The University of Southern Mississippi

The Aquila Digital Community

Master's Theses

Summer 8-2017

Evidence of Multidecadal Recruitment in the Ocean Quahog, *Arctica islandica* in the Western Atlantic Ocean

Sara M. Pace
University of Southern Mississippi

Follow this and additional works at: https://aquila.usm.edu/masters_theses

Part of the Marine Biology Commons, and the Population Biology Commons

Recommended Citation

Pace, Sara M., "Evidence of Multidecadal Recruitment in the Ocean Quahog, *Arctica islandica* in the Western Atlantic Ocean" (2017). *Master's Theses*. 313.
https://aquila.usm.edu/masters_theses/313

This Masters Thesis is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Master's Theses by an authorized administrator of The Aquila Digital Community. For more information, please contact aquilastaff@usm.edu.

EVIDENCE OF MULTIDECADAL RECRUITMENT IN THE OCEAN QUAHOG, ARCTICA ISLANDICA IN THE WESTERN ATLANTIC OCEAN

by

Sara Margaret Pace

A Thesis
Submitted to the Graduate School,
the College of Science and Technology,
and the School of Ocean Science and Technology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

August 2017

EVIDENCE OF MULTIDECADAL RECRUITMENT IN THE OCEAN QUAHOG, ARCTICA ISLANDICA IN THE WESTERN ATLANTIC OCEAN

by Sara Margaret Pace

August 2017

Approved by:

Dr. Eric N. Powell, Committee Chair
Professor, Ocean Science and Technology

Dr. Roger Mann, Committee Member
Professor, Marine Science, Virginia Institute of Marine Science, William & Mary

Dr. Chet F. Rakocinski, Committee Member
Professor, Ocean Science and Technology

James S. Franks, Committee Member
Senior Research Scientist, Ocean Science and Technology

Dr. Robert J. Griffitt,
Chair, Division of Coastal Sciences, School of Ocean Science and Technology

Dr. Karen S. Coats
Dean of the Graduate School

COPYRIGHT BY

Sara Margaret Pace

2017

Published by the Graduate School

THE UNIVERSITY OF
SOUTHERN
MISSISSIPPI

ABSTRACT

EVIDENCE OF MULTIDECADAL RECRUITMENT IN THE OCEAN QUAHOG, ARCTICA ISLANDICA IN THE WESTERN ATLANTIC OCEAN

by Sara Margaret Pace

August 2017

Ocean quahogs (*Arctica islandica*) are the longest-lived, non-colonial animals known today, with a maximum life span exceeding 500 years. Limited information is available regarding recruitment, making the sustainable management of this valuable fishery a challenge. The objective of this research was to describe the age structure and growth rates for four populations of ocean quahogs from the mid-Atlantic stock to evaluate long-term recruitment trends. Clams were sectioned for age estimation to develop population age frequencies. Initial colonization began approximately 175-250 years ago depending upon site. All sites experienced an increase in recruitment beginning in the late 1800’s to early 1900’s, after which the populations reached and remained at carrying capacity, characterized by more or less continuous low-level recruitment. Growth rates for select individuals from the Georges Bank site were evaluated using three growth models. The ALOG model was more suitable because it allows for early, rapid growth and for persistent indeterminate growth into old age. Growth rates for clams from all sites were analyzed to investigate both geographical and temporal differences. A substantive increase in the age at which animals reach 60, 80, and 90 mm has occurred, as well as an increase in average growth rates to 60, 80, 90, and post-90 mm, at the two sites in the southern portion of the stock since initial colonization, likely in response to increasing bottom water temperatures since the end of the Little Ice Age. These results have important implications for fishery management and will be used to inform management decisions.

ACKNOWLEDGMENTS

Funding for this research was provided by the National Science Foundation (NSF) Industry/University Cooperative Research Center SCeMFiS (Science Center for Marine Fisheries) through membership fees under the direction of the Industry Advisory Board (IAB). SCeMFiS administrative support is provided by NSF award #1266057. I would like to thank my advisor, Dr. Eric N. Powell, and Dr. Roger Mann, for their contributions to my thesis research and for their advice and support throughout my time at the Gulf Coast Research Laboratory and Virginia Institute of Marine Science. I would also like to thank my other committee members, Dr. Chet F. Rakocinski and James S. Franks for their assistance and feedback on my thesis work. I am also thankful for the guidance in shell preparation techniques provided by Chase Long, and would also like to thank Melissa Southworth for her help in shucking and sorting all of the samples.

TABLE OF CONTENTS

CHAPTER III - COMPARISON OF AGE FREQUENCY DISTRIBUTIONS 29

LIST OF TABLES

LIST OF FIGURES

CHAPTER I – BACKGROUND

Parts of the information from this chapter have been published in the Journal of Shellfish Research or have been submitted for publication to the Marine Ecology Progress Series or the Journal of Experimental Marine Biology and Ecology.

Pace, S. M., E. N. Powell, R. Mann, C. M. Long, & J. M. Klinck. 2017. Development of an age-frequency distribution for ocean quahogs (*Arctica islandica*) on Georges Bank. J Shellfish Res 36:41-53

Pace, S. M., E. N. Powell, R. Mann & C. M. Long. Submitted. Comparison of Age-Frequency Distributions for Ocean Quahogs (*Arctica islandica*) on the Western Atlantic US Continental Shelf. Mar. Eco. Prog. Ser.

Pace, S. M., E. N. Powell & R. Mann. Submitted. Two-hundred year record of increasing growth rates in the ocean quahog (*Arctica islandica*) in the western Atlantic Ocean. J. Exp. Mar. Biol. Ecol.

The ocean quahog, *Arctica islandica* (Linnaeus, 1769), is a long-lived bivalve mollusc, with a life span exceeding 500 years (Schöne et al. 2005a, Ridgeway & Richardson 2011). A pan-boreal species, the ocean quahog is distributed along both coasts of the North Atlantic basin (Merrill & Ropes 1969, Dahlgren et al. 2000, Begum et al. 2010). In the northwest Atlantic, ocean quahogs range from Cape Hatteras, NC to St. George's Bay, Newfoundland. On the northeastern side of the basin, they are found along the European coast from the Bay of Cadiz in Spain to Norway, including Iceland, the British Isles, the Faroe and Shetland Islands, and the Baltic, White, and Barents Seas (Merrill & Ropes 1969, for additional documentation of the North Atlantic range; see Brey et al. 1990, Rowell et al. 1990, Ragnarsson & Thórarinsdóttir 2002, Butler et al.

2009). Ocean quahogs grow to a maximum shell length of about 130 mm and attain a life span commonly exceeding 200 years. Current estimates have aged the oldest specimen at 507 years (Butler et al. 2013), possibly making it the longest-lived, non-colonial animal known to science (Wanamaker et al. 2008, see Wisshak et al. 2009, Titschock et al. 2010 for other long-lived examples) and certainly making it the longest-lived non-colonial biomass dominant in the marine world.

Ocean quahogs inhabit sandy, muddy, and gravelly sediments on the continental shelf, and are commonly found at depths of 25-80 m (Morton 2011), tolerating bottom temperatures up to 16° C and a salinity range between 22-35 (Schöne 2013). These sediment burrowing suspension feeders feed on phytoplankton and algae at the sediment-water interface via short, inhalant siphons (Cargnelli et al. 1999a, Winter 1978); however, at self-induced, irregular intervals, and during unfavorable environmental conditions such as periods of low oxygen, ocean quahogs burrow even deeper into the sediment typically for 1-7 days, or longer, at which point they close their shells and switch to an anaerobic metabolism (Taylor & Brand 1975a, Taylor 1976). The species is notable for its ability to tolerate long periods without oxygen (Oeschger 1990, Philipp and Abele 2010).

The ocean quahog has been a commercially important species in U.S. waters since the fishery began in 1967 (NEFSC 2009). The species supports commercial fisheries throughout much of its range (Gilkinson et al. 2005, Thórarinsdóttir & Jacobson 2005). At the historic start of the ocean quahog fishery in the U.S., most fishing effort was off Delmarva and southern New Jersey. By the early 1990's, 40% of the fishing effort shifted north of Delmarva to the south of Long Island. Landings peaked at 22,000 mt in 1992 (NEFSC 2009). In the late 1990's, fishing effort shifted to the Southern New England region. Early in the 2000's, the Long Island region became a focus area (NEFSC 2009). Annual ocean quahog landings in recent years, from 2010-2014, have ranged from about 14,000-16,000 mt. The northern shift of the ocean quahog fishery over the past few decades is in part a response to declining catch rates in the Delmarva and New Jersey fishing grounds (NEFSC 2009); however, an additional important driver is the fact that the more valuable surfclam fishery has shifted north in response to increasing bottom water temperatures (Cargnelli et al. 1999b, Weinberg 2005), and many commercial boats fish in both the surfclam and ocean quahog fishery. A small commercial fishery for ocean quahogs began in Iceland in 1995 but is limited to one fishing vessel (Thórarinsdóttir & Jacobson 2005, Thórarinsdóttir et al. 2010); the Icelandic fishery is currently artisanal and catches have been negligible since 2005.

The growth rates of ocean quahogs vary both spatially throughout the range of the stock and temporally through the lifetime of an individual. Juveniles grow rapidly typically until the onset of maturity with about 50% of these animals reaching maturity at a length of approximately 60 mm (NEFSC 2017a, Thórarinsdóttir & Jacobson 2005). Following maturity, growth is slow and indeterminate, with animals continuing to grow for as long as they live. Limited information is available about the long-term recruitment patterns of ocean quahogs throughout the range of the U.S. stock. Recruitment events are thought to be sporadic and regional, occurring one or two times every two to four decades (Powell & Mann 2005). The infrequency of recruitment and characteristically slow growth of ocean quahogs have led to concerns that these animals are susceptible to overexploitation (Thórarinsdóttir & Jacobson 2005) and that, if overfishing did occur, the recovery of the stock may be delayed considering that these animals do not reach a size that is available to the commercial fishery for several decades after settlement (Ropes et al. 1984, Rowell et al. 1990, Thórarinsdóttir & Steingrímsson 2000). Thus, it is imperative to understand population dynamics by investigating the variable growth rate and long-term recruitment trends throughout the range of the stock to alleviate management concerns of potential overexploitation.

