomic degradation should indicate time-since-death of the living organism (Butler et al., 2020). Determining if a shell is young (recently dead) or old (less recently dead) can help identify the timing of living occupation which is often obscured by time averaging within the death assemblage (Adomat et al., 2016; Rodrigues and Simōes, 2010; Powell et al., 1989; Powell et al., 1992; Butler et al., 2020). Powell and Davies (1990) document the rare case where physical condition of a bivalve shell provides information on time-since-death. Unfortunately, much more commonly, the taphonomic signature (sensu Davies et al., 1989; Staff and Powell, 1990) of the skeletal remnant provides limited evidence of time-since-death, thereby restricting the ability to sort the temporal sequence of skeletal remains entering the death assemblage. Constraints to sorting the sequence of remains includes the coarseness of the semiquantitative taphonomic metrics (Davies et al., 1990; Staff and Powell, 1990; Powell et al. 2011a), the difference in taphonomic degradation for different species (Callender et al., 1994; Lockwood and Work, 2006; Powell et al. 2011b), and varying taphonomic rates among environments of deposition (Best and Kidwell, 2000; Powell et al. 2011a).

The limited reliability of taphonomic signature has resulted in a dependency on other means to determine time-since death. Although a variety of options have been implemented (Szabo et al., 1981; Powell and Davies, 1990; Muhs and Kennedy, 1985; Powell et al., 1991), radiocarbon dating (e.g., Ritter et al., 2013; Kosnik et al., 2015; Adomat et al., 2016; LeClaire et al., in press) and amino acid racemization dating (e.g., Kowalewski et al., 1998; Krause et al., 2010; Tomašových et al., 2014; Kosnik et al., 2015; Ortiz et al., 2005) have proven to be the most efficient. A determination of time-since-death is a critical component of studies designed to define the rate of taphonomic processes (Meldahl 1987; Meldahl et al., 1997), the extent of time averaging, (Kowalewski et al., 1998; Dominguez et al., 2016), and the clarification of the time history of community change consequent of anthropogenic processes (Bizjack et al., 2017) or climate change (Maclntyre et al. 1978; Powell et al., 2020). Thus, species' skeletal remains need to be aged, using radiocarbon dating or amino acid racemization dating. Despite the value of studying death assemblage to address spatial and temporal changes in community composition, due to climate change or anthropogenic impact, (Kidwell, 2007; Negri et al., 2015; Bizjack et al., 2017; Arkle et al., 2018), there is limited application of these studies because of the expense of dating large sample sizes (e.g., Butler et al., 2020). Having known indicators of age can help with shell selection for 14C dating and support 14C calibration of amino acid dating, particularly for geographically extensive datasets such as documented in Powell et al. (2020), preventing a waste of funds on random, uninformed sample selection (Butler et al., 2020).

Arctica islandica has proven to be an important species documenting climate change due to its relatively narrow temperature tolerance and its widespread distribution throughout most boreal seas of the northern hemisphere (Dahlgren et al., 2000; Witbaard and Bergman, 2003; Wanamaker et al., 2011; Hemeon et al., in press;) extending observations back in time beyond the already extensive time period representing by the lifespan of this long-lived species. The usefulness of species remain is only being limited by the ability to determine time-since-death of animals. In this study, shells from dead *Arctica islandica*, commonly known as the ocean quahog, were collected from the Mid-Atlantic Bight, offshore of the DelMarVa Peninsula (LeClaire et al., in press). These shells have radiocarbon dates spanning time from recently dead (60 cal years BP) to much less recently dead (4,400 cal years BP), documenting major transgressions and regressions of the species' range across the continental shelf coincident with warming and cooling climatic episodes and strongly suggesting that this species might be used to track the dimensions of climate change throughout much of the North Atlantic Ocean and adjacent seas. Such a study would be simplified if taphonomic signature could be used to assess the limited age range of a specimen for future radiocarbon or amino acid racemization dating. The aged shells reported by LeClaire et al. (in press) have varying degrees of discoloration and various percentages of remaining periostracum. So, the question is: can ocean quahogs of varying times-since-death be distinguished using discoloration and periostracum condition? A similar question has been asked by Butler et al. (2020) who found limited applicability of taphonomic signature in identifying time-since-death, a common finding in comparison to the large body of literature on the relative change in shell condition with time-since-death. Although, exceptions do exist, finding taphonomic indicators linked to the time spent in the death assemblage (e.g., Powell and Davies, 1990). In the present study, radiocarbon dates were used to determine if the taphonomic condition of dead A. islandica shells from the Mid-Atlantic Bight continental shelf can be used to determine time-since-death. Dead shells were sampled and radiocarbon dated to determine time-since-death. Then, taphonomic condition of these dead shells was compared to the radiocarbon age.

3.2 Materials and Methods

3.2.1 Sample Collection

Dead ocean quahogs were collected along the continental shelf with a 2.54-m wide hydraulic dredge on a commercial clam vessel, the F/V Betty C, offshore of the DelMarVa Peninsula in August 2019 (Fig. 1). The vessel was a typical clam boat with a standard hydraulic dredge used throughout the ocean quahog fishery (Parker, 1971). The dredge was lined with 1-inch-square wire on the bottom and knife shelf, and 1x2-inch rectangular wire on the sides, back, and door. The wire lining retained clams ~≥40 mm. Tows had a swept area of approximately 118 m2 with tow distance limited to prevent overfilling of the dredge. Ocean quahog shells were manually picked from the dredge haul as it was carried along a central conveyor belt.

3.2.2 **Shell Imaging**

Dead shells were selected and labelled for processing. All dead shells were disarticulated. Internal and external sides of each shell valve was photographed using a

Canon camera to capture the exterior condition of the valve before cutting the valve for radiocarbon dating (Fig 2). Color swatches in the Munsell Book of Color were matched to the colors present on the shell valve and included in the image for comparison (Fig 2).

3.2.3 **Radiocarbon dating**

Once shells were imaged, the valves were cut using a Kobalt wet tile saw. A remaining half of the valve was ground using 240 grit silicon carbide abrasive paper to remove any contaminants. Using a Dremel tool, shell powder samples were extracted from the ground valve half. The Dremel tool was used to grind the edge of the shell near the hinge and umbo to collect carbonate powder from the youngest part of the shell, deposited during the early years of life. The resulting shell powder sample (>10 mg) was sent to the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine for analysis. Radiocarbon ages of samples will be denoted hereafter as birth years to clarify that the ages represent the beginning of the lifespan of the ocean quahog from which the shell came (LeClaire et al. in press).

3.2.4 **Date Calibration**

Radiocarbon ages (±15-25 years depending on sample) were calibrated using the Marine13 reservoir age of 400 years (Reimer et al., 2013). Off the DelMarVa Peninsula, ocean quahogs live in the Cold Pool, a cold-water near-bottom water mass trapped by thermal stratification during the summer on the outer continental shelf. The Cold Pool derives water in varying proportions from Arctic and North Atlantic sources depending on the year (Wang et al., 2019; Chen and Curchitser, 2020; Chen et al., 2021; Miles et al., 2021), providing some uncertainty in this correction factor given that the marine reservoir effect differs both temporally and spatially (Alves et al., 2018; Heaton et al., 2020).

Given the absence of a regional marine reservoir age correction for the Mid-Atlantic Bight offshore continental shelf, live A. islandica were collected off New Jersey, Long Island, and Georges Bank as described by Hemeon et al., (2022) and Sower (unpublished data). These live animals were shucked and their shells aged and radiocarbon dated. A correction factor of 400 years was confirmed based on the comparison between the radiocarbon birth year and the visual birth year obtaining by counting the annual growth lines (LeClaire et al., in press). The residual median when comparing the two aging methods was -5 year, a mean of -7 year, and a standard deviation of ±38.67 year. More research is need to further constrain the potential error when calibrating marine carbon dates in this region over a long time period, during which the Cold Pool likely varied in intensity. Nonetheless, the radiocarbon ages obtained in this study were corrected assuming that bottom water conditions during the lifetime of the sampled shells were consistent with the Marine13 marine reservoir age.

Some dead ocean quahog shells were alive after 1950; hence, they were exposed to bomb produced carbon-14 from the atmospheric detonation of the atomic bombs. To estimate radiocarbon birth year post-1950, a reference time series of Δ14C (‰ deviation of the sample from the radiocarbon standard defined by Stuiver and Polach, 1977) determined by Kilada et al. (2007) was applied to radiocarbon values (Scourse et al., 2012).

3.2.5 **Taphonomic Evaluation**

Assessment of taphonomic condition was limited to shell discoloration and percent periostracum coverage. All shells were whole and disarticulated. Surfaces showed evidence of dissolution, but the degree of dissolution was not easily quantified.

Arctica islandica is relatively resistant to taphonomic attack of this kind (Powell et al., 2011b) and evidence of endobionts was very rare. Epibionts were not observed. For periostracum, the dead shell was divided into a series of standard shell areas, as used in Staff and Powell (1990), and the percent coverage recorded for each section (see Brett et al., 2011 for an example of this type of analysis). Shells were also allocated into two simple categories: periostracum present (1) or absent (0) (Fig. 2). The dominant color on the shell was recorded, and discoloration from the original shell color was characterized as present (1) or absent (0) as most discoloration covered the entire valve (Fig 3). Periostracum coverage percentages were arcsine square-root transformed (Sokal and Rolff, 1998) to conduct a one-way ANOVA and fit with a generalized additive model (GAM) using the "mgcv" package in R. Logistic regressions were run using the statistical package on R to determine the probability of a dead shell being discolored or having periostracum remaining on the shell.

3.3 **Results**

3.3.1 **Periostracum**

One hundred and seventeen dead A. islandica shells were radiocarbon dated and evaluated for taphonomic condition. These 117 shells had radiocarbon dates ranging from 61-4,392 cal years BP (LeClaire et al., in press). The majority of the shells were dated within the previous 300 years (67 of 117), with the remainder exceeding 500 years (50 of 117). The taphonomic condition of shells ranged from having almost all of the periostracum intact (99.7%) to no periostracum remaining on the shell (Fig. 4). Of the 117 shells, 73 had periostracum remaining. Of those 71, 63 shells dated within 67-300 cal years BP (Fig. 4). Two shells with periostracum were born in the 800s cal years BP, and

6 shells had radiocarbon ages in the 1200s cal years BP (Fig. 5). These 8 shells dated between 858-1,223 cal years BP and had less than 16% of the original periostracum remaining on the shell surface (Fig. 4). A one-way ANOVA was conducted on the shells with remaining periostracum to evaluate the relationship between the percent remaining. relative to radiocarbon age. The relationship was statistically significant (F=27.88, p=1.46e-06). The GAM fit to the transformed periostracum percentages showed a significant relationship between the radiocarbon age of a shell and the remaining periostracum, with a fast decline of remaining periostracum with age from present to about 700 cal years BP before leveling off (Fig. 5).

The probability of periostracum being present decreased in a logistic fashion with time-since-death. A logistic curve (Eq 1) fit to the probability of the presence of retaining any periostracum on a shell of a given radiocarbon age between 0-4,000 years cal BP (Fig. 6) yielded.

$$\text{Eq (1) } p = \frac{e^{3.2406-0.0028x}}{1+e^{3.2406-0.0028x}}$$

where *p* is the probability and *x* is cal years BP. The midpoint (p = 0.5) occurs at 1,157 cal years BP. The 10% and 90% probability values are 1,942 cal years BP and 372 cal years BP. Thus, the majority of shells lose all periostracum over a ~2,000-year time period. The 10% value is near the oldest animal so far found living in the Mid-Atlantic region of 310 years (Hemeon et al., in press) and consistent with the GAM results showing that most periostracum is lost in the first ~700 years after birth, with a substantial portion of this loss occurring during the extended lifespan of $\gg$200 years.

3.3.2 **Discoloration**

Coloration of shells fell into four categories: white, white-grey, orange, and orange-blue-grey (Fig. 3). White was deemed the original condition of the shell with all other categories being a variation of shell discoloration. The samples included 64 white shells, 2 white-grey shells, 46 orange shells, and 5 orange-blue-grey shells (Fig 3).

Grey discolored shells were rare and scattered across a number of stations and birth times. Of the 7 shells that had grey discoloration, 4 shells with orange-blue-grey were collected at station 3 and aged between 3,427-3,467 cal years BP. The other orange-blue-grey shell was collected at station 30 and dated at 2,017 cal years BP. The two white-grey shells were collected at station 26 and both aged at 1,187 cal years BP. A significant relationship did not exist between time-since-death and the occurrence of grey discoloration ($P>0.05$). Nonetheless, grey appeared to be an indicator of an older shell based on the comparison between discoloration and radiocarbon age.

The majority of shell discoloration was orange discoloration and orange shells were collected at a wide range of stations and represented a wide range of radiocarbon ages. Logistic regression was used to analyze the relationship between radiocarbon age, and orange shell discoloration. In contrast to grey discoloration, orange discoloration did bear a significant relationship with time-since-death ($P<0.001$). Normally the entire shell surface was discolored orange.

The great majority of the orange-discolored shells dated to >302 cal years BP (Fig. 7). A logistic curve (Eq 2) was fit to the probability of orange discoloration and a given radiocarbon age between 0-4,000 years cal BP (Fig. 7):

$$\text{Eq (2)}\ \ p = \frac{e^{-2.088+0.0021\text{x}}}{1+e^{-2.088+0.0021\text{x}}}$$

where p is the probability and x is cal years BP. The midpoint (p=0.50) occurred at 994 cal years BP. The 20th percentile occurred at 334 cal years BP, once again in the time frame of the oldest animal collected living in the Mis-Atlantic region (310 yr, Hemeon et al., in press). Most (90%) of shells were discolored by 2,040 cal years BP.

3.4 **Discussion**

Comparing the calibrated radiocarbon ages of shells to the taphonomic condition revealed that older shells usually had no remaining periostracum and normally were characterized by discoloration (Fig. 3, 7). Almost always this discoloration was an orange pigmentation. The generality of this condition is particularly remarkable when considering the retrieval of these shells over most of the sampled region which includes almost 1.5 degrees of latitude (LeClaire et al., in press). Such a wide range of taphonomic similarity is not routinely recorded (e.g., Tanabe and Arimura, 1987; Best and Kidwell, 2000; Powell et al., 2011a). Increasing time-since-death increases the probability of discoloration and loss of periostracum (Fig. 5, 6, 7), but the trend is substantially both nonlinear and non-exponential, strongly suggesting a profoundly different time dependency in the rate in comparison to previous analyses of taphonomic processes and time averaging (Powell et al., 1986; Powell et al., 2006; Krause et al., 2010; Powell et al., 2011a; Tomašových et al., 2014). Figure 7 shows that the probability of a shell being discolored increases along a logistic curve as the radiocarbon age increases, with dead shells older than 2,500 years always having some discoloration. Additionally, Figure 6 depicts a decreasing probability along a logistic curve of dead shells having any remaining periostracum as radiocarbon age increases. Dead shells older than 2,500 years have a 0% chance of having any periostracum remaining on the exterior surface of the shell.

Similar to Powell and Davies (1990), our results depict a clear relationship between the discoloration of a shell and a longer time-since-death. As well, the presence of periostracum is also an indicator of time-since-death, with an absence of periostracum for all old (less recently dead) shells. These findings differ from recent studies, such as Butler et al., (2020) who determined that old, dead A. islandica shells have no discernable taphonomic characteristics, including remaining periostracum, to help identify the timing of death of the animal. However, Butler et al., (2020) infers that this may be an aspect of the specific environment in which the dead shells are retained. An important impediment to the application of the results reported herein to a broader geographic area is the limited information on periostracum condition after death for most species and locales studied. A primary reason is the use of coarse semi-quantitative scales for assessment, a tradition routinely used in previous studies (e.g., Frey and Howard, 1986; Davies et al., 1990; Lockwood and Work, 2006; Powell et al., 2011a), a tendency clearly shown to be inadequate by this study, at least for species with well-developed periostracum such as A. islandica. Although considerable is known about the breakdown of the organic matrix in a shell after death (e.g., Kimber and Griffin, 1987; Powell et al., 1989; Powell et al., 1991 Mitchell and Curry, 1997; Clark, 1999), supporting the use of amino acid racemization as a means of determining time-since-death, the process of periostracum decay is poorly studied (Poulicek et al., 1981; Poulicek and Jeuniaux, 1987) though bacterial attack would seem to be of potential importance (Dungan et al., 1989; Paillard et al., 2004).

Additionally, the scale of time passed can change the effectiveness of discoloration and presence of periostracum. While ‘old’ shells have no periostracum and an orange discoloration, this state applies to shells that died over 2,000 years ago. So, the usefulness of these characterizations depends on how old the shells are within a sample. The difficulty of discerning between young and old shells increases on smaller scales, such as comparing a 100-year-old shell and a 1,000-year-old shell. Nonetheless, the scale of time observed is consistent with the scale of time averaging in some assemblages (Carroll et al., 2003; Kosnik et al., 2009; Dexter et al., 2014; Ritter et al., 2017). Time averaging has been modeled as an exponential process (Carroll et al., 2003; Kosnik et al., 2009. Tomašových et al., 2014) while, in contrast, the taphonomic rates measured here are strongly non-exponential. Rather, a threshold-type process is present, well-modeled by a logistic function and suggesting a rapid change in the degree of taphonomic degradation initiating about 350 cal years BP, reaching a mid-point approximately 1,000 cal years BP, with the process essentially reaching completion by about 2,000 years. The initiation time is remarkably similar to the oldest living animals collected in the region suggesting that A. islandica shells begin to degrade rapidly on a time scale similar to the species’ lifespan. The entire time trajectory of degradation is reminiscent of the rapidly changing rates of certain taphonomic processes by Powell et al. (2011a) in being highly nonlinear and clearly non-exponential, though the time scale is very different, and suggests that rapid time-dependent changes in taphonomic rates are likely a normal condition.

Discoloration is rarely an important taphonomic characteristic for fossil shells, but its application to the taphonomic signature of death assemblages has received wide attribution. Discoloration of the shell is most likely a result of the chemistry of the surrounding environment in which dead shells were retained. Colors as wide ranging as brown, green, orange, grey, and black have been noted, some of them commonly and some definitively associated with certain environments of deposition (e.g., Cutler, 1995; Lazo, 2004; Rodrigues and Simões, 2010; Powell et al., 2011a).

Grey to black discoloration is one of the most common shades of discoloration (MacIntyre et al., 1978; Frey and Howard, 1986; Pilkey and Curran, 1986; Thieler et al., 2001; Walker, 2001; Best 2008, Powell et al., 2011a) and normally is the result of exposure to hydrogen sulfide. The shells that contained grey discoloration were found at three of the 25 stations sampled. This local occurrence may indicate a specific difference in the habitat surrounding the death assemblage at these stations. However, few samples collected (7/53) were grey, with the dominant discoloration on the shells in this study being orange, suggesting that the grey endpoint of discoloration is not an important process on this region of the continental shelf.

Orange is a relatively rarely noted discoloration (Lazo, 2004; James et al., 2005; Best, 2008; Powell et al., 2011a). Our dataset showed an uncommon frequent and geographically extensive distribution of discoloration compared to specimen remains in other studies, with orange being the dominate form of discoloration and grey appearing infrequently. The orange color may be a result of iron oxidation, a common process on the seafloor and a potential explanation for the limited appearance of grey to black discoloration, with the oxidized mineral product forming orange and yellow pigments (Powell et al., 2008). In species like Mercenaria mercenaria, pyrite is incorporated into the shell (Clark and Lutz, 1980) and can result in orange discoloration after oxidation

(Powell et al., 2008)   Exposure to seawater for extended periods of time can result in sulfide infusion into the shell and pyritization on the shell surface, either of which might support a subsequent chemical change in the shell due to direct oxidation or microbial production (Powell et al., 2008). Products of pyrite (and presumably sulfide) oxidation include a variety of iron oxy-hydroxides varying in color from yellow to orange to red, including the minerals schwertmannite and goethite, characterized by an orange pigment (Edwards et al., 2004; Li et al., 2011; Mitsunobu et al., 2021). The geographic distribution of this form of discoloration suggests a widespread geochemical process on the Mid-Atlantic Bight continental shelf emphasizing the oxidation of iron compounds resulting in a long-term stable discoloring process.

3.4.1 **Summary**

Assessing the potential for taphonomic condition as indicators of time-since-death, this study utilized the dead shells of the long lived, bivalve Arctica islandica to evaluate whether old shells could be visually identified. Such an option would greatly improve the ability to trace range shifts over Holocene time on the continental shelf as this method could be used to inform sample selection when choosing which specimen to date and retain for further analyses. Present data support such an increase in efficiency. The data also suggest further analyses to determine the chemical processes behind the discoloration of these shells and its relation to time-since-death and the processes controlling decay of the periostracum, which happens on a time scale distinctly shorter than that of discoloration. Both processes obey a logistic model, suggesting that taphonomic degradation is highly nonlinear in time. The logistic nature of the process does provide an important dichotomy permitting efficient sorting of shells into relatively young and relatively old age groups. Whether other taphonomic processes might impose a similar dichotomy given a sufficiently long period of observation remains unexplored.

3.5 **Figures**

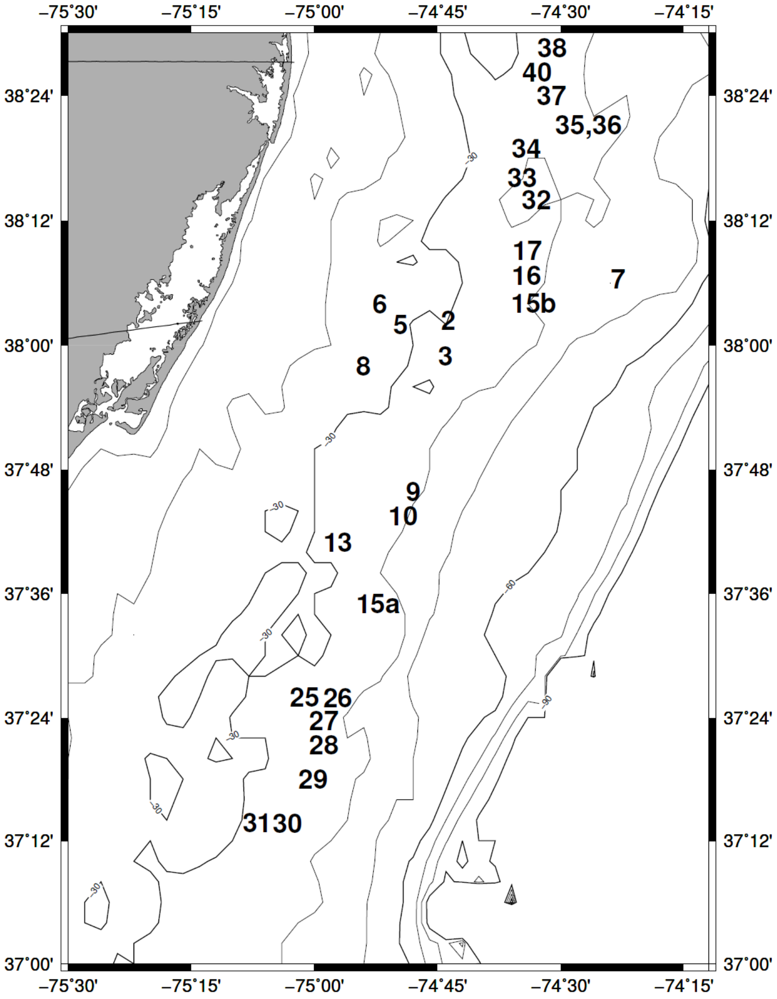


Figure 3.1 Map of stations where Arctica islandica were collected via dredge onboard the *F/V Betty C* in August 2019.

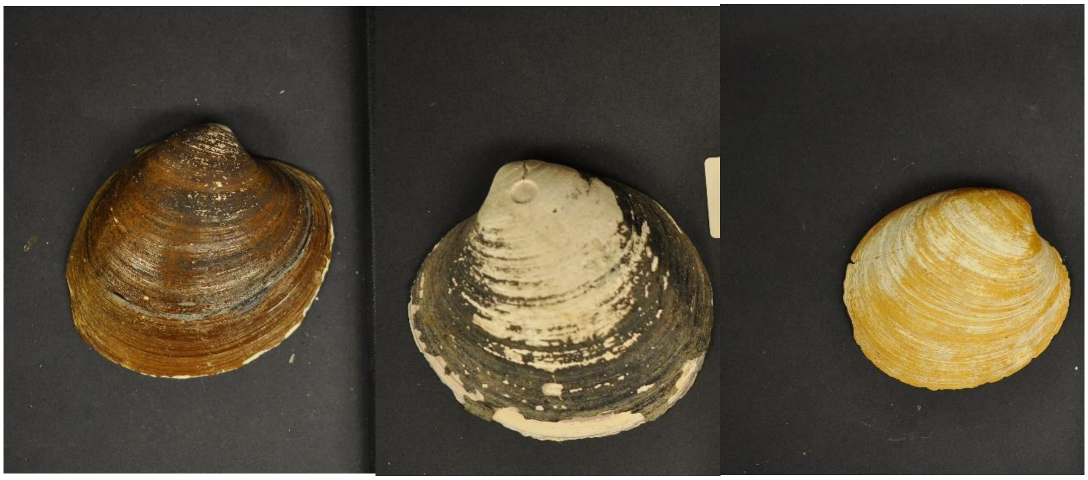
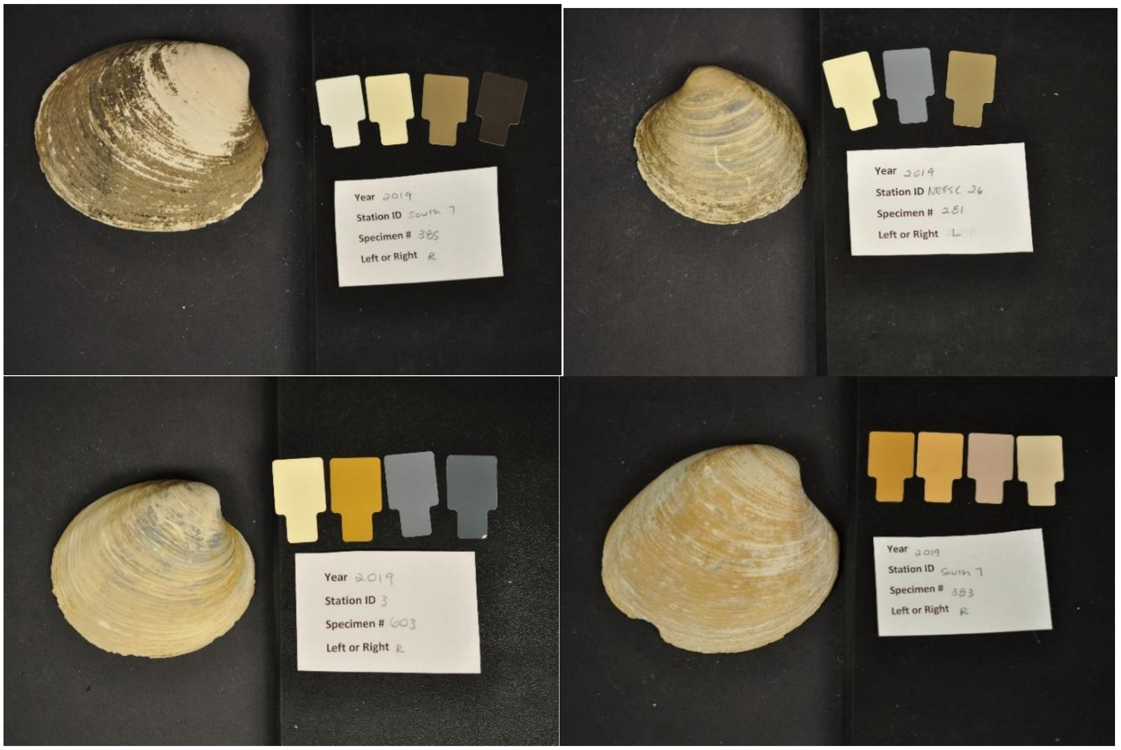