The objective of this research was to develop age-frequency distributions for ocean quahog populations throughout the range of the U.S. stock in order to evaluate population dynamics such as growth rates and long-term recruitment trends, information that is essential to the sustainable management of this commercially valuable species. To do this, a single population from the Georges Bank region was first investigated (Chapter II) through the development of an age-length key for the population in order to generate a population age-frequency distribution to examine historic recruitment patterns. The growth rates of the five oldest individuals were also examined using three growth models. Chapter III introduces the three other populations that were studied. Population age frequencies were developed for these sites and the results synthesized with that of the Georges Bank population. Finally, Chapter IV investigates the growth of animals from all four sites, as the growth rates of these populations vary both spatially and temporally throughout the range of the stock. The knowledge gained from this research will help further understanding the life history of ocean quahogs, and will contribute to the improved management of the commercial U.S. stock.

CHAPTER II – DEVELOPMENT OF A POPULATION AGE FREQUENCY

This chapter has been published in the Journal of Shellfish Research.

Pace, S. M., E. N Powell, R. Mann, C. M. Long & J. M. Klinck. 2017. Development of an age-frequency distribution for ocean quahogs (*Arctica islandica*) on Georges Bank. J. Shellfish Res. 36:41-53.

Introduction

Although considerable information exists on the growth and physiology of *A. islandica*, limited information is available regarding recruitment; accordingly, the sustainable management of the fishery is a challenge. The ocean quahog stock is considered to be relatively unproductive. Recruitment events in ocean quahogs appear to be regional and are thought to be infrequent, with recent larger events occurring once or twice every 20-40 years (Lewis et al. 2001, Powell & Mann 2005, Harding et al. 2008, see also Witbaard & Bergman 2003, Thórarinsdóttir & Jacobson 2005). While recruitment appears to be rare in the context of the fishery, as these animals commonly exceed 200 years in age, recruitment appears to be frequent considering their longevity. Yet as a result of their slow growth, ocean quahogs do not recruit to the fishery for several decades after settlement (NEFSC 2009). Thus, any increase in stock productivity anticipated from fishing down the stock, judged to have been at carrying capacity in 1980 (NEFSC 2009), would likely be delayed due to the time lag between settlement and recruitment to the fishery (Powell & Mann 2005).

Consideration has been given to the challenge of sustainably managing such a long-lived species (Hennen 2015). The possible infrequency of recruitment suggests that ocean quahogs are vulnerable to overexploitation (Thórarinsdóttir & Jacobson 2005). The limited information available on ocean quahog recruitment, even if providing sufficient information on recent recruitment, does not lend any insight on past recruitment events and the potentially daunting time span for rebuilding, should the stock collapse, and the uncertainty of response as the species is fished down from carrying capacity urge precaution if recruitment capacity is truly limited. Improved management of the ocean quahog fishery and increased confidence in the potential of achieving sustainability is dependent upon the development of a long-term recruitment index that will provide guidance as to the frequency and significance of recruitment in ocean quahogs over the extended life span of the species.

The objective of this study was to develop information regarding long-term recruitment patterns of ocean quahogs in the Georges Bank region from the age frequency of the living population. To do so, ocean quahogs were collected from Georges Bank and aged by counting annual growth lines using photographs of a cross-section of the hinge plate of each shell. Analysis of the annual growth increments of selected individuals allowed for the assessment of growth rates using three different growth models. Information on age at length enabled the development of an age-length key, permitting reconstruction of the population age frequency, which could then be used to evaluate long-term recruitment trends.

Methods

Sample Collection

Samples of ocean quahogs were collected from Georges Bank (40° 43.66’N, 67° 48.32’W) in May 2015 using a hydraulic dredge deployed from the *F/V Pursuit* and towed for five minutes. The *F/V Pursuit* dredge is nearly 100% selective for clams 80 mm and larger, which is the size range upon which this project is focused. Two dredge tows were required to obtain a sufficient sample size; however, the second tow was taken as close as possible to the location of the first so that the same local population was assessed. The two tows were treated as one sample of the local population.

The shell length (anterior-posterior dimension) of each clam was measured (mm). The first 400 clams measured were retained for analysis. An additional 400 clams were retained that exceeded the upper 20th percentile of the size-frequency distribution established by the initial 400 so that samples for ageing contained sufficient numbers of the rarer largest individuals.

Sample preparation

Clams were shucked and the paired valves dipped in diluted bleach, rinsed in water, and air-dried overnight. Both valves (if intact) of each individual were measured (mm), labeled, and archived. A subset of about 20 clams to be aged was haphazardly selected from each 5-mm size interval present in the collection, beginning with the 80-<85-mm size class. Hereafter, the size classes will be referred to using the lower size class boundary, e.g., 80-mm for animals 80 to <85 mm. Clams were sectioned along the shell height axis as close to the origin of the umbo as possible using a modified commercial tile saw to expose the hinge region. The sectioned edge was ground and polished using a wet polishing wheel on 400-µm and 600-µm sandpaper grit, and then polished with 6-µm and 1-µm diamond suspensions on polishing pads.

The hinge region of each clam was photographed using a high definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software. This software permits photographs of the hinge region to be captured at a resolution high enough to distinguish annual growth lines without the use of a stain or acetate peel; however, many photographs were needed to produce a single continuous image of the hinge at high magnification. The individual images were stitched together automatically by the imaging software. To estimate the age for each clam, its hinge image was analyzed by annotating each annual growth line using the Object J plugin in the software ImageJ. This plugin also measures the growth increments, the distance between consecutive growth lines, which allowed for the examination of growth rates of selected individuals.

Identification of annual growth lines

The age of 156 ocean quahogs with known shell lengths was estimated from the Georges Bank region. Ocean quahogs deposit distinct annual growth lines along the hinge and along the ventral margin of the shell. The deposition of annual growth lines has been validated through mark-recapture (Murawski et al. 1982) and continuous sampling experiments (Jones 1980), as well as through stable carbon and oxygen isotope analysis (Schöne 2005a, 2005b).

Either of the growth records from the hinge plate or along the ventral margin can be used to determine the age of an individual. A disadvantage in counting growth lines along the entire valve is that many shells are damaged during the collection process and thus do not have fully intact records, and many animals with fully intact shells often exhibit growth anomalies and disturbances which inhibit accurate identification of annual growth lines. In addition, records in the hinge region can be incomplete, especially in old specimens and those that lived in a harsh environment because years of abrasion can result in erosion of the oldest growth lines near the umbo. Furthermore, during periods of extended shell closure, anaerobic glycolysis results in the production of acidic metabolites, which can result in partial dissolution of the hinge plate region (Schöne 2013). These processes can eliminate growth lines, resulting in an underestimate of an individual's age. Thus, the hinge was used for the determination of age and growth increment.

One challenge that arises when aging ocean quahogs is that sub-annual growth lines are visible in addition to annual growth lines, especially in the early years of life. These sub-annual growth lines are typically less distinct than annual growth lines, but are still clearly visible without the use of a stain or acetate peel. Harding et al. (2008) used a combination of grayscale imaging of the hinge and scanning densitometry of the image to distinguish sub-annual growth lines of lower intensity from the higher intensity annual growth lines. Based on Harding et al. (2008), sub-annual growth lines were omitted from the age count. To confirm that the sub-annual growth lines were consistently excluded, age counts performed by multiple individuals were compared, as were age estimates using the hinge plate and the entire ventral margin of the valve. Growth rates estimated for the first few decades of life, when sub-annual growth lines commonly occur, agreed with previous analyses by Jones (1980), Harding et al. (2008), and Murawski et al. (1982).

Another challenge encountered when aging ocean quahogs is the presence of closely spaced consecutive growth bands, often referred to as doublets (Butler et al. 2009). Little information is available in the literature regarding the explanation of doublets. Foster et al. (2009) claim that the doublet is generated by a growth check preceding an annual growth band and thus should only be considered a single year. In contrast, Butler et al. (2009) suggest that the doublet is generated by a year of unusually slow growth; thus, each line in a doublet should be counted as a distinct annual growth band. While ontogenetic growth rates of ocean quahogs vary from one individual to another, overall, a population of ocean quahogs inhabiting the same area should all experience the same general increases and decreases in growth rates due to environmental factors, or variations in food supply. To investigate further whether doublets should be counted as a single growth increment or two discrete annual growth increments, the annual growth lines of three randomly selected clams were counted in two different ways: with all doublets treated as a single year and counting each doublet as two years. The distance between each annual growth line in each of the aforementioned scenarios was measured and the time series of yearly changes in growth increment compared among the three individuals.

In the test scenario where all doublets were counted as a single annual growth increment, the resulting ages were underestimated considering the sizes of ocean quahogs that were collected. The latter age estimation method also produced a better fit to a general trend of increases and decreases in population growth that is expected throughout the lifetime of the three individual clams, taking into account the uncertainty that exists when identifying annual growth bands in an ocean quahog, which is likely not greater than ±5 years (Butler et al. 2013). When doublets were treated as two years, the age estimation along the hinge and the entire ventral margin did not differ by more than ±3 years, nor did it differ by more than ±3 years when age counts from the hinge region from multiple readers were compared for the same clam. For these reasons, and in consideration of the recommendation by Butler et al. (2009) that doublets should be treated as discrete annual growth bands, doublets were counted as two discrete years.

Creating the age-length key

The data for Georges Bank are composed of the shell length and age of all aged individuals. An observed population age frequency was generated by applying the probability of finding the observed ages within each 5-mm size class to the complete size frequency of shell lengths measured. To create an age-length key from the sampled individual ages-at-length, the probability of encountering every age within the size range at each site must first be established; however, this is a challenge because the range of ages within any 5-mm size class will be vastly larger than the number of individuals aged unless scores of individuals are aged in each size class. Though technically feasible, the number of aged animals required to meet standard age-length key requirements is prohibitive in practice. Even in relatively data-rich cases, the problem of missing or inadequately sampled lengths or ages within age or length classes can require estimation (e.g., Kimura & Chikani 1987, Harding et al. 2008, Stari et al. 2010).

In the sampled Georges Bank population, as an example, which is composed of animals of 80-115 mm in shell length, ages range from 54 to 198 years. Thus, a sample size of about 150 individual clams would only assign an average of approximately one individual per year assuming no duplicates in age. As shown later, the range of ages within a 5-mm size class is a substantive fraction of this entire age range; thus, any probability function established only on the basis of observed ages will likely considerably bias the probability of occurrence of any specific age because it is highly likely that animals are present in the population with ages not found among the subset of animals aged.