Figure 3.2 Images showing shells with varying levels of periostracum coverage. The first shell on the left has almost all periostracum intact. The middle photo depicts a shell with some periostracum remaining. The exact percentage was estimated using the methods from Staff and Powell (1990). The image on the right depicts a shell with no remaining periostracum



Year 2019
Station ID South 7
Specimen # 385
Left or Right R

Year 2019
Station ID NEFSC 26
Specimen # 281
Left or Right L

Year 2019
Station ID 3
Specimen # 603
Left or Right R

Year 2019
Station ID South 7
Specimen # 383
Left or Right R

Figure 3.3 Images showing the original color of shells (top left: white) and the three variations of discoloration that were seen in the collected samples (top right: white-grey, bottom left: orange-blue-grey, bottom right: orange). Color swatches are from the Munsell Book of Color (top left: N 9.25, 2.5Y 9/2, 10YR 5/2, 10YR 2.5/1; top right: 2.5Y 9/2, 10B 5/2, 10YR 5/2; bottom left: 2.5Y 9/2, 10YR 6/6, 10B 5/2, 10B 4/2; bottom right:10YR 8/2, 7.5 YR 7/6, 7.5YR 6/6, 2.5YR 7/2).

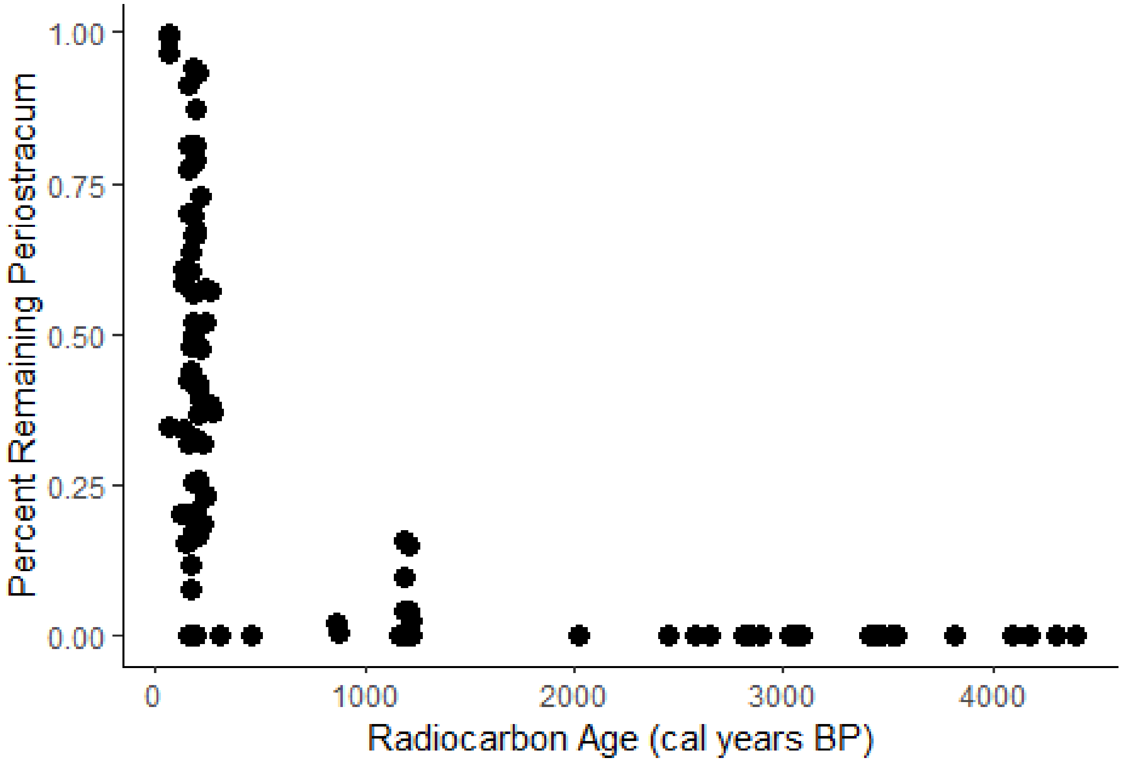


Figure 3.4 Estimated percent of remaining periostracum compared to the radiocarbon age of the shell sample.

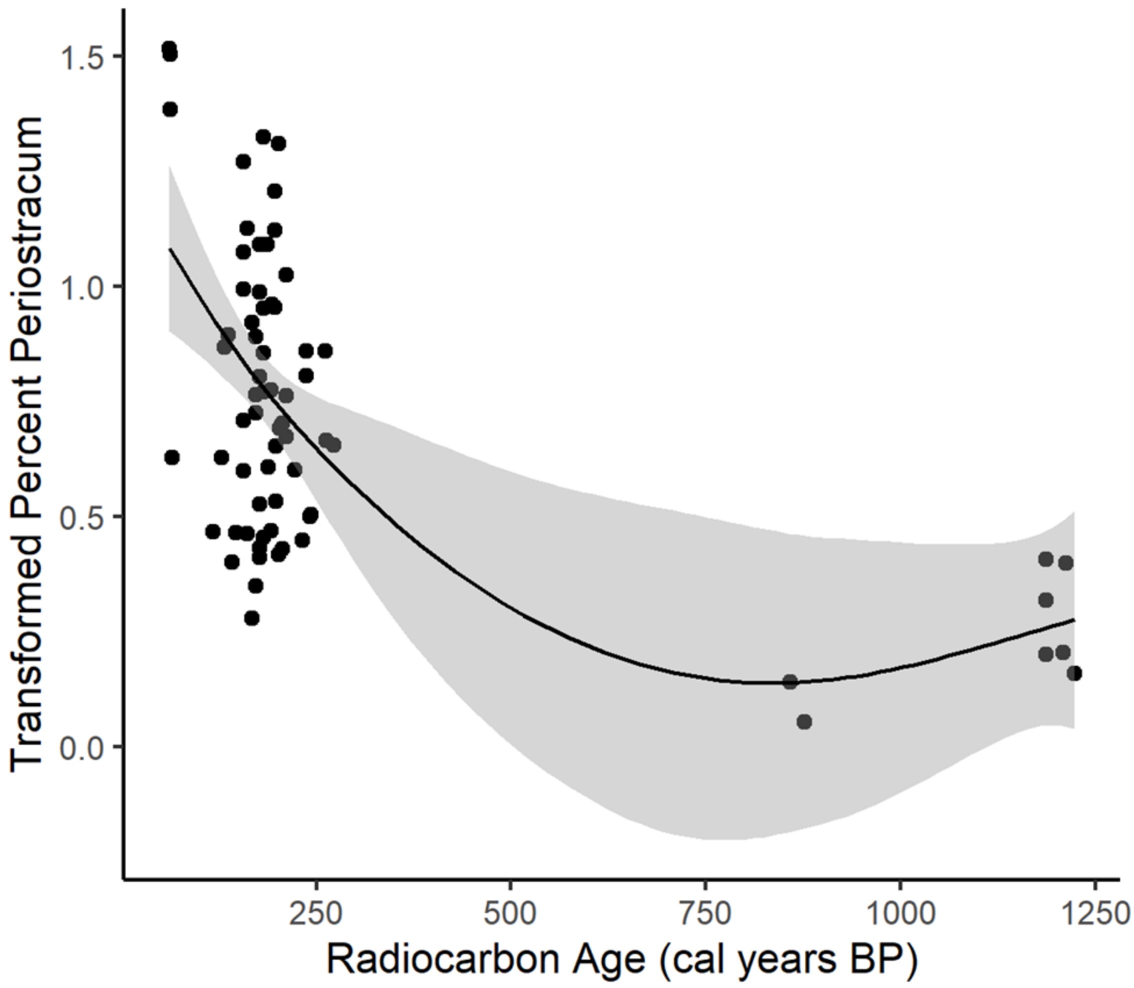


Figure 3.5 Generalized additive model (GAM) fit to the arcsine square-root transformed percent coverage of periostracum on shells with periostracum still present. Plotted points represent the raw transformed values and the blue line represents the fitted GSM. The grey shaded area represents the error around the fitted values.

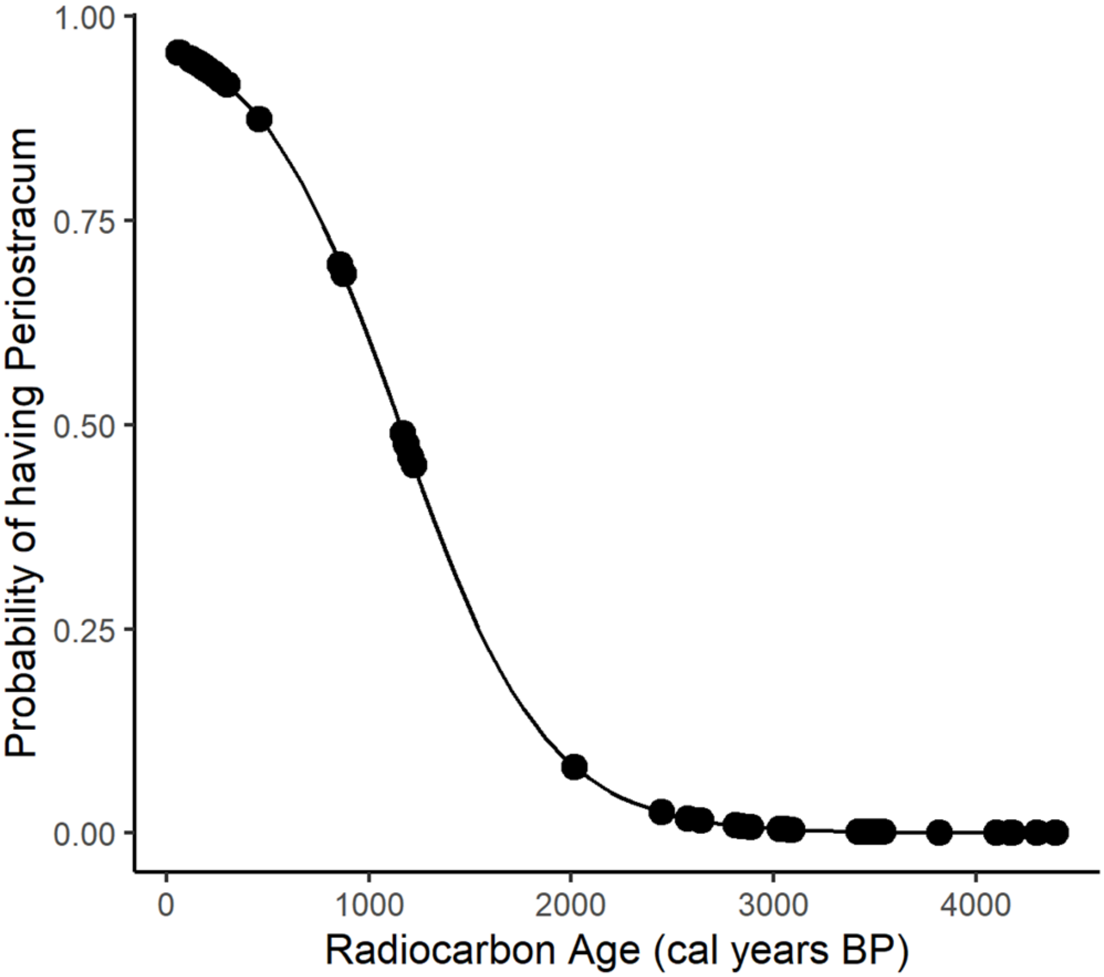


Figure 3.6 Logistic curve shows the probability of a dead *Arctica islandica* shell of a known radiocarbon age having any periostracum remaining on the external shell surface.

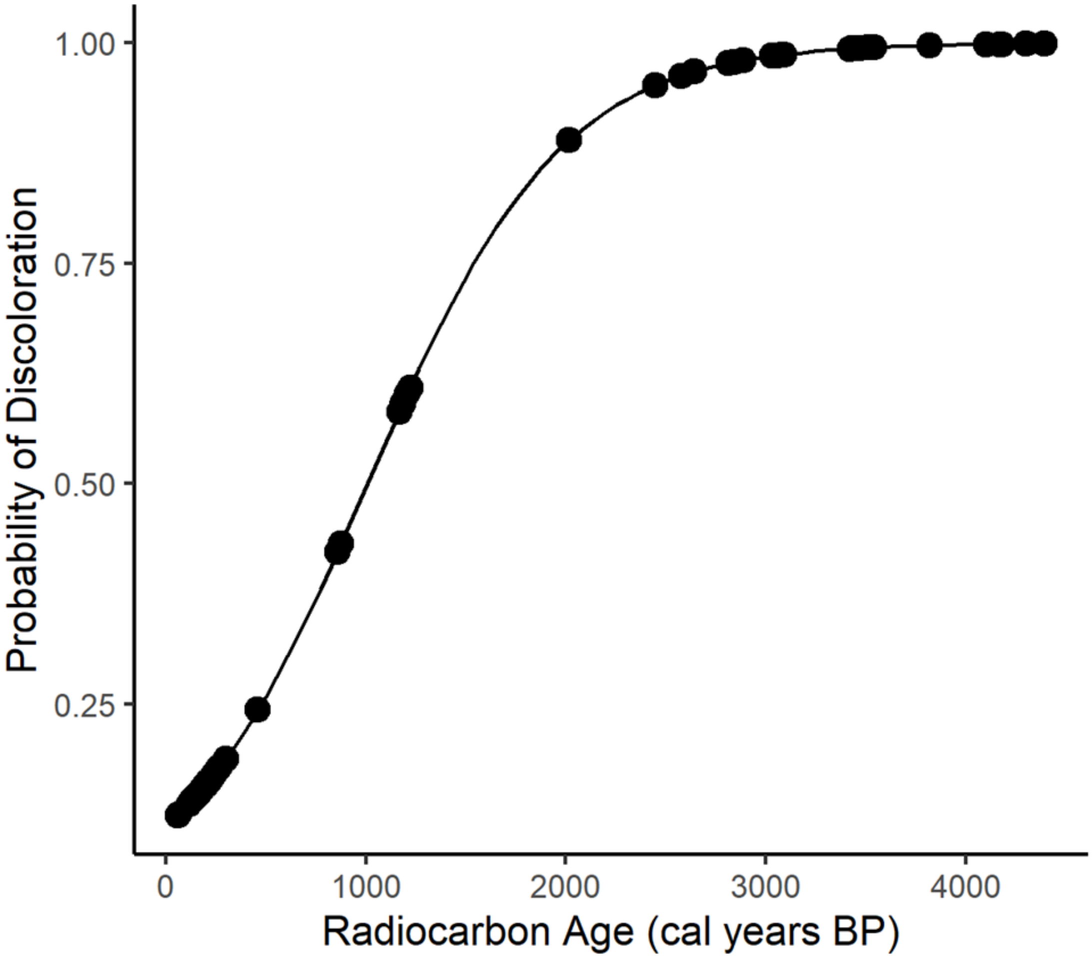


Figure 3.7 Logistic curve showing the probability of a dead *Arctica islandica* shell of a known radiocarbon age being discolored.

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CHAPTER IV TEMPORAL AND SPATIAL GROWTH COMPARISONS OF OCEAN QUAHOGS (ARCTICA ISLANDICA) ON THE NORTH ATLANTIC CONTINENTAL SHELF

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4.1 **Introduction**

Animal growth is controlled by ontogeny, genetics, and the environment (Sebens 1987, Hemeon et al., 2021a). Comparing growth over time between cohorts within populations and between populations can permit the effects of a surrounding environment to be isolated to determine the influence of environmentally-driven changes in growth of an organism (Grissino-Mayer 2001, Black et al. 2008, Peharda et al. 2018, Hemeon et al. 2021a). By comparing temperature regimes and climatic events to known periods of growth, the beneficial, neutral, or detrimental effects on growth often can be inferred from chronological growth increments recorded in the hard parts of an organism (Richardson, 2001; Killam and Clapham, 2018). For example, annual lines (annuli) deposited in the shells of bivalve molluscs, similar to the rings in a tree, capture a record of environmental information from the surrounding habitat (Peterson et al., 1985; Richardson, 2001; Kraeuter et al., 2007; Ridgeway et al., 2011; Peharda et al. 2019). These annuli result from a slower rate of carbonate deposition during periods of slower growth relative to the continuing deposition of organic matrix. Hence, substantial value can accrue from sampling bivalves from a range of spatial, temporal, and environmental settings to provide consistent and accurate records of the individual chronological age and the local climate (Jones et al., 1984; Austad, 1996; Brey et al., 2011; Ridgeway et al., 2011; Shirai et al., 2018).

Arctica islandica, commonly called the ocean quahog, is a boreal clam with a range extending along the mid-Atlantic continental shelf and throughout most boreal seas in the northern hemisphere. Ocean quahogs have a well-known sensitivity to temperature, with an upper thermal limit of ~15℃, and an extensive lifespan, often exceeding 300 years in age with the oldest yet aged being 507 years (Butler et al., 2013). These characteristics make *A. islandica* well suited for documenting the spatial and temporal influence of climate change. Investigations of this clam species cover the majority of the North Atlantic, including the Mid-Atlantic region (Witbaard, 1996; Dahlgren et al., 2000; Witbaard and Bergman, 2003; Wanamaker et al., 2011; Butler et al., 2013; Reynolds et al., 2017; Hemeon et al., 2021a).

In the Mid-Atlantic, on the U.S. continental shelf, *A. islandica* is found at latitudes well south of the normal boreal provincial boundary (Hale, 2010). This unusual southern extension in range is due to the presence of the Cold Pool, a body of cold bottom water trapped by thermal stratification during the late spring to early fall which maintains mean summer temperatures typically a 13.5°C or lower, with fall temperatures when stratification breaks down rarely exceeding 16°C (Lentz, 2017; Chen et al., 2018; Friedland et al., 2020, 2022).

Given the information archived in the growth record of these animals, many studies have been conducted examining the determinants of growth in this long-lived species, with particular emphasis on temperature and food supply (Schöne et al., 2005; Wanamaker et al., 2009; Begum et al., 2010; Vihtakari et al., 2016; Ballesta-Artero et al., 2017). Ocean quahogs are unique in their tendency for continuous growth into old age which limits the application of growth models that describe asymptotic growth at old age, typical of most bivalve species (e.g., McCuaig and Green, 1983; Devillers et al., 1998; Luquin-Cavarrubias et al., 2016). Hemeon et al., (2021a) determined that the best-fit growth model for ocean quahogs is a modified Tanaka model (MT) when compared to both traditional Tanaka model (Tanaka, 1982, 1988) proposed by Pace et al. (2017a) and the often favored von Bertalanffy model. The original Tanaka growth model, a power growth function, fits animals with indeterminate growth, such as is found in some marine invertebrates (McShane & Anderson 1997, Velázquez-Abunader et al. 2016, Pace et al. 2017a), but it tends to underestimate growth of *A. islandica* at old age. Consequently, Hemeon et al. (2021a) modified the traditional Tanaka model (Tanaka 1982, Sebens 1987, McShane & Anderson 1997, Pace et al. 2017b) by adding an additional parameter, *g*, which permits the model to better estimate length at old age.

4.1.1 **Objectives**

A primary objective of this study is to implement the Tanaka growth model to compare growth dynamics in ocean quahog populations from the U.S. Mid-Atlantic region, using information obtained from existing and extinct populations. LeClaire et al. (2022) documented the presence of dead *A. islandica* shells distributed over a substantial region of the Mid-Atlantic continental shelf off the Delmarva Peninsula (DMV). LeClaire et al. (2022) identified evidence of ocean quahog occupation inshore of their present range with animals born throughout the Holocene Epoch since the Holocene Climate Optimum (60-4400 cal years BP), including all four of the major cold events: the two cold period events during the Neoglacial, the Dark Ages Cold Period, and the Little Ice Age. LeClaire et al. (2022) proposed that the Cold Pool had transgressed and regressed across the continental shelf a number of times in the past and that during the transgressions associated with colder climates *A. islandica* occupied the inner to middle portion of the continental shelf well inshore of their range today. The objective of this research is to compare the growth rates of these ocean quahogs both spatially and temporally amongst themselves and with recently documented growth rates for living *A. islandica* from four different regions (Delmarva, New Jersey, Long Island, and Georges Bank (Hemeon et al., 2021a; Hemeon et al. in prep.; Sower et al. in prep.). Of note, Pace et al. (2017b), Hemeon et al. (in prep.) and Sower et al. (in prep.) document the extraordinary variability in *A. islandica* growth rates as a function of birth year for animals still living in these Mid-Atlantic populations. Animals born in a given birth year integrate the subsequent climatology over their lifetimes developing a growth curve that can vary from animals born in other birth years. These differences document the sensitivity of the species to temperature change. This sensitivity produces a differential growth dynamic based on the differential in temperature exposure for each cohort. Hence, these comparisons can describe differences in growth over space and time, revealing the influence of biogeographic location and climate change on ocean quahog growth. These findings will potentially provide the ability to identify the temperature history of the dead populations identified by LeClaire et al. (2022) based on comparisons to the still-living populations.

4.2 **Materials and Methods**

4.2.1 **Sample processing**

Growth data for living ocean quahogs were obtained from three different studies, including animals collected off New Jersey (39 50.40’N, 72 49.20’ W; Sower et al. in prep.), George’s Bank (40 43.66’N, 67 48.32’W; Hemeon et al., 2021a), and Long Island

(40 5.95N, 73 00.74W; Hemeon et al., in prep.). Growth data from dead shells were obtained from collections off the Delmarva Peninsula reported by LeClaire et al. (2022) (Fig 4.1). Live and dead ocean quahogs were collected along the continental shelf using a hydraulic dredge towed by commercial clam vessels. For live animals, a standard commercial ocean quahog hydraulic dredge was used. For subfossil collections, the dredge was lined with 1-inch-square wire on the bottom and knife shelf. Material collected by the dredge was sorted, by clam species, along the central conveyor belt aboard the vessel. Live ocean quahog samples were shucked, and both live and dead shells were retained and archived for later analysis. Samples selected from the archive were processed through a standard procedure described by Pace et al., (2017a) and Hemeon et al., (2021b). Each shell was cut along the long axis of growth using a Kobalt wet tile saw. After being cut, shells were then ground using abrasive paper of increasing grit size (at 240, 320, 400, and 600) and polished with a polycrystalline diamond suspension fluid (6 µm and 1 µm diamond sizes) (Pace et al. 2017a, Hemeon et al., 2021b) to obtain a mirror finish. Shell hinges were imaged using a high-definition Olympus DP73 digital microscope camera. After photographing the hinge, shell powder samples were extracted using a Dremel tool to obtain carbonate from the edge of the shell near the hinge and umbo. Grinding was focused on the youngest part of the shell hinge, where carbonate was deposited during the earliest growth. The powder sample (>10 mg) was sent to the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine for analysis. Radiocarbon dates were calibrated according to the methods in LeClaire et al., (2022).

4.2.2 **Aging**

Following the methods described in Hemeon et al. (2021b), *A. islandica* shells were aged using images of the shell hinge pate and ImageJ annotation software to estimate age. Precision was verified using multiple readers and blind samples (Hemeon et al. 2021b). Annual growth increments were measured in pixels by the ObjectJ plugin for ImageJ (Hemeon et al. 2021b). Annual lines observed on the shell hinge plate are proportional to increments on the outer shell valve (Thompson et al. 1980); therefore, annual growth increments on the hinge plate were converted to annual growth increments of the total shell length (Hemeon et al. 2021b) using the ratio of the hinge plate length to total length after conversion of pixel dimension to mm.

4.2.3 **Growth Model**

The growth increments for each shell were cumulatively summed to create a growth curve for that specific individual. Using the Akaike information criterion (AIC), Hemeon et al. (2021a) determined that the modified Tanaka model was the best-fit growth model for ocean quahog growth (Eq 1).

Eq (1) $$L_t = d + \frac{1}{\sqrt{f}}\, log\left(2f(t-c) + 2\sqrt{f^2(t-c)^2 + fa}\right) + gt^{2.5}$$

where L_t is the shell length in mm at a given time (t). The MT model parameters can be understood as follows. Parameter c (years) denotes the age at maximum growth rate. At the age of maximum growth, c, the growth rate is $1/\sqrt{a}$. So, parameter a ($yr^2\ mm^{-2}$) describes the maximum growth rate which will occur at age c. Parameter f (yr^{-2}) controls that rate at which growth declines with increasing age. For older animals, growth rate reduces to $1/(t\sqrt{f})$ were t is age (yr). Parameters d (mm) and g ($mm\ yr^{-1}$) are scalers of size, with g influencing the rate of growth rate decline with increasing age determined by parameter f. All MT model parameters except d, were forced to be ≥0 during model convergence to prevent the estimation of negative square roots and logarithms.