As shown later, the distribution of ages within a length class was typically highly skewed and relatively unpredictable from one age class to another. Thus, the problem of missing ages was attacked using an approach that did not require knowledge of the underlying distribution function. Rather, four metrics were defined for each of the sets of measured ages from the 5-mm size classes; namely, the mean age, the variance in age, the mean differential in years between consecutive ages ordered from youngest to oldest, and the variance in the mean differential between consecutive ages. For each 5-mm size class, 1,000 sets of ages were first drawn of the same number as the number of animals aged. These were drawn randomly with replacement from a range of ages established by the youngest and oldest ages in the size class expanded by the average distance between consecutive ordered ages. The observed value of each of the four considered metrics was compared to the distribution of metric values from the 1,000 drawn sets. The probability of the observed value occurring by chance could thereby be established. The 1,000 simulated age groups were then searched to identify individual sets that fell within a 10th percentile of the position of the observed age group for all four metrics. These select age groups were taken as equally valid estimates of the probability of age within the 5-mm size class. Minimally, 10 such age groups were retrieved and these plus the observed age group were used to construct the probability of age at length for each 5-mm size class.

Considering the small sample size in comparison to the age range, a reasonable concern is whether an increased sample size would change the population age-frequency distribution significantly and, as well, whether the simulated expansion of age-at-length data as previously described provided a realistic probability distribution. To address this matter, 20 additional animals were aged in the 100-mm size class. This size class was chosen because it had the age distribution least expected to occur by chance based on the four considered metrics. The original set of individuals had ages from 73 to 198 years old. Two questions were posed. First, how many of the ages in the new set were not represented in the old set? The expectation is that this number would be large, indicating that the probability of missing ages in the set of animals aged in any 5-mm length class was high, thus requiring application of a method to fill in missing ages. Second, did the second set of ages differ significantly in distribution as measured by the four afore-defined metrics from the first set? The expectation is that the first set was adequate to establish the age distribution function within a 5-mm size class with sufficient accuracy to be used to estimate the age distribution for the age-length key as previously described. A permutation test was used in which 1,000 sets of ages were drawn with replacement from the original set and the second set compared to the distribution obtained thereby (Noreen 1989) to evaluate the probability that the observed mean and variance of ages of the second set could have been obtained from the first. Note that the other two metrics, which depend on the difference between adjacent ages, cannot be tested using a random draw with replacement because replacement increases the number of zero differences between adjacent ages and thus biases the test. As a consequence, a variant of the afore-described test was run in which 1,000 sets of ages of a number equivalent to the original set of ages were drawn without replacement from the combined dataset and the second set of ages compared to the distribution obtained to determine if the new set represented a random draw from the total. All four metrics were evaluated using this test. In addition, a population age frequency was also established by generating the estimated ages from all measured shell lengths using the ALOG growth curve (see subsequent section) for comparison to the one generated from the age-length key.

Growth

The measurements of growth increment width, the distance between two consecutive annual growth lines, were recorded for the five oldest clams. Growth increment widths were determined through the annotation of each annual growth line using the Object J plugin, which provides measurements in units of pixels. The total shell length of an individual divided by the cumulative sum of all growth increment widths allowed a conversion of pixels into mm. Three growth models (von Bertalanffy, Gompertz, and ALOG) were used to analyze the data. The first two, both frequently evaluated as growth models for shellfish (e.g., McCuaig & Green 1983, Solidoro et al. 2000, Appleyard & DeAlteris 2001, Chintala & Grassle 2001, Urban 2002), were calculated as:

$$\text{von Bertalanffy: } L_t = L_\infty \, (1 - \exp(-K(t - t_0))), \qquad (1)$$

and

$$\text{Gompertz: } L_t = L_\infty \exp(-\exp(-K(t - t_0))), \qquad (2)$$

where L_t (mm) is the shell length at age t (years), L_∞ is the asymptotic shell length, K is the growth coefficient, and t_0 is the hypothetical age when shell length would be zero. The third growth model,

$$\text{ALOG: } dL_t = \frac{1}{\sqrt{f(t-c)^2 + a}}, \qquad (3)$$

was developed for species with continuous indeterminate growth (Tanaka 1982, Tanaka 1988). By integrating equation (3) over age, the relationship between age and shell length for ocean quahogs was described using the 4-parameter ALOG growth model (Eq. 4):

$$L_t = \mathrm{d} + \frac{1}{\sqrt{\mathrm{f}}} \log(2\mathrm{f}(\mathrm{t} - \mathrm{c}) + 2\sqrt{f^2(\mathrm{t} - \mathrm{c})^2 + \mathrm{fa}}) \quad (4)$$

where *a* is a measure of the maximum growth rate, *c* is the age at which the growth rate reaches a maximum, *d* is a parameter that shifts the body size at which growth is maximum, and *f* is a measure of the rate of change in growth rate (Tanaka 1988). The ALOG curve was fit using a two-stage fitting process, first by fitting the length data to the ALOG length equation (4), and then by fitting both the change in length (Eq. 3) and length (Eq. 4) relationships simultaneously starting from the solution of the length fit.

Results

Growth

Length-at-age was fit with three models; the von Bertalanffy and Gompertz curve fits are shown in Figure 1. Parameter estimates and associated standard errors are shown in Table 1. The observations of growth increment width-at-age and length-at-age also were fit to the ALOG growth curve equation (Figure 2). Note in Figure 2 that the curve fits both the growth increment relationship and the relationship of length at age. Note also that the latter fit includes both the rapidly ascending early portion of the animal’s life and also the extended period at older age of slow but continuous growth. Importantly, the ALOG curve retains a rational ascending limb at old age that cannot be accomplished by the asymptotic von Bertalanffy and Gompertz curves. In addition, the ALOG curve provides rational ages early in life that likewise fail to be accurately fit by the other two growth models. The parameter estimates for the 4-parameter ALOG equation are: a =

0.044932; c = 2.007; d = 92.7737; f = 0.0023936. The mean and standard deviation of the residuals to the growth increment curve (Figure 2, left) are -0.0516 ± 0.4172. The same analysis for the integrated 4-parameter expression for age versus length (Figure 2, right) yields $1.34 \times 10^{-6} \pm 3.731$. Perusal of Figure 2 (right) shows that the individual growth curves are bimodally distributed about the fitted line at old age. Thus the mean of the residuals tends to be small while the standard deviation tends to be large. The origin of this bimodality remains uncertain, although the possibility that male and female ocean quahogs grow at different rates cannot be discounted (Ropes et al. 1984, Steingrímsson & Thórarinsdóttir 1995).

Age dynamics within size class

The size-frequency distribution from all individuals collected in the two dredge hauls is shown in Figure 3. The shell lengths for 2,780 individuals were recorded. Of these measured clams, 156 individuals ≥80 mm in length were aged. Ocean quahogs from this area ranged in age from 54 to 198 years old, with animals growing to a maximum length of 116 mm. The observed ages of the sampled animals are shown in Figure 4. These clams have a large age range within each size class (Figure 5), with the smallest age range of 59 years and the largest age range of 125 years within a 5-mm size class. Similarly, a large variation in size exists at age throughout much of the observed age range (Figure 4). Thus, the relationship between age and size is highly variable even within narrow age and size categories.

Table 2 shows the statistics for each of the four metrics used to determine if the originally sampled ages were randomly distributed within each size class. Non-random test statistics are shaded. The 100-mm size class is the most non-random with three out of four test metrics diverging significantly from random; this is also the size class which had an age range spanning 125 years. The 80-mm size class was the best behaved, not surprisingly as differential growth rates at age should accrue over time and, thus, should introduce increasingly non-random distributions into the larger size classes. Interestingly, it is an intermediate size class that shows the largest deviance from randomness, despite the expectation for the largest size class to be the most non-random.

A second group of animals in the 100-mm size class was aged. Table 3 shows the estimated ages of the original 20 clams and the resampled age estimates for the second set of 20 clams. Eighteen clams in the second set had ages that were not present in the original set of 20 ages. This confirms the expectation that many animals would need to be aged in order to define the age-length relationship solely from a set of observed lengths and ages.

The statistics listed in Table 2 accordingly were used in the simulation of 10 additional age groups for each size class to identify groups that fell within the shown percentile of the position of the observed age group for all four metrics. The 10 selected simulation groups were used in addition to the observed age group to construct the probability of age at length for each 5-mm size class.

Evaluation of sample size

A series of permutation tests were run to determine whether the second set of 20 clams aged from the 100-mm size class were significantly different from the first set. In the first case, the two datasets were directly compared using the observed mean and variance of ages. The two data sets were not significantly different by either metric. In the second group of tests, the likelihood that the second group of ages was a random draw from the combined group was considered. Results indicate that none of the four metrics were significantly different; that is, the second group of ages was a random draw from the combined dataset (Table 4). The lack of statistically significant differences indicates that the age distribution of the first 20 clams sampled does not differ from the second set of 20 clams and suggests that the number of animals aged is sufficient to determine the distribution function for ages within a length class. Additionally, the simulated age groups can be expected to also be representative of that distribution function.

Age-length key

The age-length key (Table 5) was generated by establishing the age probability for each known size class, based on the observed age group plus the 10 simulated groups that were taken as valid estimates of the probability of age within the 5-mm size class. For ease of presentation, the key is shown using 5-mm length classes and decadal age classes. Calculated age frequencies shown subsequently, however, used individual ages rather than a decadal age class. Table 6 shows the estimated number of individuals at age obtained from the two 5-minute dredge tows, and was generated by applying the total number of individuals measured (Figure 3) to the probabilities from the age-length key. Shaded boxes indicate ages with the highest probability of occurring. Table 7 shows the observed age frequency, based only upon the 156 sampled ages, which results in many ages being apparently absent from the population. Earlier analysis of the second set of animals in the 100-mm size class demonstrates the invalidity of the expectation that this many ages are truly absent. Although the observed and generated age frequencies differ, both show some of the largest numbers of individuals with ages in the late 60’s and between 86-96 years old. The simulated dataset suggests that the peaks of animals at older ages in Table 7 are unlikely, in that many more potential ages exist than could be filled even by one animal given the sample size. Table 6 suggests that the numbers at older ages are more evenly distributed and this expectation is reinforced by Table 3.

Population age frequency

The population age-frequency distribution for Georges Bank is shown in Figure 6. This figure was generated from the data in Table 6. The age structure consists of a smattering of animals older than 125 years of age, a much larger number of animals in the 100-125-yr age range, and an even larger number of animals in the 65-100-yr age range (Figure 6). The population age frequency indicates that ocean quahogs have been present in this region of Georges Bank for about 200 years, since the early 1800’s. Given that the oldest animal is substantively younger than the oldest known age for this species and given that the subsampling of the catch included a focus on ageing a subset of the largest animals which averaged modestly older than the smaller individuals (Figure 5), it is likely that had many animals exceeding 200 years of age been present, at least a few would have been aged. Thus, occupation of this site, while possibly earlier than the birthdate of the oldest animal, was at least very limited in comparison to the age potential of this species.