For comparison with data from Hemeon et al. (2021a, in prep.) and Sower et al. (in prep.), dead shells reported in LeClaire et al., (2022) that were born after 1700 were divided into 20-year groups by birth year.

4.2.4 **Death Dates**

The age-at-death of each dead shell collected off Delmarva and reported in LeClaire et al. (2022) was added to the radiocarbon age (assumed to approximate the birth year of the animal), to determine the year of death.

4.2.5 **Temperature Model**

Using data from Hemeon et al. (2021a), animals collected from Georges Bank and Long Island were compared to bottom water temperatures for these collection locations from 1958-2017(GLORYSv12). A generalized additive model (GAM) was fit to the yearly maximum values obtained from the X model compared to the yearly growth of animals to describe the relationship between growth and temperature. The GAMs were fit using the mgvc package in R. Growth was the response variable with maximum yearly temperature, sex, location, and animal age in that growth year were used as predictor variables to explain the differences in growth.

4.3 **Results**

Comparison of the MT growth curves for the dead shells taken off Delmarva that had birth dates contemporaneous with living populations from New Jersey, Long Island, and Georges Bank, animals born after 1700 BCE), showed that the ocean quahogs from

Delmarva (DMV) grew faster than those from all other regions, with animals from George's Bank (GB) following, then those from Long Island (LI) and New Jersey (NJ) being essentially the same, although NJ animals were larger than LI animals as the animal increased in age (Fig 4.2). When comparing populations with contemporaneous birth dates (1700-2017 BCE) from GB, LI, NJ, and DMV, maximum growth rate (i.e., smaller a) was highest for DMV (Table 4.1), followed by GB and then by NJ and LI. The age at maximum growth rate (c), was youngest at GB, with LI, NJ and DMV demonstrating increasing age at max growth rate (Table 4.2). All of these ages at maximum growth fell within the first 4 years of life, however. The rate of decline of growth rate with age was lowest at DMV (higher f), then NJ, LI, and GB. A scale of body size, (d) was largest at GB, then DMV, LI, and NJ2 (Table 4.1).

Figures 4.3-4.4 depict temporal and spatial trends in growth from 1740-1940 BCE at DMV, GB, and LI respectively. Modified Tanaka growth curves (Figure 4.4) for animals born during major climate events in the Holocene illustrate the temporal changes in growth during major events including: the Little Ice Age (LIA) (207-462 cal years BP), Medieval Warm Period (MWP) (877cal years BP), Dark Ages Cold Period (DACP) (1167-1223 cal years BP), Roman Warm Period (RWP) (2,447 cal years BP), Neoglacial part 1 (Neo1) (3,418-3,542 cal years BP), Neoglacial part 2 (Neo2) (3418-3542 cal years BP), and the Meghalayan stage boundary (Meg) (3817-4302 cal years BP). The growth of dead ocean quahogs collected from DMV was always greater than or equal to the growth of ocean quahogs from LI, GB, and NJ. Growth was fastest during the RWP and the DACP, followed by the MWP. Growth during the Meghalayan stage boundary was almost the same during the earliest part of the Neoglacial, with the late Neoglacial shells growing slightly faster. Growth during the LIA and between 1740-1960 BCE was very similar.

Dead shells from Delmarva lived between 16-247 years of age (Figure 4.5). These ages-at-death were well distributed across radiocarbon birth years between 60-4400 years ago (Figure 4.5). Analyzing the *A. islandica* that died in the past 200 years, younger animals become less common closer to present time, with their near disappearance starting about 120 years before present (Figure 4.6).

The GAM showed a negative relationship between the annual maximum temperature of the Cool Pool at collection locations and the growth of *A. islandica* at both GN and LI during the 1958-2017 time period (Figure 4.7).

4.4 **Discussion**

4.4.1 **Spatial and temporal comparisons in growth rates**

The MT growth models change over time, throughout the birth year groupings, describing the growth rate of living ocean quahogs, as anticipated from detailed analyses by Hemeon et al. (2021a, in prep.) and Sower et al. (in prep.). Spatial differences in growth of ocean quahogs are observed for living *A. islandica* across the three study regions. As Hemeon et al. (in prep.) reported, GB *A. islandica* exhibit faster growth rates than LI. Growth of ocean quahogs from NJ and LI had very similar rates, nearly identical until animals reached an old age (Figure 4.2, Table 4.1).

The MT growth models also shows consistent differences between growth rates for these living populations and dead animals taken off DMV with birth dates contemporaneous with living animals and clams from each of earlier the Holocene cold climate events. In addition, Unexpectedly, DMV dead ocean quahogs collected inshore of the species’ present-day distribution grew as fast or faster than animals from other studied regions. Previous to this study, both Hemeon et al. (in prep.) and Pace et al., (2018) found ocean quahogs from GB to have the highest growth rates in the Mid-Atlantic among living populations so far studied; however, even growth rates at GB were equaled or exceeded by growth rates obtained from subfossil shells off DMV in the current study.

Ocean quahogs born post-1700 had higher growth rates in the DMV populations compared to all other regions, maintaining a higher rate of growth across all 20-year groupings supporting comparisons. These continuously higher rates of growth observed, when comparing the total population born between 1740-1960 offshore of DMV, support the inference that the DMV populations lived in conditions that may have maximized growth prior to the mortality event that eradicated the population. So, observed high growth rates for dead populations off DMV suggests that environmental conditions, supporting optimal growth, were present during the lifetime of these clams. Bottom temperatures may have supported maximum growth before reaching intolerable levels that eventually led to the death of all ocean quahogs, prior to the 1980s (Fig. 4.6). Given suitably warm temperatures, increases in food supply also produce increasing rates of growth (Schöne et al., 2005; Mette et al., 2016; Ballesta-Artero et al., 2017).

Growth rate increase with increasing temperature, to a point, until optimal temperature is exceeded and growth rates decline. This parabolic relationship of physiology and temperature is well described in general (Woodin et al., 2013) and physiologically based in the relationship of filtration rate and respiration rate in bivalves, which are primary determinants of scope for growth (Ren and Ross, 2001; Hofmann et al., 2006; Munroe et al., 2013). The GAM model (figure 4.8) shows the influence of a temperature regime today at the LI and GB sites that tends to exceed optimal for periods during the summer, a product of the rapid warming of this region of the Mid-Atlantic (Lucey and Nye, 2010; Pershing et al., 2015; Saba et al., 2016). If such conditions were present for dead shells off DMV, one would not expect to observe the higher growth rates consistently present for DMV animals relative to rates observed for living animals from LI and GB.

Accordingly, one could infer that increased temperatures relative to today seems an unlikely explanation for the increased growth rate, and this is further supported by the fact that growth rates for dead animals born in the 19th and early 20th century off DMV are higher than contemporaneous animals still living at LI and GB. Yet, evidence clearly indicates that growth rates for LI and GB were lower in the 19th century than observed today (Pace et al., 2018; Hemeon et al. 2021a). Thus, only an increase in temperature appears insufficient to support the observed higher growth rates for dead shells collected off DMV, alive throughout the Holocene. The shells from ocean quahogs with birth years during most cold and warm events, during the Holocene, were growing as fast or at faster rates than the present populations in GB, LI, and NJ. Again, this fast rate of growth indicates that conditions off DMV were most suitable to growth and success of the resident *A. islandica* population at that time, but increased temperature does not provide a sufficient explanation, supporting the inference of an additional increased food supply. However, little is known about the influence of warming temperatures on phytoplankton production in the studied region (Friedland et al., 2018, 2020b), though considerable attention has been given to the influence of warming temperatures on phytoplankton production in general (e.g., Oviatt, 2004; Richardson and Schoeman, 2004; Osman et al., 2019; Lotze et al., 2019). Moreover, detailed knowledge of the influence of the inshore-offshore depth gradient on phytoplankton production is limited in the studied region (Yoder et al., 2002; Mouw and Yoder, 2005; Munroe et al., 2013). Despite the lack of studies, it is clear that phytoplankton production cannot meet the food supply requirements of the largest bivalve in the region, the Atlantic surfclam, *Spisula solidissima* (Munroe et al. 2013). Munroe et al. (2013) argue that benthic primary production is a critical supplement to phytoplankton production to support Atlantic surfclam biomass. The dead ocean quahogs with radiocarbon from known cold periods since the Holocene Climate Optimum, were collected at study sites off DMW, with depths considerably shallower than the present range of this species south of Long Island. Sea level at the earliest cold times recorded by the DMV animals was slightly lower than today (Engelhart et al., 2011), indicating animals would have lived at depths shallower than presently recorded at sites. *Arctica islandica* are found well inshore off Long Island, as well as elsewhere in the north Atlantic (Ragnarsson and Thórarinsdóttir, 2002; Strahl et al., 2011; Begum et al., 2019); hence, this species has no shallow-water depth restriction. Growth rates for inshore Long Island populations are not available. Nonetheless, the depth range of past occupation off DMV is not unusual for the species. The shallower depth, being much higher in the photic zone, could permit enhanced benthic primary production (Munroe et al. 2013), leading to increased availability of food and therefore increased growth rates.

GB ocean quahog growth was comparable to growth off DMV during the Neoglacial and the Meghalayan stage boundary (Fig 4.4) and somewhat lower than subsequent cold periods (the DACP and LIA) suggesting that the relatively slower growth rates may indicate that bottom waters were exceptionally cold during these periods off DMV, resulting in a decreased rate of growth. Of note is the strong suggestion from this study, and LeClaire et al. (2022), that the Cold Pool, a key oceanographic feature of the region, has waxed and waned across the continental shelf off the U.S. east coast, consistent with known cold and warm periods in the past and the community structure of the continental shelf.

4.4.2 **The dynamics of range regression in ocean quahogs**

The studied record of occupation by ocean quahogs of the inner-to-middle continental shelf off DMV represents periods of transgression of cold water inshore, including individuals in the death assemblage radiocarbon dated from the LIA through recent times. Death assemblages tend to err on the side of small (young) animals because the process of natural mortality usually adds a declining number of animals as the cohort ages and increases in size (Hallam, 1967; Cummins et al., 1986; Tomašových, 2004); however, taphonomic processes normally bias the assemblage against the preservation of the smallest size classes (Staff et al., 1986; Powell and Stanton, 1996, Kidwell, 2001). Nonetheless, as larger animals were selected for processing, ages-at-death are likely older than an unbiased sampling of the assemblage would otherwise provide. Hence, increased numbers of animals at smaller size are expected with decreasing age-since-death, as the most recent cohorts added to the death assemblage tend to be most numerous (Olszewski, 2004; Kosnik et al., 2009; Tomašových et al., 2014, 2018). Surprisingly, the opposite was observed (Figure 4.6). Considering the dead animals that lived contemporaneously with living animals (in the past 200 years), young animals become less common after approximately 120 years before present (Figure 4.6). This shift in age distribution is not abrupt, but rather shows a steady loss of increasingly old animals as time progresses, with the animals of oldest age-at-death having died most recently. This pattern infers recruitment decreased dramatically around 120 years ago, leading to the disappearance of younger animals prior to the death of older animals.

Older animals likely have a higher tolerance to high temperatures as a result of their ability to burrow deeper into the sediment (Tylor, 1976; Strahl et al., 2011) to escape the higher temperatures that occur routinely in the Cold Pool when stratification breaks down in the fall, before winter temperatures arrive. Temperature conditions similar to the annual maximum temperatures depicted in figure 4.7 result in a negative trend in growth and likely forecast a future cessation of growth, followed by death as higher temperatures remain for longer periods in the fall. This finding supports the conclusion that recently-dead-shells collected off DMV are the product of an increase in bottom temperature that cause the mortality of young *Arctica* and eventually older animals. The analysis of age-at-death, depicted in figure 4.6, provides a unique mechanism utilized to observe the rate of range regression in *A. islandica*. Unlike many bivalves, such as Atlantic surfclams (e.g., Narváez et al., 2015), large ocean quahogs are less sensitive to increasing temperatures. Evidence of the recession of the inshore range boundary will be found first in the timeseries of abundance of the juvenile animals. Most importantly, a shift in range in *A. islandica* is a100+ year process on the trailing edge of the range, rather than sub decadal as in many bivalve species (Jones et al., 2010; Hofmann et al. 2018; Baden et al., 2021).

4.5 **Summary**

Ocean quahogs represent a long-term record of climate change on the U.S. northeast-coast continental shelf. This species transgressed and regressed across the shelf numerous times in accordance with cold and warm climatic periods. The growth rates of this species provide a unique view of climatic conditions during the times of occupation. Living ocean quahogs from multiple regions across the North-Atlantic shelf (George's Bank, Long Island, New Jersey) were compared to shells collected from a region off Delmarva inshore of the species' present range. These populations had different growth rates, with DMV clams growing the fastest. Moreover, ocean quahog growth compared between regions and 20-year groupings from 1740 to 1940 showed both regional and temporal differences in growth, indicating that ocean quahogs that once occupied the inner-to-middle continental shelf off DMV continued to grow faster than animals from living populations taken from other regions throughout this timespan. Earlier populations occupying the studied region off DMV representing each of the cold periods after the Holocene Climate Optimum grew as fast or faster than living populations in the Mid-Atlantic region, possibly due to increased food supply in shallow water. *Arctica islandica* growth changed throughout the Holocene, reflecting the changes in environmental conditions throughout the epoch, with periods of the Neoglacial most closely representing modern-day growth rates suggestive of colder temperature conditions inshore during that time period. Examining ocean quahogs with a shorter time-since-death from DMV, the quahogs with the most recent radiocarbon dates were older than animals born closer to 1800, with clam births ceased about 120 years ago. This trend describes the characteristics of range contraction in *A. islandica* and might be a result of greatly diminished recruitment about 120 years ago, and the subsequent slow disappearance of live animals without replacement with the oldest dying most recently. The age-dependent mortality may be the product of the increased capability of older animals to burrow deeper than younger clams to escape high fall temperatures. This is the largest spatial and temporal growth comparison of *A. islandica* ever recorded and the first record of the process by which this species inshore range regresses as temperatures rise. Continuing to explore the relationship between the spatial and temporal difference in growth, birth, and age at death is important to interpret the current population dynamics of the *Arctica islandica* stock and to make future predictions as climate change continues.

4.6 Tables

Table 4.1 Georges Bank, Long Island, New Jersey 2, DelMarVa modern population Modified Tanaka model parameters.

Group	Parameter	Georges Bank		Long Island		New Jersey 2		Delmarva	
		Estimate	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Contemporary Population	*a*	7.36E-03	7.34E-04	1.57E-02	7.29E-04	1.69E-02	6.07E-04	7.91E-03	9.17E-04
	c	7.62E-01	7.62E-02	1.77E+00	6.88E-02	2.40E+00	6.55E-02	3.76E+00	1.72E-01
	d	8.78E+01	2.03E-01	7.73E+01	1.53E-01	7.61E+01	1.62E-01	8.00E+01	8.41E-01
	f	3.00E-03	2.82E-05	3.90E-03	3.48E-05	4.34E-03	4.30E-05	6.99E-03	4.21E-04
	g	6.04E-06	4.29E-07	5.07E-06	2.66E-07	9.34E-06	3.86E-07	4.59E-05	5.68E-06

Table 4.2 Geoges Bank, Long Island, DelMarVa 20y cohort Modified Tanaka model parameters.

Cohort	Parameter	GB Population		LI Population		DelMarVa Population	
		Estimate	SE	Estimate	SE	Estimate	SE
1740	a	6.55E-03	9.64E-03	9.91E-03	9.63E-03	8.54E-03	5.13E-03
	c	0.00E+00	8.07E-01	0.00E+00	5.85E-01	2.94E+00	1.03E+00
	d	8.10E+01	1.45E+00	7.09E+01	7.68E-01	8.72E+01	4.89E+00
	f	2.19E-03	1.34E-04	2.91E-03	1.26E-04	4.60E-03	1.21E-03
	g	9.14E-06	1.01E-06	1.46E-05	5.97E-07	7.29E-06	2.76E-05
1760	a			4.46E-02	2.83E-02	7.21E-03	1.41E-03
	c			0.00E+00	1.22E+00	2.96E+00	2.75E-01
	d			7.36E+01	1.29E+00	7.99E+01	1.22E+00
	f			2.56E-03	1.76E-04	6.52E-03	5.63E-04
	g			1.58E-05	9.69E-07	3.08E-05	6.19E-06
1780	a	1.14E-02	6.26E-03	1.46E-02	8.31E-03	3.15E-03	2.99E-03
	c	0.00E+00	4.09E-01	0.00E+00	4.77E-01	1.50E+00	8.12E-01
	d	8.42E+01	6.49E-01	6.98E+01	6.71E-01	1.03E+02	4.56E+00
	f	2.61E-03	8.21E-05	2.84E-03	1.01E-04	2.94E-03	5.23E-04
	g	7.67E-06	6.34E-07	2.02E-05	6.73E-07	0.00E+00	1.49E-05
1800	a	5.74E-03	6.39E-03	1.33E-02	5.85E-03	8.08E-03	1.05E-03
	c	0.00E+00	5.14E-01	0.00E+00	3.52E-01	2.42E+00	2.20E-01
	d	8.78E+01	1.01E+00	7.24E+01	5.46E-01	9.22E+01	1.17E+00
	f	2.53E-03	1.15E-04	2.83E-03	7.92E-05	3.73E-03	1.97E-04
	g	6.91E-06	1.17E-06	2.10E-05	6.53E-07	3.64E-05	6.29E-06
1820	a	9.56E-03	4.31E-03	2.50E-02	9.59E-03	1.04E-02	1.60E-03
	c	0.00E+00	3.24E-01	0.00E+00	4.73E-01	3.48E+00	2.86E-01
	d	8.95E+01	6.58E-01	7.54E+01	6.61E-01	8.42E+01	1.36E+00
	f	2.41E-03	6.72E-05	2.99E-03	1.07E-04	5.73E-03	4.83E-04
	g	9.31E-06	8.87E-07	2.49E-05	9.34E-07	2.95E-05	8.94E-06
1840	a	9.48E-03	4.35E-03	4.37E-03	4.27E-03	1.31E-02	3.02E-03
	c	2.64E-01	3.63E-01	0.00E+00	3.12E-01	2.63E+00	4.63E-01
	d	9.11E+01	8.51E-01	7.77E+01	6.29E-01	8.59E+01	1.85E+00
	f	2.52E-03	8.96E-05	3.21E-03	1.04E-04	3.90E-03	3.57E-04
	g	9.38E-06	1.50E-06	2.60E-05	1.24E-06	3.53E-05	7.55E-06
1860	a	1.12E-02	2.63E-03	4.62E-03	3.72E-03	1.55E-02	6.00E-03
	c	9.50E-01	2.62E-01	1.51E-01	3.05E-01	2.77E+00	9.63E-01
	d	8.82E+01	7.35E-01	8.00E+01	7.24E-01	8.98E+01	4.74E+00
	f	2.91E-03	9.38E-05	3.16E-03	1.11E-04	3.67E-03	7.63E-04
	g	1.91E-05	1.87E-06	3.13E-05	1.78E-06	0.00E+00	2.97E-05
1880	a	1.01E-02	1.67E-03	1.43E-02	3.30E-03	3.60E-03	1.32E-03
	c	1.08E+00	1.84E-01	8.66E-01	2.89E-01	2.20E+00	9.14E-01
	d	8.69E+01	5.93E-01	8.33E+01	8.02E-01	1.58E+02	2.41E+01
	f	3.11E-03	8.17E-05	2.99E-03	1.06E-04	1.36E-03	5.30E-04
	g	1.79E-05	2.04E-06	3.01E-05	2.59E-06	0.00E+00	9.72E-04
1940	a	1.06E-02	9.45E-04	1.25E-02	5.62E-04	1.70E-02	3.78E-02
	c	2.21E+00	1.65E-01	2.74E+00	9.12E-02	0.00E+00	6.27E+01
	d	8.31E+01	9.85E-01	7.39E+01	5.22E-01	7.14E+02	2.65E+03
	f	4.27E-03	1.93E-04	5.60E-03	1.63E-04	7.03E-05	5.00E-04
	g	7.39E-05	1.30E-05	9.39E-05	8.46E-06	0.00E+00	1.18E-02

SE, standard error

Table 4.3 Modified Tanaka model parameters for dead shells from DelMarVa grouped by climate event.

Climate Event	Parameter	DelMarVa	
		Estimate	SE
Modern	*a*	7.91E-03	9.17E-04
	c	3.76E+00	1.72E-01
	d	8.00E+01	8.41E-01
	f	6.99E-03	4.21E-04
	g	4.59E-05	5.68E-06
LIA	*a*	8.77E-03	4.07E-03
	c	1.74E+00	6.79E-01
	d	1.00E+02	2.98E+00
	f	2.79E-03	3.20E-04
	g	0.00E+00	1.02E-05
MWP	*a*	3.89E-03	6.43E-04
	c	4.10E+00	1.19E-01
	d	8.32E+01	1.14E+00
	f	1.02E-02	8.89E-04
	g	6.67E-05	3.41E-05
Dark Ages	*a*	1.03E-03	7.28E-03
	c	0.00E+00	2.57E+00
	d	1.59E+02	4.74E+01
	f	1.04E-03	7.05E-04
	g	0.00E+00	2.03E-03
RWP	*a*	4.17E-03	1.81E-03
	c	1.60E+00	8.25E-01
	d	1.23E+02	1.74E+01
	f	2.18E-03	8.41E-04
	g	0.00E+00	1.19E-03
Neo1	*a*	3.53E-03	5.72E-03
	c	1.01E+00	8.77E-01
	d	8.60E+01	2.69E+00
	f	3.75E-03	5.43E-04
	g	0.00E+00	6.41E-06
Neo2	*a*	3.67E-03	9.30E-03
	c	0.00E+00	1.02E+00
	d	9.36E+01	2.77E+00
	f	1.97E-03	1.89E-04

	g	0.00E+00	2.80E-06
Meg	*a*	1.11E-02	2.93E-03
	c	3.24E+00	4.49E-01
	d	7.16E+01	1.58E+00
	f	6.61E-03	7.83E-04
	g	7.74E-05	7.33E-06

4.7 **Figures**

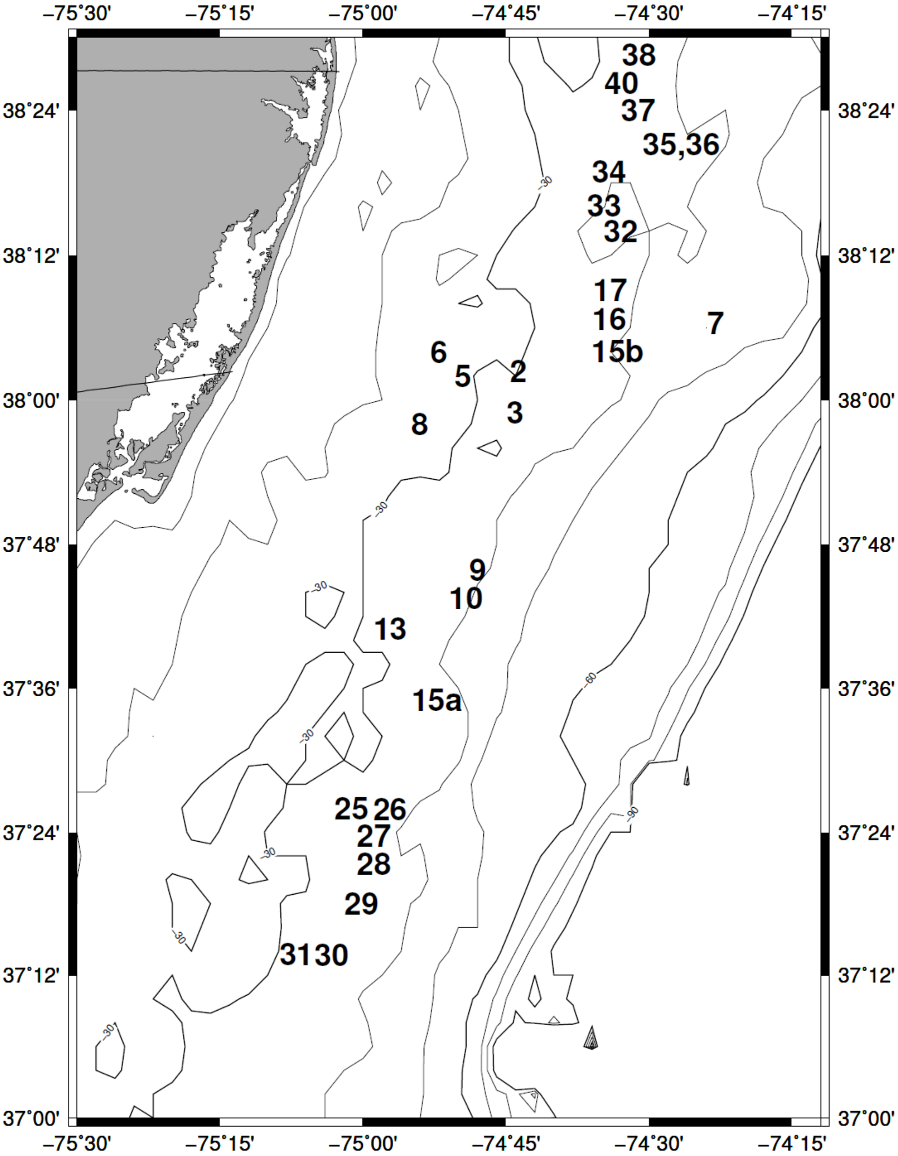

Figure 4.1 Map of ocean quahog shell collection sites from offshore of the Delmarva (DMV) Peninsula (see LeClaire et al. (2022) for further explanation.