Assuming that the mortality rate did not vary substantively over the time span represented by the aged animals, the population size remained low for an extended period of time after initial colonization, approximately 70 years, after which the population began to increase in size. This increase began approximately 125 years ago, around the 1890’s. Proliferation of the population occurred rapidly over a 5-10 year period reaching a stability point around 1900, a relatively short period of time considering the longevity of these animals. The population expansion occurred in two phases with the second phase beginning circa 1915 and approaching a second and higher asymptote circa 1920; thus over an approximately 30-year period, the population expanded dramatically from a minimal level to its present-day robust population density. After 1920, the population apparently stabilized, with recruitment approximately balancing mortality through the mid-1950s, whereupon the record of measured ages ceases to effectively describe the population age distribution. That is, the decrease in the number of individuals younger than about 65 years is due to the artificial truncation of the data set at shell length ≥80 mm, not to a reduction in recruitment or an increase in mortality. Aging smaller animals would fill out the younger ages, but the problem of age truncation would persist unless animals of all sizes, including young of the year, were aged.

Comparison to ALOG

The population age frequency was also generated using the age estimated from the ALOG curve for each measured length (equation 4) (Figure 7). For lengths where the ALOG curve predicted multiple ages, that is, for cases where a 1-mm increase in length covered more than a single year increment in age, the total number of individuals was apportioned evenly over the predicted ages for each length. The age-frequency distribution generated from the ALOG curve can be compared to the previously generated distribution (Figure 6). Both age-frequency distributions have a similar general shape but differ in substantive ways. In particular, the ALOG approach over-predicts the abundance of old animals and expands the age range well beyond the oldest observed animal. The two distributions differ significantly (Kolmogorov-Smirnov two sample test, $P < 0.05$). Thus, the ALOG curve cannot be used to predict the age structure of the

Georges Bank population. Perusal of the age-length key (Table 5) in comparison to Figure 2 showing the ALOG growth model shows that the variability inherent in the population in the age at length at large lengths and old ages is primarily responsible for the failure of the growth model to provide sufficient information to generate a population age frequency.

Discussion

Growth

Historically, ocean quahog growth has been modeled using the von Bertalanffy growth curve (e.g., Sager & Sammler 1983, Brey et al. 1990, Steingrímsson & Thórarinsdóttir 1995, Thórarinsdóttir & Jacobson 2005). The von Bertalanffy growth curve, as well as other growth curves such as the Gompertz curve, lack an inflection point and approach an asymptote (Karkach 2006). The ALOG growth curve (Tanaka 1982, Tanaka 1988) was designed to model an early lag and initial period of exponential growth followed by an indefinite period of continuing albeit perhaps declining indeterminate growth; this type of growth is characteristic of ocean quahogs. The relationship was originally developed for application to the lantern clam *Laternula anatina*, but it has been more widely applied to model the growth of sea urchins (Ebert et al. 1999, Ebert & Southon, Flores et al. 2010). Note that the relationship proves unrealistic for animals where growth asymptotes as it cannot be used to estimate infinite size (Rogers-Bennett et al. 2007)

The ALOG growth curve is the best descriptor of growth in ocean quahogs. This is not surprising considering that the growth of ocean quahogs matches the characteristics of the ALOG growth curve. Growth in ocean quahogs is not asymptotic and, thus, asymptotic growth models often fail to fit growth at old age. While the von Bertalanffy curve has frequently been used to describe ocean quahog growth in the past, both this curve and the Gompertz curve describe an animal that grows to a maximum size, hence the asymptote that both of these curves approach. Unlike most animals, ocean quahogs have the capacity to live for centuries and continue to grow indefinitely, albeit at a very slow rate.

Moreover, the ALOG growth curve is characterized by a relatively strong change in slope that occurs at an age of approximately 20 years and a size of about 60 mm on Georges Bank. Whether this change in growth rate marks sexual maturity is unknown, but the size demarcation is consistent with the maturity curve presented by Thórarinsdóttir and Jacobson (2005) and Thórarinsdóttir and Steingrímsson (2000), relatively consistent with Ropes et al. (1984), and somewhat larger than inferred from Rowell et al. (1990). Boukal et al. (2014) describe an analogous growth model with similar characteristics dependent upon a change in energy allocation at maturity. The metabolic energetics of ocean quahogs beyond the interestingly lower metabolic rate (Begum et al. 2009, Ungvari et al. 2013), the extended capacity for anaerobiosis (Oeschger 1990, Philipp & Abele 2009), and the tolerance to sulfide exposure (Butterworth et al. 2004) are too poorly known to permit a complete metabolic explanation for the growth curve.

The tendency to model the growth of the ocean quahog using asymptotic growth stems from the general agreement of these models with the central more or less two-thirds of the growth trajectory; however, neither the von Bertalanffy nor Gompertz curve can capture the exponential growth exhibited by juvenile ocean quahogs unlike the

ALOG curve nor can they capture the continual growth at old age (e.g., Steingrímsson & Thórarinsdóttir 1995, Ridgway et al. 2012).

The age-length key and generation of a population age frequency

The 100-mm size class had the most unusual age distribution, spanning an age range of 125 years. This size class also had the most non-random distribution with three out of four statistically significant test metrics. Based on these considerations, the 100-mm size class was chosen to sample an additional 20 clams to determine if the age distribution of the 20 resampled clams significantly differed from that of the 20 original ages. A series of permutation tests revealed no significant differences between the two groups of aged animals in the four metrics chosen to evaluate the age distribution within a 5-mm size class. This suggests that a sample size of 20 individuals per 5-mm class is sufficient to represent the dispersion of ages present in that size class, although not sufficient to represent all ages likely to be present. Given this result for the size class with the most irregular age distribution, encompassing a range of 125 years within a single 5-mm class, a reasonable assumption follows that the other size classes with a sample size of 20 individuals comprising smaller age ranges with less extreme age distributions are also representative of their respective age distributions.

The number of new ages in a second set of 20, however, confirms the expectation that a large number of aged animals per size class would be required to directly assess the probability of age at size within a size class. Many ages present in the 5-mm size class are not identified in a single sample of 20 individuals. Thus, obtaining a representative age-length key requires assumptions of the underlying age distribution function within a size class, unless one is prepared to age many hundreds of clams. Two options were compared. In one case, ages were estimated from the ALOG growth curve of Tanaka (1982). In a second case, a simulation approach was used that required that a set of 20 individuals meet four criteria in comparison to the observed set, a mean age close to that observed, a variance in age close to that observed, a mean age differential between pairs of individuals ordered by age close to that observed, and a mean variance in the age differential close to that observed.

In the case of estimating ages from the ALOG growth curve, the ages predicted do not align with those produced by the observed age frequency. This is due to the high variability in size at age (Figure 2), especially for the older animals, so this method cannot be used to predict the population age frequency of ocean quahogs. The simulation approach produced a distribution similar to the age frequency that is produced from only the observed ages. The simulation approach distributes individuals in the observed age frequency to ages that were absent due to the low sample size. A direct test of the assumption that many ages likely to be present were not observed demonstrated the verity of this expectation, as shown in Table 3 where only two ages in the second dataset were present in the first. Thus, the simulation approach likely provides a more realistic age distribution among all ages within the observed age range.

The age frequency of a Georges Bank population – implications

As the last surviving member of the family Arcticidae, ocean quahogs have inhabited areas along the continental shelf of the North Atlantic basin and adjacent European seas since the Late Mesozoic (Morton 2011). Considering that these animals have been present along the boreal North Atlantic shelf for such an extended period of time, it is perhaps surprising to find animals no older than about 200 years on Georges

Bank, suggesting colonization sometime very early in the 1800's. One possible hypothesis is that the establishment of the ocean quahog population on this portion of Georges Bank co-occurred with the ending of the Little Ice Age, which is thought to have ended sometime in the early to mid-19th century (for more on the Little Ice Age, see Schöne et al. 2005b, Mann et al. 2009, Cronin et al. 2010). During the Little Ice Age, bottom water temperatures would have been much colder on Georges Bank than observed today. As the end of the Little Ice Age approached, warming waters would have permitted movement of the ocean quahog population into the region of Georges Bank sampled for this study. Recent examination of the distribution of ocean quahog shells on Georges Bank lends credence to this scenario as shells, but no live animals, are found at shallower depths on the bank today (Powell et al. submitted), in a region that arguably would have had more appropriate bottom water temperatures for ocean quahogs in earlier times.

Regardless, once the initial recruits were established where ocean quahogs now live on Georges Bank, the population remained at low levels for about 70 years, evident from the long tail in the population age frequency (Figure 6). Taking the analogy of a species invasion for this colonization event, time lags after initial colonization are not uncommon (Diederich et al. 2005, Facon & David 2006, Karatayev et al. 2011). The time lag from a small population size until the propagation of the population is likely a result of delayed maturity in ocean quahogs. As ocean quahogs do not reach maturity for several decades following settlement, the population perforce would have to remain small in size for many years, unless recruitment from outside the region increased. Evidence suggests that it did not. Of course, one cannot discount the possibility that the occupation remained limited because the environment remained suboptimal until the late 1800s.

The rapid expansion of the population late in the 1800s suggests that one of several events occurred. Once enough animals reached maturity, a local Allee effect might have been overcome, permitting much enhanced recruitment. Fertilization efficiency can be expected to be poor in sparse populations of relatively immobile molluscs (Shepherd et al. 1998, Hodgson et al. 2007, Luttikhuizen et al. 2011). Alternatively, increased water temperatures or a change in food supply might have permitted increased spawning and enhanced survivorship to maturity (Hofmann et al. 1992, Munroe et al. 2013, Svensson & Marshall 2015). Less likely, perhaps, but still possible given the extended larval life span (Lutz et al. 1982), increased recruitment from outside the region may have occurred. The latter is not consistent with the limited larval connectivity of Georges Bank with external regions observed today (Zhang et al. 2015), but such connectivity may not have been required if ocean quahogs occupied a shallower portion of the bank in the 1800s.