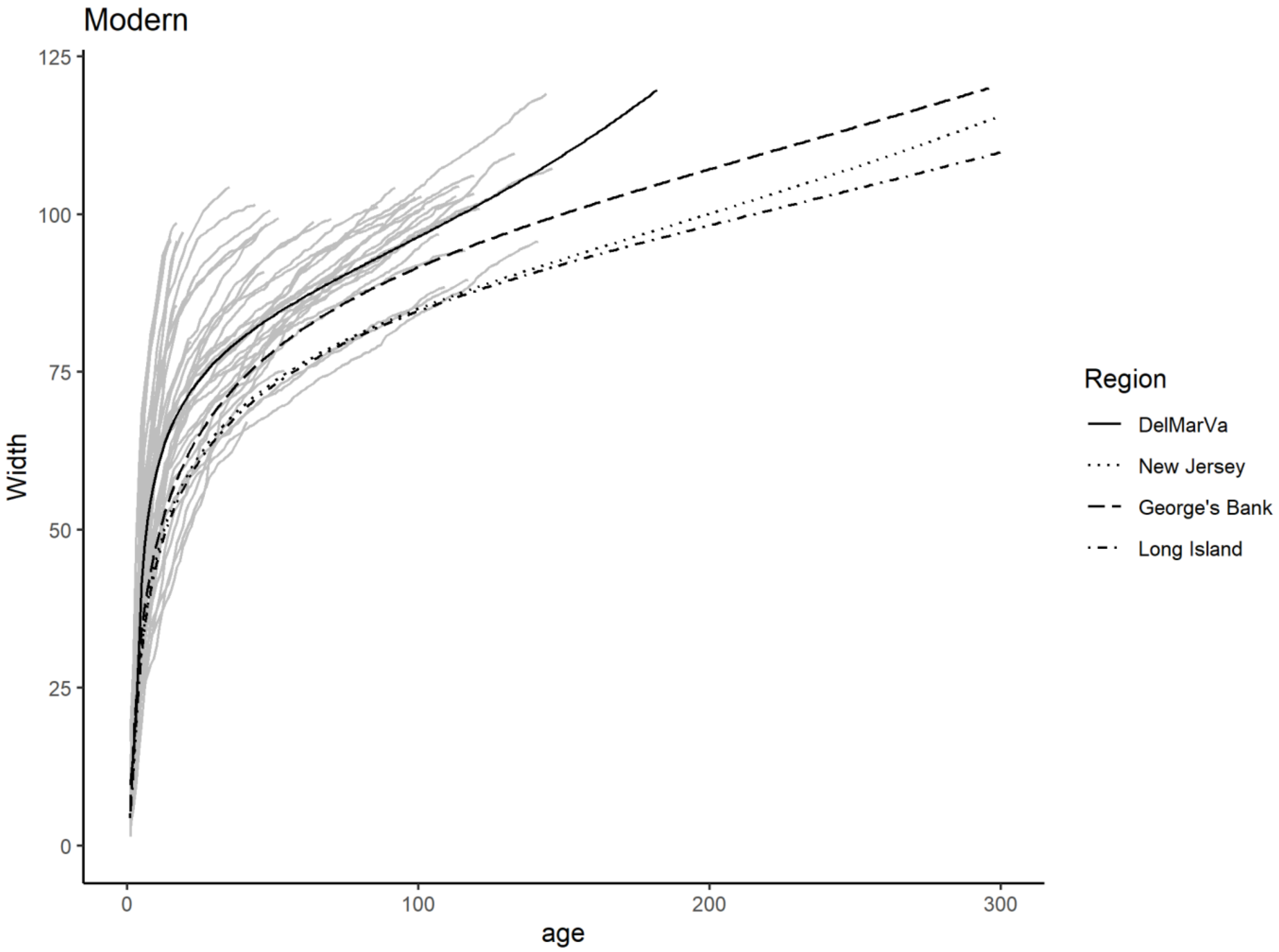

Figure 4.2 Modified Tanaka curves (black lines) from ocean quahogs born after 1700 BCE compared across regions: Delmarva (solid line), New Jersey (dotted line), George’s Bank (dashed line), and Long Island (dot-dashed line). Light grey lines represent the cumulative growth throughout life of each animal in the sample.

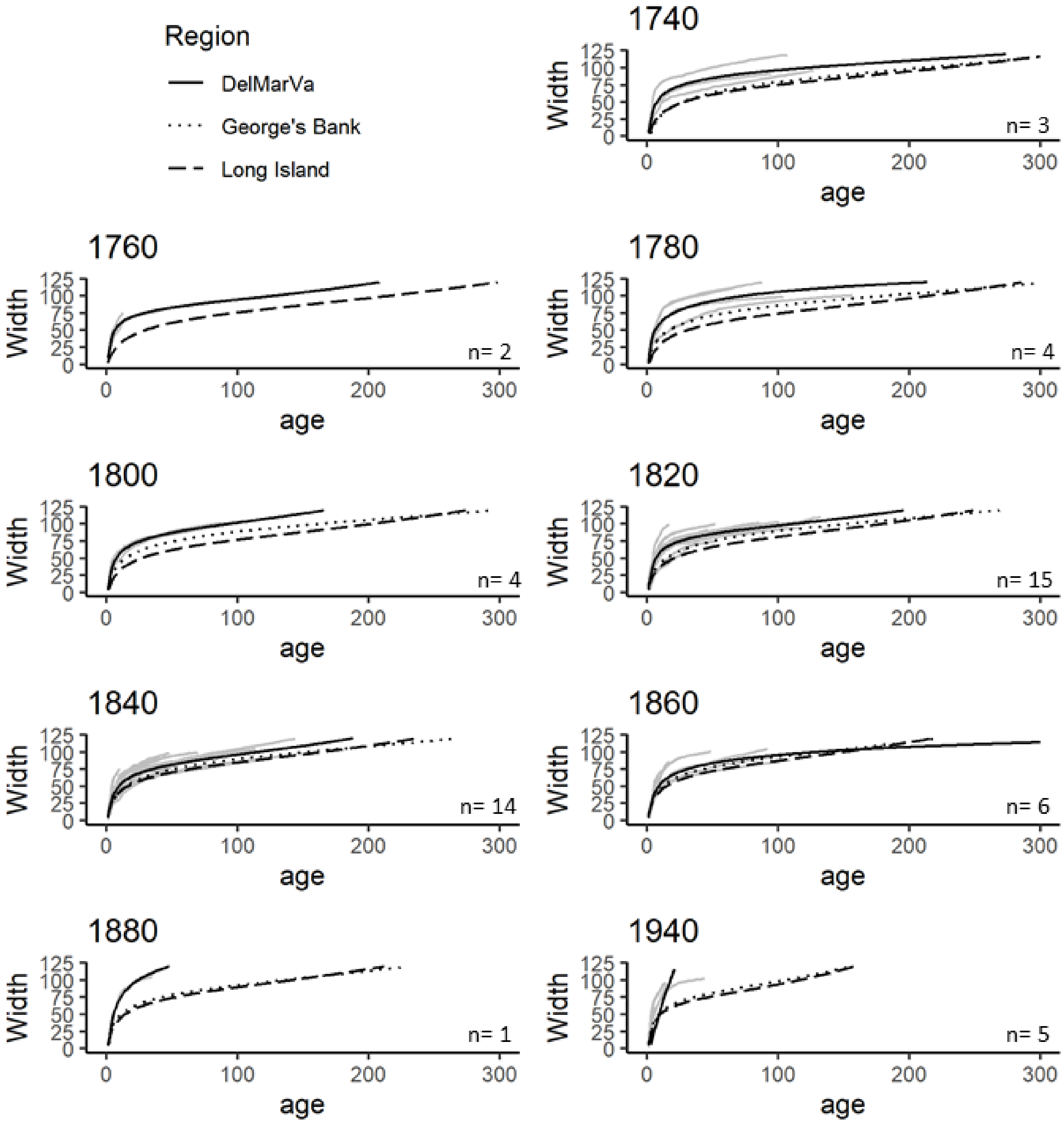

Figure 4.3 Modified Tanaka curves (black lines) compared across regions and 20-year groupings by birth date including, Delmarva (solid line), Long Island (dashed line), and George’s Bank (dotted line). Light grey lines represent the cumulative growth throughout life of each animal in the sample.

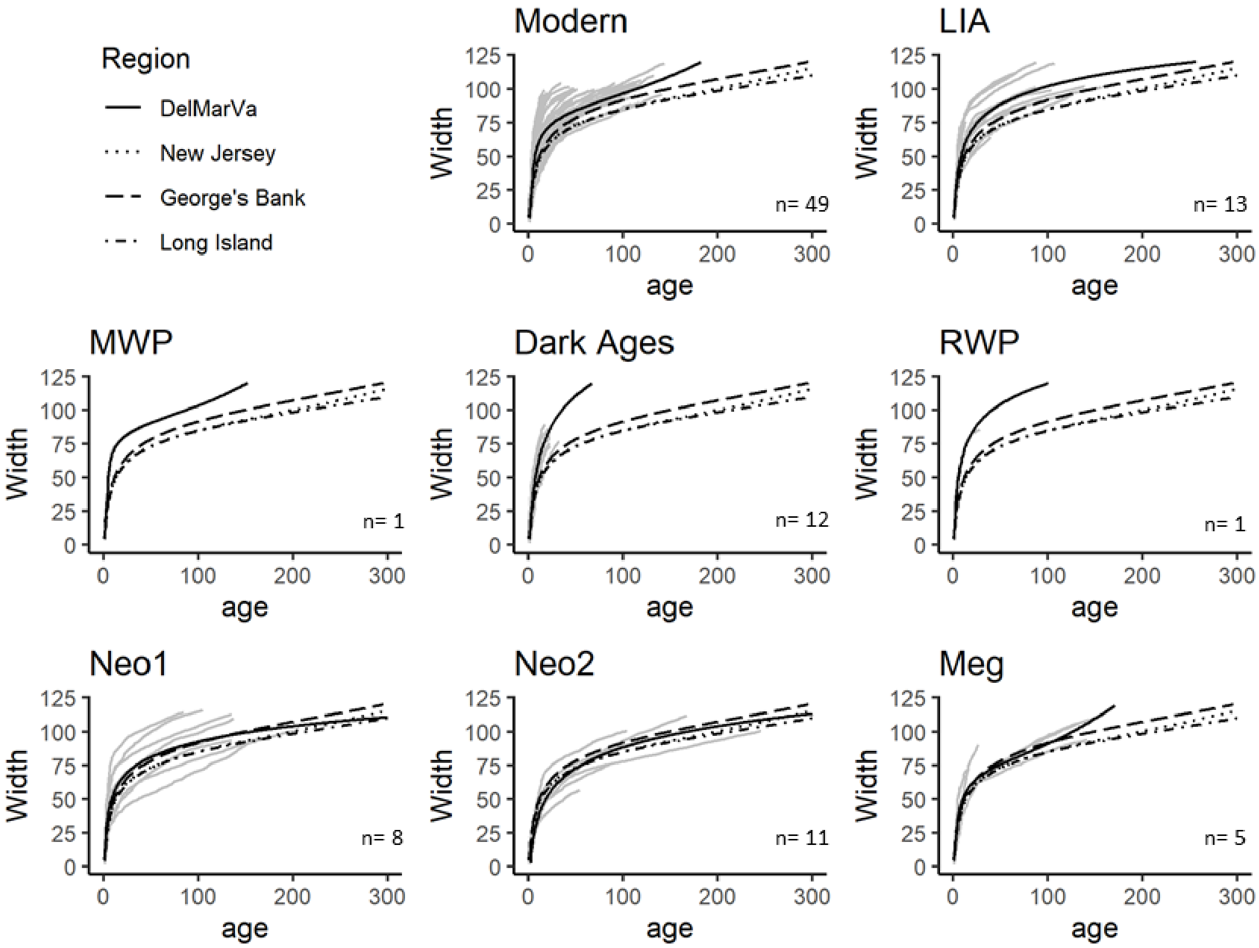

Figure 4.4 Modified Tanaka growth curves (black lines) for shells born off Delamrvaa during major climate events in the Holocene: Modern (60-203 cal years BP), Little Ice Age (LIA) (207-462 cal years BP), Medieval Warm Period (MWP)(877cal years BP), Dark Ages (1167-1223 cal years BP), Roman Warm Period (RWP) (2447 cal years BP), Neoglacial part 1 (Neo1)(3418-3542 cal years BP), Neoglacial part 2 (Neo2)(3418-3542 cal years BP), Meghalayan stage boundary (Meg)(3817-4302 cal years BP). The solid line represents the dead shells sampled off the Delmarva Peninsula. Curves from New Jersey, George’s Bank, and Long Island represent living animals born after 1700. The dotted line represents the growth for living *A. islandica* off the coast of New Jersey, the long dashes represents George’s Bank, and the dot-dash line represents Long Island. Light grey lines represent the cumulative growth throughout life of each animal in the sample.