Once the population expansion occurred in the late 1800s, the population rapidly approached an asymptote and stabilized, suggesting that the population probably reached carrying capacity. This is supported in the literature, as ocean quahog populations in the Mid-Atlantic were considered to be at carrying capacity prior to the beginning of the fishery in the late 1960's (NESFC 2009) and the stock on Georges Bank effectively has never been fished. The rapid population expansion, then, encompassing about 30 years, is not inconsistent with molluscan population dynamics (Carlton et al. 1990, Zolotarev 1996, Brandt et al. 2008), but is surprising given the population dynamics of many long-lived species, and perhaps counterintuitive with the lower metabolic rate of this species in comparison to other bivalves (Begum et al. 2009, Ungvari et al. 2013). As the population stabilized early in the 1900s, recruitment was essentially continuous, though low enough to balance mortality. Currently the ocean quahog stock is considered to be relatively unproductive, with literature suggesting that the recruitment rate is low and infrequent (Powell & Mann 2005). This type of recruitment is characteristic of a stock that is expected to be near carrying capacity, wherein recruitment is in balance with the low mortality rate characteristic of a long-lived species. Nonetheless, the record of colonization on Georges Bank suggests that the species is a capable and rapid invader once environmental conditions are met and once the initial restriction on spawning success produced by low population density and slow growth to maturity is overcome.

The age-frequency distribution bears many similarities to the one presented by Ridgway et al. (2012) for the Belfast Lough, Northern Ireland and by Steingrímsson and Thórarinsdóttir (1995) for Iceland. Both Ridgway et al. (2012) and Steingrímsson and Thórarinsdóttir (1995) observe an approximately 100-yr period of low abundance beginning about 200-220 years BP, followed by a rapid rise in numbers at age over an approximately 20-year period. The subsequent record also asymptotes at what might be interpreted as carrying capacity. Ridgway et al. (2012) record only minor breaks in what is a generally consistent recruitment record over the time span represented by the age frequency, also similar to our results. Steingrímsson and Thórarinsdóttir (1995) document less consistent recruitment with what might be considered broad age classes, although the overall pattern of recruitment as determined from abundance at age remains similar.

Whether this type of colonization record is typical of ocean quahogs is unclear, but the similarity between the three sites, well separated in space, poses an interesting possibility.

CHAPTER III - COMPARISON OF AGE FREQUENCY DISTRIBUTIONS

This chapter has been submitted for publication to Marine Ecology Progress Series.

Pace, S. M., E. N. Powell, R. Mann & C. M. Long. Submitted. Comparison of Age-Frequency Distributions for Ocean Quahogs (Arctica islandica) on the Western Atlantic US Continental Shelf. Mar. Eco. Prog. Ser.

Introduction

Results of Chapter II suggest that recruitment on Georges Bank has been nearly continuous since the late 1800's, though at low levels to balance the low mortality characteristic of long-lived species, as the stock is considered to have been at carrying capacity since 1980 (NEFSC 2009, NEFSC 2017b). Yet, the size at which ocean quahogs fully recruit to the fishery is not reached until several decades following settlement (Ropes et al. 1984, Rowell et al. 1990, Thórarinsdóttir & Steingrímsson 2000); accordingly, an increase in stock productivity, the expected result of fishing down a stock from carrying capacity, would not be evident to the survey gear for many years (Powell & Mann 2005). This poses a problem for fishery management because long-term recruitment potential cannot be gleaned from the recruitment index obtained over the history of the survey time series which extends back a mere 35 years. To better define the characteristics of a sustainable ocean quahog fishery, which includes understanding the time line for rebuilding should overfishing occur and the sensitivity of the stock to potentially decadal or longer periods of low recruitment, development of a long-term recruitment index is necessary. As described in Chapter II, such data are needed to inform fishery managers of the frequency and significance of recruitment events in ocean quahog populations throughout the range of the stock.

In addition, recruitment rates for long-lived species are generally thought to be inherently low. Broodstock-recruitment relationships for long-lived finfish often show low steepness, a characteristic of a species with limited recruitment capacity and an extended time frame for population recovery following a decline in biomass (Goodwin et al. 2006, Mangel et al. 2010). The same may be true for many long-lived invertebrates, although documentation is more limited (e.g., Peterson & Summerson 1992, Peterson 2002). Indeed, broodstock-recruitment relationships are rarely reported (e.g., Hancock 1973, Honkoop et al. 1998, Kraeuter et al. 2005, Powell et al. 2009). Often, recruitment rates are low despite high fecundity due to larval and post-settlement mortality (e.g., Thorson 1950, Ólafsson et al. 1994, van der Meer 2003), but Allee effects can also be present (Kraeuter et al. 2005). For ocean quahogs, the time necessary to build a population to carrying capacity after initial colonization or to rebuild a population after overfishing and the ability of the population to remain at carrying capacity through years of variable recruitment and mortality is extremely poorly known. Ocean quahogs, being extremely long-lived and certainly the most successful of the extremely long-lived non-colonial marine invertebrates, offer a particularly interesting opportunity to study the population dynamics of recruitment during population expansion and when at carrying capacity. Indeed, results from the Georges Bank population suggest that recruitment capacity is high, but scarcely evident at carrying capacity where only limited recruitment is necessary to balance the low natural mortality rate characteristic of the species.

The objective of this study was to evaluate long-term recruitment patterns of ocean quahogs from three sites throughout the Mid-Atlantic, and to compare these patterns to that of the Georges Bank population previously described (Chapter II) using the age frequencies of the existing populations. The approach used includes estimation of the age of individuals by counting annual growth lines using photographs of a cross-section of the hinge plate, followed by development of age-length keys for each site from the observed ages at length. These then were used to reconstruct the population age frequency from which an evaluation of long-term recruitment patterns could be deduced.

Methods

Sample collection

Ocean quahog samples were collected from New Jersey and Long Island from the *F/V Christy* in March 2015; samples from Southern New England and Georges Bank were collected in May 2015 from the *F/V Pursuit* (Figure 8). All samples were collected using hydraulic dredges towed for five minutes. Ocean quahogs with shell lengths (anterior-posterior dimension) ≥80 mm were targeted by this project, as the sampling gear is nearly 100% selective for this size range (NEFSC 2017). All sites except the Southern New England site required multiple tows in order to obtain sufficient sample sizes; however, all additional tows were taken from as close to the same location as possible so that each sample comprised animals from the same local population.

To ensure that each sample contained an adequate number of the largest animals present in the populations, two collections of about 400 clams each were made at each site. In the first collection, the shell length of all 400 clams was measured and all clams were retained. For the second collection, all shell lengths were measured but only clams in the largest 20th percentile of the size-frequency distribution as determined by the first collection were retained.

Sample preparation

Shucked clams were dipped in diluted bleach, rinsed in water, and air-dried. Intact valves were measured again, labeled, and archived. At each site, a selection of approximately 20 clams from each 5-mm size class was haphazardly chosen from the collection, starting with the 80-mm size class through the maximum available size for each site.

Each clam chosen to be aged was sectioned, ground, and polished (see details in Chapter II). The hinge plate of each clam was photographed using either a high definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software or a high definition Olympus America microscope camera using Olympus MicroSuite software. Neither camera could capture a single image of the hinge plate at a magnification high enough to discriminate annual growth lines; multiple images of the hinge were required to produce a complete hinge image. The Olympus cellSens microscope imaging software automatically stitched images of the hinge together; the hinge photographs taken using the alternative software were stitched together using the open source software ImageJ (FIJI) to create a complete image of the hinge section. Both cameras provided images at a resolution sufficient to distinguish annual growth lines without the use of acetate peels or staining methods. To estimate the age for each clam, its hinge image was examined and each annual growth line annotated using the Object J plugin in the software ImageJ (Figure 9).

Creating age-length keys

As shown in Chapter II, the range of observed ages for a sample size of less than 200 individuals at a sample site greatly underrepresents the entire age range present in a population. Consequently, estimating the probability of age at length based only on observed ages likely biases the probability of any age occurring at a given length; in particular, some ages present in the population are not observed. At each site, the age distributions were typically right-skewed within each 5-mm size class. That is, animals of younger age had a higher probability of occurrence than animals of older age, and a long tail comprising the rarer and much older animals was present. To address the problem posed by unobserved ages within the observed age range without having knowledge of the underlying age distribution within each size class, four metrics were defined for each set of ages within each 5-mm size class; namely, the mean age, the variance in age, the mean differential in years between consecutive ages ordered from youngest to oldest, and the variance in the mean differential between consecutive ages. Sets of ages were simulated within each 5-mm size class using a Monte Carlo routine, and at least 10 individual sets that fell within a 10th percentile of the position of the observed age group for all four metrics were selected and considered valid estimates of the age probability in addition to the observed group. These age groups were used to construct the probability of age at length within each size class (for further details on the methodology used, see Chapter II).

To investigate the representativeness of the set of 20 animals aged per 5-mm size class, a size class with a particularly skewed distribution was chosen from each site. This was a size class that was significantly different from a random draw of ages within the observed age range; that is, a size class with the age distribution least likely to occur by chance based on the four defined metrics previously described. An additional 20 animals were haphazardly chosen from the original set of animals obtained that fell within that size class. These animals were aged. This second set of ages was compared to the first set using a permutation test in which 1,000 sets of ages were drawn without replacement from the combined dataset and the second set of ages was then compared to the distribution obtained from the probabilities of the four metrics to determine the representativeness of the second set of ages and, by inference, the additional 10 sets of simulated ages (Noreen 1989).

Cases in which the second age distribution represented a random draw from the combined dataset supported the assumption that a sample size of 20 individuals within each size class was sufficient to represent the age distribution. For cases where the second set did not represent a random draw from the combined dataset, the combined dataset was resampled again 1,000 times, each selection of 20 individuals again evaluated using the permutation test, and the probability of each metric recorded. In this way, the likelihood of the original second set being fairly drawn from the combined dataset could be evaluated. For example, if the original second set of 20 was significantly different from the first for a given metric and that outcome occurred only a few times out of the 1,000 independently drawn sets of 20, this analysis would suggest that the age distribution of the second set drawn was highly unlikely to occur again by chance if 40 different clams had been aged. To further investigate the effect of significant differences in age distribution between two sets of 20 individuals from the same size class, two population age frequencies were generated, the first using the age estimates from the original sample only; the second using the ages from the resample. A Kolmogorov-Smirnov two-sample test (Daniel 1978) was run to determine if the two population age-frequency distributions differed significantly.

Results

Age and length dynamics

The size-frequency distributions obtained from the measurement of all individuals retained by the dredge at each site are shown in Figure 10. The total number of clams measured was 2,448 (New Jersey), 2,443 (Long Island), and 2,453 (Southern New England). Of these measured clams, 189 individuals ≥80-mm were aged from New Jersey, 154 from Long Island, and 118 from Southern New England.

The distribution of observed ages at length for ocean quahogs from each site is shown in Figure 11. Within each 5-mm size class, ocean quahog populations exhibited a large age range (Figure 12). The youngest clam sampled from New Jersey was 24 years old; the oldest 220 years, covering an age range of nearly 200 years. The largest animal aged was 125-mm. Clams from Long Island ranged in age from 44 to 248 years. The largest animal aged was 115-mm. Clams from Southern New England covered a narrower age range from 73 to 172 years old. The largest animal aged was distinctly smaller than at other sites at 105-mm. As reported in Chapter II, clams from a Georges Bank site ranged from 54 to 198 years, with the largest animal 116-mm in length.

A large size range at age also exists throughout most of the observed age range at all sites (Figure 11). That is, the age and length relationship for market-size ocean quahogs at each of these sites is highly variable whether described in terms of age at length or length at age. Moreover, at all sites, the intermediate size classes displayed the largest age ranges. Ages in the 95-mm size class from New Jersey spanned 108 years. Long Island had the largest age range of 188 years in the 95-mm size class. In the Southern New England population, ages spanned 93 years in the 90-mm group.

The test statistics for each metric used to identify whether the sampled ages within each size class were randomly distributed are shown for each site in Table 8. Shaded boxes indicate cases where the distribution of observed ages was unlikely to be obtained from a random draw of ages within the observed age range. As evident in Table 8, size classes with the most non-random distributions varied throughout the size-class range. In New Jersey, the 90-mm and the 115-mm size classes had the most non-random age distributions, which might have been anticipated considering the old-age outliers present in both groups (Figure 12). The Long Island population provided the most non-random distributions, with three of four metrics significantly non-random in the three smallest size classes, whereas the two largest size classes did not diverge from a random distribution in any metric. The Southern New England population had one size class (90-mm) with three of four metrics significantly diverging from random, with the most non-random distribution coinciding with the 5-mm size class with the largest age range. Chapter II describes a similar pattern in a Georges Bank population in the 100-mm size class, which exhibited the largest age range of 125 years, with three of four significantly non-random metrics.

Based on the statistics shown in Table 8, 10 age groups having a similar age distribution pattern were obtained as simulated datasets. These distributions retained the statistical characteristics for the four metrics in that they fell within the shown percentiles and were used in addition to the observed age dataset to establish the probabilities for age at length within each 5-mm size class.

Representativeness of aged subsets

Based on the statistics shown in Table 8 and Figure 12, a 5-mm size class with a highly skewed age range was chosen from each site and an additional 20 ocean quahogs were aged to evaluate the representativeness of the original 20 aged animals. Size classes with additional animals sampled were as follows: 95-mm (New Jersey), 90-mm (Long Island), and 90-mm (Southern New England). Table 9 shows the ages for the original and resampled set of animals from each site. Analyses from the Georges Bank population reported in Chapter II are also included. Shaded boxes indicate cases where an age present among the resampled 20 individuals was also present in the original set of ages. At all sites, the second set of individuals contributed only a few duplicate ages found also in the first set. Southern New England had 14 individuals in the second set of animals with ages that were not found in the original set. In New Jersey, 15 of 20 ages were present in the second set but not in the first set. The second set of 20 individuals aged from Long Island had only a single animal with an age also present in the first set; 19 of the 20 resampled ages were not found in the first set of animals. As reported in Chapter II, only two ages were found in both datasets for a Georges Bank site. Thus, at all sites, the addition of a second set of 20 animals added a large number of ages that were not represented in the first set of ages, confirming that many more animals would need to be aged in order to establish an age-length relationship based solely upon observed ages and lengths.

For each site, a permutation test was run to determine whether the distribution of age estimates from the resampled set deviated significantly from that of the combined set of ages. At two of the three sites, none of the four metrics were significantly different;

that is, the resample dataset could be obtained as a random draw from the combined set of ages (Table 10). This was also true for the Georges Bank site. The absence of test metrics diverging from random at the Long Island and Southern New England sites suggests that the age distribution derived from the first 20 animals aged adequately represented the distribution function for the age range within that 5-mm length class. As the analyzed size classes were chosen because the age distributions were ones showing significant deviations from a random distribution of ages, by inference, the age distributions for the remaining size classes are likely also to be representative.

In contrast to the other three sites, three of four test metrics for the resample differed significantly from the combined dataset for the New Jersey population (Table 10). This suggests that the first sample of 20 did not sufficiently describe the age distribution within this size class. Perusal of Table 9 shows that the primary difference between the two datasets is that the resample contains many ages falling within a large age gap (116 to 153 y) in the first set. These two datasets came from the same group of clams, each chosen haphazardly from the group. To further examine this issue, the combined set of 40 was randomly split in half 1,000 times and the permutation test run each time to evaluate the probability of obtaining a split providing two datasets as deviant as were the observed two. The set of statistical comparisons for the 1,000 divisions was examined to evaluate the likelihood of the outcome initially observed. For the comparison of the observed mean, the probability of an outcome as unlikely as observed occurred in only two out of 1,000 cases. For the observed variance, an outcome as unlikely as observed occurred in only three cases in 1,000. For the observed variance in the differences obtained from the set of ordered ages, an outcome as unlikely as observed occurred seven times out of 1,000. These results suggest that obtaining the observed split from the set of 40 aged animals is statistically highly improbable. By inference, one would assume that a second set of 20 drawn from any of the remaining 5-mm size classes would demonstrate a selection of ages diverging in detail from the original set as shown in Table 9, but not diverging in the distribution function for that size class. Inasmuch as it was infeasible to age several scores of animals within each size class from each population due to the time required, even using the advanced camera technology employed in this project, and because at the other three sites, 20 animals sufficiently described the age distribution of the most extreme 5-mm size class, for the purposes of this study, 20 animals within each 5-mm size class was taken as an acceptable sample size to describe the dispersion of ages within a 5-mm size class.

Age-length keys

Age-length keys for New Jersey (Table 11), Long Island (Table 12), and Southern New England (Table 13) were generated by establishing the probability for each age within each size class, based on the observed age group plus the 10 simulated age groups for each 5-mm size class. For simplicity of presentation, each key displays decadal age groups and 5-mm size classes; zero probabilities in the tables indicate the absence of animals at that size and age given the sampling constraints. Population age frequencies shown subsequently, however, were obtained using the probabilities of each observed age in each 5-mm size class rather than the decadal age groups shown in Tables 11-13.

The population age frequencies are shown for New Jersey (Table 14), Long Island (Table 15) and Southern New England (Table 16). The age frequencies display the estimated number of individuals at age in the population sample obtained at each site.

The population age frequencies were generated from age-length keys that included observed ages and the 10 simulation groups. Tables 17-19 show the population age frequencies had the 10 simulated groups not been included, for comparison. The observed age frequencies clearly miss many ages that one may expect are present in the population (see Table 9) given the results of the resampled age classes (Table 9), but are absent from the observed dataset due to the small sample size.

Two additional age frequencies were generated for the New Jersey site to address the issue of significantly different results obtained from the permutation test when the resample was included, the first using only the original set of ages to represent the 95-mm size class, and the second using only the resampled ages. Significant differences between the population age-frequency distributions were not detected (Kolmogorov-Smirnov two-sample test, $D = 0.107898$, $P > 0.05$), despite the significant difference between the age distributions of the two sets of 20 age estimates for this size class. Thus, the differences in the age distributions of the two samples in the 95-mm size class did not significantly affect the population age-frequency distribution derived for this population.

Population age frequency

The population age-frequencies for all four sites, including the Georges Bank population reported in Chapter II, are shown in Figure 13. The age structure differs substantially throughout the New Jersey to Georges Bank region, which encompasses the majority of the U.S. ocean quahog stock. The ocean quahog populations at the New Jersey and Long Island sites have age ranges spanning at least 200 years. New Jersey had the youngest animals that were fully recruited to the fishery, with animals ≥80 mm as young as the low 20s, indicating that ocean quahog populations in New Jersey have the most rapid growth rate of the four sites. Compare this to the Southern New England site, where the youngest animals ≥80 mm were in the low 70s.

Table 20 displays a summary of the age structures, as well as the beginning and ending of the period over which the populations expanded in size, including data from Chapter II. Unlike the three other sample sites, the New Jersey population does not display a particularly long tail of low numbers of older animals on the right side of the distribution. A few animals over 200 years old were present, but the oldest relatively common animals recruited circa 1835, with the population expanding in size relatively continuously from 1855 until approaching an asymptote around 1900 when the population apparently stabilized. The population consists of a small number of animals over 140 years, a larger number of animals between 100-140 years, and the largest number of animals less than 100 years. An extended period of relatively low recruitment occurred from 1950-1965. The decrease in number of ocean quahogs <25 years is due to the artificial truncation of the dataset at shell length 80 mm, not to a reduction in recruitment or an increase in mortality. All sizes including young of the year would have to be aged in order to completely fill out the population age-frequency distribution. This same truncation and ineluctable misleading decrease in numbers at young age occurs for all sites.

The Long Island population has the longest tail, suggesting that with the exception of a particularly large year class around 1880, the population remained small in size following establishment circa 1765 until approximately 1895. After 1895, the population expanded rapidly over about 40 years and stabilized circa 1935. The population age structure in Long Island consists of a small number of animals between

120-255 years, with the majority of the population between the ages of 40-120 years; no obvious hiatuses in recruitment exist, however.

The Southern New England site has been occupied by ocean quahogs since the 1840's, the most recently settled of the four sites. The population apparently remained small in size until approximately 1900; fifteen years later, by 1915, the population had apparently approached carrying capacity. The population consists of a large number of animals between about 70-100 years old, fewer animals between 100-115 years old, and a consistently low number of animals 115-175 years old. Recruitment hiatuses are not apparent.

As a comparison, the Georges Bank population (Chapter II) was initially colonized about 200 years ago, circa 1815, after which the population remained small in size for about 70 years, as indicated by the small number of animals older than 125 years. Around 1890, the population began to increase in size very rapidly, reaching about half of its final asymptotic state in only 5-10 years; a second population expansion occurred around 1915 and approached a higher asymptote within approximately five years. The population consists of a large number of individuals between the ages of 65-100 years, with a smaller number of animals in the 100-125 year range. Following population expansion, recruitment hiatuses are not apparent.