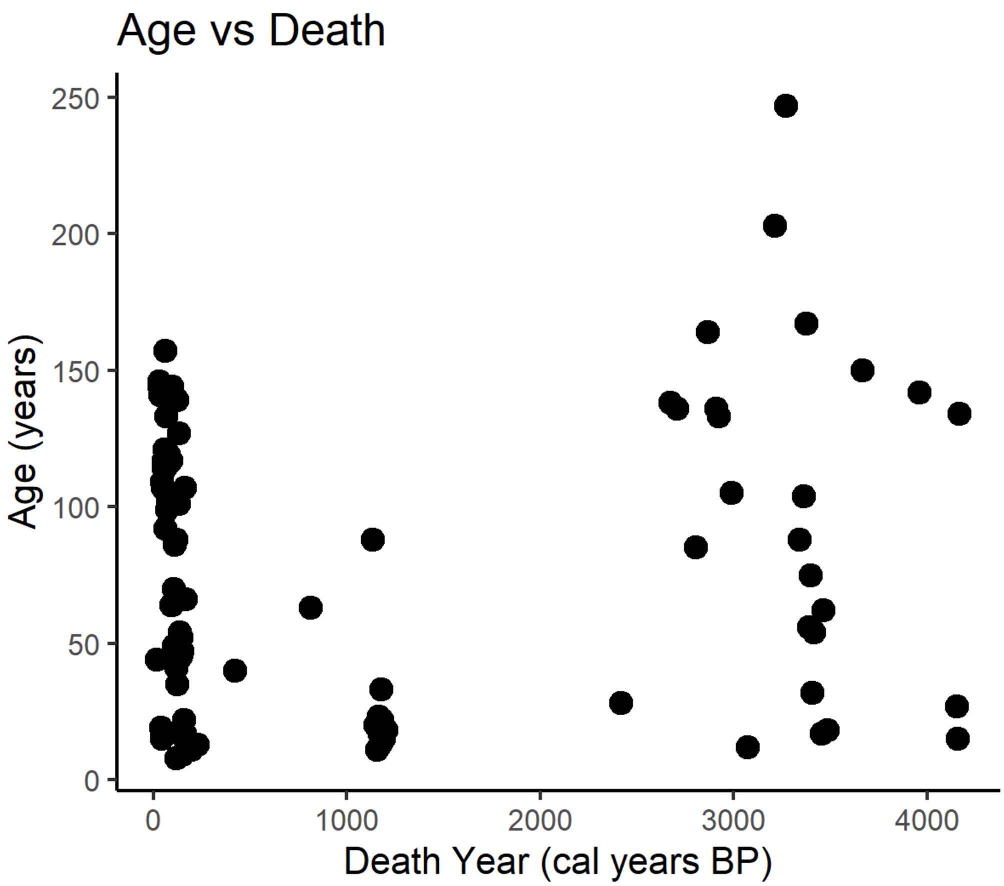

Figure 4.5 Age of ocean quahog at death compared to the time (death year) that the animal died. Death years are in years before present, focusing on animals that died between 62-4400 years ago.

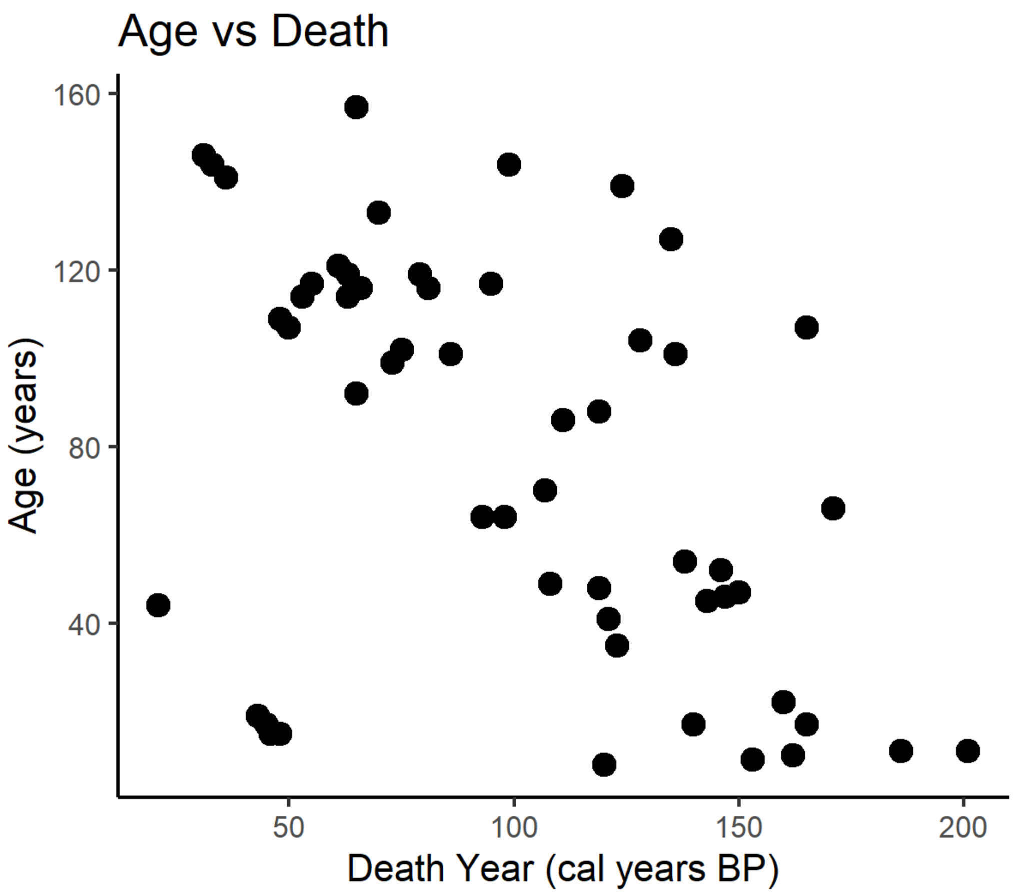

Figure 4.6 Age of ocean quahogs at death compared to the time (death year) that the animal died. Death years are in years before present, focusing on animals that died in the past 200 years.

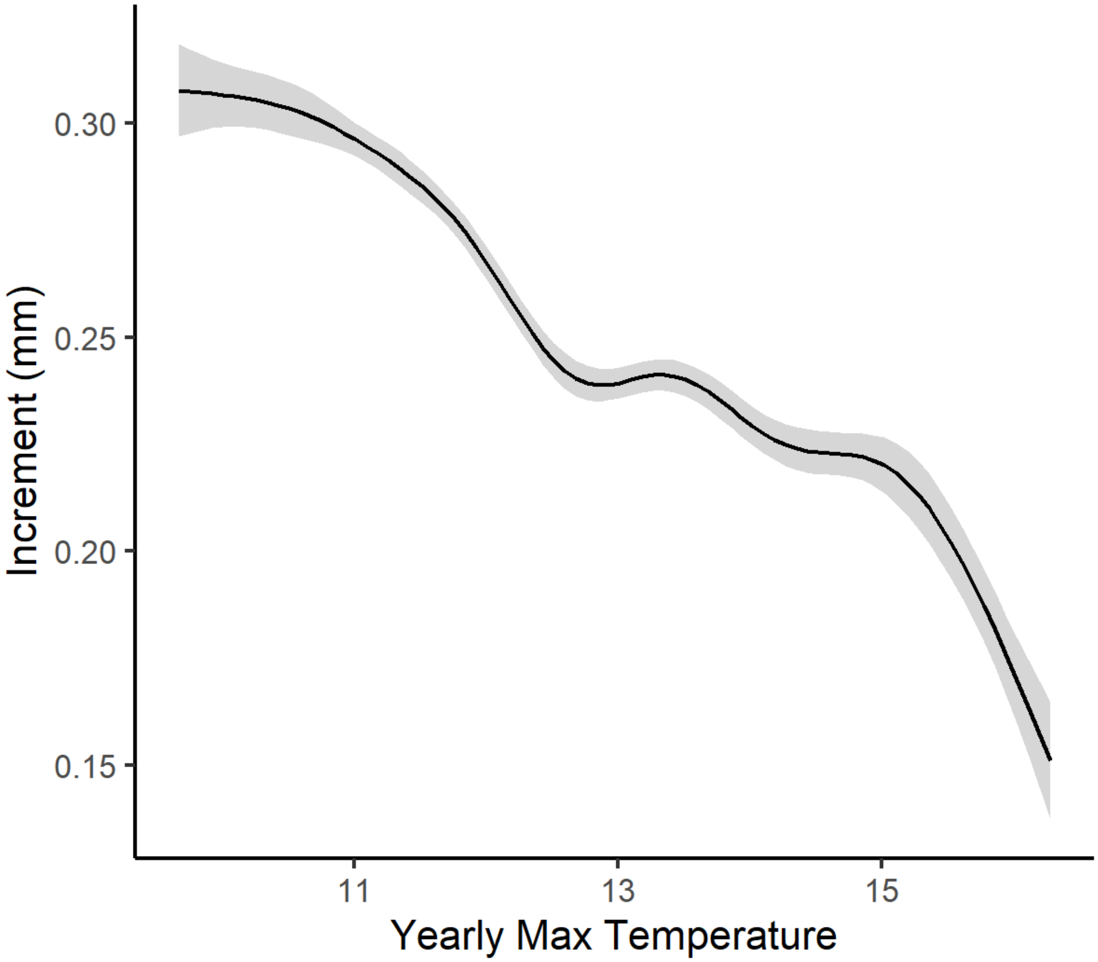

Figure 4.7 General additive model of yearly growth increment over yearly maximum temperature between 1958-2017.

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Supplementary information on *A. islandica* shell processing procedures can be found at: https://www.vims.edu/research/units/labgroups/molluscan_ecology/publications/topic/ocean_quahog_arctica/index.php

CHAPTER V CONCLUSIONS

5.1 Biogeographic Range Shifts

The Holocene, starting approximately 11.7 cal ka, is characterized by distinct periods of warming and cooling. Despite these known climate events, few temperature proxy data to describe them exist for the northwestern Atlantic Ocean. One potential record of past water temperatures is preserved in the marine fossil record. Shell growth of ocean quahogs (*Arctica islandica*), a long-lived bivalve, can provide records of past environmental conditions. *Arctica islandica* habitat includes the Mid-Atlantic Bight (MAB), an area rapidly warming as a consequence of climate change. The Cold Pool, a bottom-trapped water mass on the outer continental shelf within the MAB, rarely rises above 15°C. Ocean quahogs inhabiting the MAB are confined to the Cold Pool as a consequence of an upper thermal limit for the species of ~15-16°C. Recently, dead *A. islandica* shells were discovered outside of the species' present-day range, suggesting that the Cold Pool once extended further inshore than now observed. Shells collected off the Delmarva Peninsula were radiocarbon-dated to identify the timing of habitation and biogeographic range shifts. Dead shell radiocarbon ages range from 4,400 cal BP to 60 cal BP, including ages representing four major Holocene cold events. Nearly absent from this record are shells from the intermittent warm periods. Radiocarbon ages indicate that ocean quahogs, contemporaneous with the present MAB populations, were living inshore of their present-day distribution during the past 200 years. This overlap suggests the initiation of a recent biogeographic range shift that occurred as a result of a regression of the Cold Pool following the Little Ice Age.

5.2 Taphonomic Indicators of Shell Age

Taphonomic indicators are often used to assess time-since-death of skeletal remains. These indicators often have limited accuracy, resulting in the reliance of other methodologies to age remains. This report evaluates taphonomic age using 117 ocean quahog shells collected from the Mid-Atlantic Bight, offshore of the DelMarVa Peninsula with radiocarbon dates extending from 60-4,400 cal years BP, with varying degrees of taphonomic alteration produced by discoloration and degradation of periostracum. To determine if a relationship exists between taphonomic condition and time-since-death, radiocarbon ages were compared with the amount of remaining periostracum and type of discoloration of the shell. Old shells (individuals that died a long time ago) were discolored orange with no periostracum while younger shells (individuals that died more recently) had their original color, white, with some periostracum. Both the disappearance of periostracum and the appearance of discoloration followed a logistic process, with 50% of shells devoid of periostracum and 50% discolored in about 1,000 years. The logistic form of long-term taphonomic degradation is first reported here, as are the longest time series for taphonomic processes in death assemblages within the Holocene record. This relationship can be utilized to triage when deciding what shells to age from time-averaged assemblages permitting more efficient application of expensive methods of aging such as radiocarbon dating.

5.3 Spatio-temporal Growth Comparisons

Ocean quahogs represent a long-term record of climate change on the U.S. northeast-coast continental shelf. This species transgressed and regressed across the shelf numerous times in concert with cold and warm climatic periods. The growth rates of this species and their availability in the death assemblage over a wide geographic and temporal range make *Arctica islandica* well suited for documenting both spatial and temporal influences of climate change in the Mid-Atlantic. The purpose of this study is to compare regional growth of dead ocean quahogs obtained off Delmarva inshore of the species' present range and representing each of the cold periods since the Holocene Climate Optimum with living animals from New Jersey, Long Island, and Georges Bank. These populations had different growth rates, with all DMV populations growing as fast or faster than the living populations. Moreover, ocean quahog growth compared between regions from 1740 to 1940 showed more rapid growth than contemporaneous living individuals born over the same time from these other regions. Higher growth rates of the A. islandica population off DMV suggest that conditions supported near maximum growth during each of the cold periods after the Holocene Climate Optimum, possibly due to increased food supply in shallow water. Considering DMV animals which lived contemporaneously with living animals (in the past 200 years), young animals become less common after approximately 120 years before present. This shift in age distribution showed a steady loss of increasingly old animals as time progressed, with the animals of oldest age-at-death having died most recently. These characteristics describe the mechanism by which range regression occurs in this species. Unlike many bivalves, evidence of range recession will be found first in the timeseries of abundance of the juvenile animals and a shift in the trailing edge of the range is a100+ year process. This study is the largest spatial and temporal growth comparison of *A. islandica* ever recorded and the first record of the process by which this species inshore range regresses as temperatures rise.