Discussion

Age-length keys

The population dynamics of ocean quahogs are highly variable over the species' range. For the populations on the U.S. East coast, regional variation is substantial, as is apparent from the age-length keys presented in Tables 11-13. A single age-length key cannot be used to estimate the age structure of populations from these different regions, considering the large variation in age at length and the size range of animals present. Perusal of Figure 11 demonstrates this large variability in both age at length and length at age, and the differences in these distributions at each of the three sites illustrates why a single age-length key would not result in accurate age estimates throughout the Mid-Atlantic. Consider that the youngest animal aged in New Jersey was as young as 24 years old at 80-mm, whereas the youngest animal of comparable size from Southern New England was 73 years old. Additionally, the variability in maximum shell length at each site would prohibit accurate age estimates throughout the species range; recall for example that the maximum shell length of animals aged at Southern New England was 105-mm, whereas the largest animal aged from New Jersey was 125-mm.

The development of an age-length key for ocean quahogs is challenged by the time required to age individual animals, the age range present in most populations, and the presence of individuals of many ages within a narrow size range. Moreover, the population is not composed of a few dominant year classes; indeed, dominant year classes appear to be remarkably rare; even dominant decadal recruitment events appear to be rare. This is true for the four populations reviewed here, and would appear to be true for other North Atlantic populations reported in the literature (Steingrímsson & Thórarinsdóttir 1995, Ridgeway et al. 2012). Moreover and more unfortunately, the range of ages in a narrow size class (e.g., 5-mm) is large and the dispersion of ages within a narrow size class is rarely random, often being highly right-skewed, and typically differing substantively from even the abutting lower and higher size group. As a consequence, a large number of animals must be aged from each size group to support a standard age-length key for a specific population and a large number of populations must be aged to characterize the regional metapopulation. These types of challenges are well known (e.g., MacDonald & Pitcher 1979, Mohn 2001, Stari et al. 2010), but ocean quahogs represent an extreme example of the common challenge of ageing sufficient numbers of animals to characterize the population demographic.

Consequently, any age-dependent analysis of population dynamics requires a way to estimate age at length from a sparse dataset. In this study, we utilized an approach that assumed that the age distribution function as observed in a length class from a restricted set of aged animals, 20 in this case, was sufficient to define the age distribution function for the length class. We also assumed that the set of ages observed was a small subset of the sets of ages that might be obtained that remained true to that age distribution function. We tested this in several ways by focusing on a few length classes that contained the most non-random distribution of ages across the observed age range.

For the Long Island and Southern New England populations, a comparison of the ages of the original 20 animals in the size class with the most unusual age distributions to that from a second set of 20 animals showed no significant differences in the metrics used to evaluate the age distribution. This lends credence to the argument that 20 animals sufficiently represent the age distribution within a 5-mm size class, although it does not adequately characterize all ages present within that size class within the population. The assumption follows that 20 animals also likely describes the age distribution sufficiently in age classes with smaller age ranges and more random age distributions. The same is true for the Georges Bank population (Chapter II). Whereas the significant difference between the age distributions of the original and resampled animals from the 5-mm size class chosen for the New Jersey population was concerning, the two were sufficiently divergent as to show that such a difference was a highly unlikely outcome and the results of the Kolmogorov-Smirnov test revealed that the two sets of data from the 5-mm size class did not materially affect the final population age-frequency distribution. That is, the population age frequency using the original ages did not differ significantly from the one using the resampled ages. In summary, these analyses suggest that a sample size of 20 animals sufficiently represents the age distribution within each 5-mm size class for the evaluation of general aspects of the age-frequency distribution, such as periods of curtailed recruitment, the presence of strong year classes, periods of population expansion, and the timing of initial colonization. Each of these can be estimated from this dataset at all four sites.

Details, however, are likely not clearly revealed. Whereas 20 ocean quahogs per 5-mm size class may accurately describe the age distribution, the number of new ages present in the second sample of 20 individuals (Table 9) affirms the postulate that many ages are present in any one 5-mm size class and that a large number of individuals would need to be aged to accurately identify the full number of ages present and to permit small-scale differences in the degree to which certain ages are better represented than others to be distinguished. At all of these sites, not more than 25% of a second set of 20 animals were of an age identified in the earlier set of 20. Taking the 40 animals as a whole, duplicate ages occurred in no more than five cases in any of the four 5-mm size classes sampled twice and as few as one in the Long Island and two in the Georges Bank cases. Triplicates occurred only twice, both in the Southern New England dataset.

A further note is that the additional ages obtained in the second resampling but not observed in the first sampling filled in a gap in the original dataset in almost every case, and expanded the age range at the New Jersey site and marginally at the Long Island site. Thus, for example, the second resampling from New Jersey added additional animals in the younger fraction of the age range, as would be anticipated as the relatively younger ages are disproportionately abundant in nearly all 5-mm size classes. However, the first 20 animals exhibited a large gap in ages between 116 and 153. Fully nine of the 20 resampled ages fell into this age gap. Similarly, for Southern New England, the second sampling showed a large age gap between 112 and 140. Six of 20 animals in the first sampling fell into this age gap. For the Georges Bank dataset (Chapter II), the first sample of 20 showed an age gap between 121 and 134. Six of 20 individuals in the resampling fell into this gap. By inference, age gaps in the datasets in most cases evidence under-sampling rather than recruitment lulls and, in fact, clear intimations of decadal or multidecadal hiatuses in recruitment or below average recruitment are rare in these datasets.

Thus, the probability that the dataset presented here represents a complete survey of all ages present in the population is extremely low and subtle details showing, for example, variations in recruitment that might be anticipated by short-term climate cycles such as the North Atlantic Oscillation, are unlikely to be resolved. The primary source of error, however, is in the poor resolution of the long tail of old animals present in most 5-mm size classes; these animals are relatively rare in the population and their presence very likely underestimates the full range of older ages in the population age frequencies.

Age frequencies and population dynamics

The rarity of old animals in the population suggests that animals older than the oldest animal aged may have been missed. However, the known long life span of ocean quahogs, our oldest animal being less than half the oldest age known (Schöne et al. 2005c, Ridgway & Richardson 2011), and the low mortality rate suggest that older animals than the ones observed are indeed rare. By inference, the record of ages suggests that the ocean quahog populations of the U.S. continental shelf initially colonized the presently inhabited area 200-250 years BP.

The two southern sites displayed the earliest inhabitation by ocean quahogs, beginning approximately 250 years ago in Long Island with evidence of colonization 220 years ago in New Jersey. Colonization of Southern New England seems to have begun approximately 170 years ago, and the earliest inhabitants of the Georges Bank population apparently became established about 200 years ago. Interestingly though, the populations at the northern sites began to expand fairly rapidly beginning in the late 1800s, and approached an asymptote presumed to be at carrying capacity within about 15 years in Southern New England and approximately 30 years on Georges Bank. At the southern sites, whereas ocean quahogs had been present longer than in the northeastern areas, the New Jersey population took nearly 80 years to approach carrying capacity although population expansion began much earlier, around 1835 and the Long Island population took about 40 years although initiation of the expansion began approximately contemporaneously with the Southern New England and Georges Bank populations.

The extended population expansion recorded by the New Jersey population would be consistent with a population at the southern end of the range. For a species with a circumboreal distribution, New Jersey, being situated dramatically farther south than is typical of the species' range, is in an area presumably nudging the maximum high temperature tolerance of the species, which could have an effect on the filtration and ingestion rate of these animals (e.g., Hofmann et al. 2006, Flye-Sainte-Marie et al. 2007, Munroe et al. 2013). Increased periods of high bottom water temperatures might inhibit survival of newly settled individuals when compared to areas with a more consistently suitable temperature range. Additionally, the larval supply and subsequent recruitment may have been more limited if this population was farther from a source population. Furthermore, although consistently small numbers of older individuals were present in the Long Island population for about 130 years, that population did not exhibit rapid growth until the early 1900's, a distinctly longer period at low abundance than observed for the two populations to the northeast, after which the population approached carrying capacity within about 25 years.

As suggested in Chapter II, initial colonization by ocean quahogs co-occurred with the ending of the Little Ice Age, an epoch that concluded in the first half of the 19th century (Schöne et al. 2005b, Mann et al. 2009, Cronin et al. 2010). Moore et al. (2017) recorded significant warming trends in the northwest Atlantic Ocean beginning in the middle of the 19th century consistent with this climate change. Warming bottom water temperatures would have allowed colonization of ocean quahogs in areas that were previously too cold to permit survival of the species. This could explain why the oldest animals are found at the southern sites, as these regions should have warmed up before the more northern sites. Regardless, once the initial recruits began to inhabit the northeastern US continental shelf, the populations remained at low levels for an extended period as is evident from the long tail in the population age frequency (Figure 13), a time span of nearly 150 years in Long Island, about 70 years on Georges Bank, and about 55 years in Southern New England, and at very low levels off New Jersey, as indicated by the rarity of animals over the first 60 years of colonization.

Like most bivalves, maturity in ocean quahogs is more clearly dependent upon length rather than age (Powell & Stanton 1985, Steingrímsson & Thórarinsdóttir 1995), with 50% of ocean quahogs reaching maturity at a shell length of about 60-mm in the mid-Atlantic (NEFSC 2017), similar to a report by Thórarinsdóttir and Jacobson (2005) of Icelandic populations reaching 50% maturity at 64-mm shell length. Ocean quahogs that recruited when these populations were initially established likely did not reach maturity for several decades following settlement due to slower growth expected in colder water, which is one possible cause of the time lag between the establishment of the populations and the rapid population growth. That is, only after many years would the newly established population be able to contribute to its own recruitment. From this perspective, the multidecadal gap in ages between about 180 and 215 years for the New Jersey dataset might suggest that a long tail is actually present in this population, but at an abundance not well recorded by this study’s sampling intensity.

Oddly enough, the Long Island site apparently experienced colonization prior to the northern sites, yet the rapid population expansion occurred at the Georges Bank and Southern New England sites, prior to the expansion in Long Island. Considering the extended period of time (one to three months) that ocean quahog larvae can remain in the water column (Lutz et al. 1982, Mann 1985), the long-distance transport of larvae would be possible. Larval connectivity at mid-shelf where ocean quahogs are found is not well documented. At shallower depths, net transport is west and south alongshore from New England to New Jersey with a larval retention gyre operating on Georges Bank (Zhang et al. 2015, Zhang et al. 2016) and with offshore transport occurring on the continental shelf south of Hudson Canyon, particularly in the fall. Although larvae spawned in the south possibly could reach the Southern New England and Georges Bank sites, a more likely original larval source for colonization is from the northeast where populations have existed for extended periods of time (Dahlgren et al. 2000, Wanamaker et al. 2009). In fact, the fossil record for ocean quahogs dates at least back to 5000-8000 BP off the western coast of Greenland (Funder & Weidick 1991). Wanamaker et al. (2008) reported that ocean quahogs have been present in the Gulf of Maine since 1030 ± 78 AD.

While speculative, one possible source population for the Mid-Atlantic colonization is documented by the presence of ocean quahogs in the northwest Atlantic Ocean for several hundred years prior to the establishment of the New Jersey and Long Island populations. The incongruity in this ready alternative is that the oldest animals in the present dataset came from the two southern sites. The fossil record of ocean quahogs in the Gulf of Maine suggests that the initial populations in the western Atlantic Ocean may have inhabited warmer, shallower waters, as the fossils were collected at a water depth of 38 m (Wanamaker et al. 2009) and Powell et al. (in press) recently have reported ocean quahog shells at shallower depths on Georges Bank than presently occupied by the living population. Thus, an alternative source population for the southwestern sites might be animals living further inshore than they do today. Regardless, explanation for the delayed response at the Long Island site between initial colonization and subsequent population expansion remains uncertain; nevertheless, the possibility that net larval transport south out of the Long Island region may have restricted population expansion off Long Island cannot be discounted and would be consistent with a recent evaluation of surfclam connectivity in the Mid-Atlantic Bight (Zhang et al. 2016).

Unexpectedly little evidence exists of strong year classes in this dataset. Two potential year classes are visible at the Long Island site both early in the population record, the first smaller year class occurring circa 1820, and the second larger year class occurring in approximately 1880. A vague indication exists of a possible year class in New Jersey that probably occurred circa 1845. In both cases, evidence for strong year classes if any only exists early on, prior to the population expansion, arguably during a time when the local population was not self-recruiting. As New Jersey and Long Island are the two most southern sites, it is conceivable that these populations were farther from the recruitment source of the early populations, which could explain the less consistent recruitment into these populations early in their history as compared to the two northern sites. Once population expansion occurred, substantial periods of low recruitment are almost nonexistent, with the only obvious case being the decadal trough in recruitment, perhaps not surprisingly, at the most southern site, New Jersey, from 1950-1965.

Fishery implications

Ocean quahogs support an East-coast commercial fishery that began circa 1967 and expanded in the early 1980s. The majority of fishing effort from the start of the fishery in 1967 was off of Delmarva and southern New Jersey until the early 1990’s when ocean quahog landings peaked, after which the fishery began to shift northwards to the south of Long Island and Southern New England (NEFSC 2009). As commercial dredges are selective for animals approximately >80 mm, the fishery removes the larger, older clams. Clams that were fully recruited to the fishery when it began have been fished for a long time, unlike the small clams that were unavailable to the dredge for some period of the last ~35 years. Thus, smaller clams may be overrepresented in the sampled populations compared to the larger clams that were available to the fishery for a longer period of time. Of the populations sampled, the New Jersey population would likely be the one most influenced by the fishery, as this region was a major focus area for the fishery for much of the last ~35 years, including the time period when commercial ocean quahog landings were highest (NEFSC 2009). Influence by the fishery on the population age structure may also be present in Long Island and to a much lesser extent in Southern New England.

Several lines of evidence suggest that the fishery has not materially influenced the age frequencies reported herein. (1) The fishing mortality rate over the history of the fishery has never exceeded the natural mortality rate and, for most of the time, has been well below it (NEFSC 2009, NEFSC 2017a). That is, the fishery has had little impact on the stock. (2) The selfsame trends in the age frequencies observed at the three fished sites are also present in the Georges Bank populations, although this population has rarely been fished and, in fact, was closed to fishing over much of the historical fishery (NEFSC 2009). Indeed, the US ocean quahog stock was considered to be at carrying capacity in the late 1960's at the historic start of the ocean quahog fishery (NESFC 2009) and remains near that today (NEFSC 2017a). An asymptote in the age frequency after population expansion at each of the four sites is consistent with this interpretation. (3) The vast majority of animals of age 80 or higher were fully recruited to the fishery prior to its inception; thus, any fishing would have decremented this group of animals equivalently. These animals are the primary contributors to the age frequencies reported herein, as ageing was restricted to animals ≥80 mm. Thus, we have not attempted to correct the age frequencies for bias in a possible over-representation of the youngest clams that grew into market size since the fishery became operational. It is unlikely that the fishery has substantively impacted the age frequencies, nor is it likely that the length frequencies have been truncated.

Conclusions

As described in Chapter II, the Georges Bank age-frequency distribution shares many similarities with the published age-frequency distributions for Iceland (Steingrímsson & Thórarinsdóttir 1995) and the Belfast Lough in Northern Ireland (Ridgeway et al. 2012). The age-frequency distributions for New Jersey, Long Island, and Southern New England also bear many similarities to that of Georges Bank, in that population levels remained low for a period of about 100 years beginning about 200-250 years ago after which the population size grew rapidly over a few decades at all sites except New Jersey, whereafter the population increased in size more slowly (Steingrímsson & Thórarinsdóttir 1995, Ridgeway et al. 2012). Similarities between locations as distant as the New Jersey continental shelf and Ireland suggest that this mode of colonization and population expansion may be characteristic of ocean quahogs throughout the North Atlantic basin.

The age-frequency distributions suggest that the living population of ocean quahogs record the entire history of colonization over a substantial portion of their present North Atlantic range. Setting aside recent non-native invasions (e.g., *Crassostrea gigas* – Troost 2010, *Potamocorbula amurensis* – Carlton et al. 1990), this species may be the only marine species for which such a record exists and very likely the only native species. The characteristics of this colonization and possible biological explanations are as follows. (1) Initial colonization began towards the end or shortly after the end of the Little Ice Age. Abundances were low as might be anticipated by dependency on an external source for recruitment. Low mortality rates and a long life span permits representatives of these initial colonizers to remain present in the living population. Year classes, albeit small, were possibly more common than later, suggesting more sporadic recruitment events from an external source. Small sample sizes, however, limit confidence in this inference. (2) At some point, local reproduction began to contribute to the larval pool; likely this occurred many years following initial colonization due to the extended time to maturity. (3) Due to local reproduction or to environmental change, the population entered into a rapid expansion that, over a relatively brief period given the life history of the species, raised abundance to near carrying capacity. The population expansion is remarkably rapid given the extended life span of the species; however, the rapid expansion is consistent with the high recruitment potential of most bivalves due to their high annual fecundity. (4) Population expansion ceased when the population reached carrying capacity. Afterwards, recruitment remained sufficient to balance natural mortality and the population remained at carrying capacity for an extended period of time, rarely interrupted by extended periods of low recruitment. This suggests that ocean quahogs have recruited regularly, certainly more frequently than decadal, to these populations.

Resiliency of the ocean quahog population of the U.S. East coast to fishing has been questioned due to the limited evidence for large recent recruitment events. The population dynamics inferred from the age frequencies described here suggest that low recruitment is the anticipated result for a population near carrying capacity, whereas a much higher recruitment capacity typical of most bivalve species is well demonstrated by the rapid population expansion that occurred during earlier times as the population abundances rose to that level. Expansion of the range northward, however, which might be anticipated with continued warming of the North Atlantic, may require an extended period of time as time-to-maturity will likely limit the response time of a newly established population in developing local recruitment potential

CHAPTER IV – TWO-HUNDRED YEAR RECORD OF INCREASING GROWTH RATES

Information from this chapter has been submitted for publication in the Journal of Experimental Marine Biology and Ecology.

Pace, S. M., E. N. Powell & R. Mann. Submitted. Two-hundred year record of increasing growth rates for ocean quahogs (*Arctica islandica*) from the northwestern Atlantic Ocean. J. Exp. Mar. Biol. Ecol.

Introduction

With life spans capable of exceeding 500 years (Butler et al. 2013), the long life span and the sensitivity of ocean quahogs to interannual variations in the environment, particularly temperature, have supported the use of time series of growth as a temperature proxy to track long-term trends in climate (Schöne et al. 2003, Butler et al. 2010, Butler et al. 2013) and shorter term climate cycles (Schöne et al. 2005c, Butler et al. 2013, Lofmann & Schöne 2013, Beierlein et al. 2015). In addition to the importance of this clam as a benthic biomass dominant and its value in elucidating long-term trends in climate, the clam also supports a commercial fishery that provides clam meat for most commercial chowders. Indeed, a commercially valuable fishery for this species has existed in the U.S. since the late 1960's (NEFSC 2009, 2017a). An essential element in the sustainable management of this fishery is information on growth rate, which controls the age at which animals reach a size that can be selected by the commercial dredge.

The growth of ocean quahogs varies substantially throughout the lifetime of an individual, and proceeds through ontogeny and into old age in a manner that is unlike the growth process of most other bivalves. Juvenile ocean quahogs grow rapidly, displaying near exponential growth until the onset of maturity, whereupon growth rate slows, yet growth continues throughout the lifetime of the individual. Although numerous authors have applied a von-Bertalanffy growth model to this species (e.g., Brey et al. 1990, Lewis et al. 2001, Kilada et al. 2007), the continuation of growth into old age contradicts the basic assumption of asymptotic growth in this model. Chapter II showed that an alternative growth model specified by Tanaka (Tanaka 1982, 1988) fits this growth dynamic by combining both the near exponential growth of the juvenile phase with the continuous indeterminate growth of the adult into old age.

Geographical differences in growth rates are also well documented (Murawaski 1982, Brey et al. 1990, NEFSC 1995, Lewis et al. 2001, Thórarinsdóttir & Jacobson 2005, Kilada et al. 2007, Ridgeway et al. 2012). Witbaard et al. (1999) suggest that the regional differences in growth rates are predominantly due to differences in primary production, but it is certain that a combination of several environmental factors contribute to the varying growth rates throughout the range of the stock and, indeed, Marali et al. (2015), Mette et al. (2016), Reynolds et al. (2017) and others have shown that variations in growth of individual animals over their life span can be explained in part by changes in sea surface, and by inference, bottom water temperatures. Additionally, sex-related differences in growth rate have been described (Ropes et al. 1984, Steingrímsson & Thórarinsdóttir 1995). Regardless of the mechanism behind the variable growth rates of this species, the result is an inability to create a single age-length key for the species, as the high variability in growth rates routinely observed throughout the range of the stock produces not only regional differences in growth rate, but also differential growth rates within each local populations such that a wide range in age at length is found throughout most of the post-juvenile size range. Thus, as described in Chapters I and II, any age-at-length key that might be developed from a local population likely would result in inaccurate age estimates for more distant populations of ocean quahogs.

Characteristics of age and growth of various ocean quahog populations from the U.S. mid-Atlantic continental shelf have been described (Murawaski 1982, NEFSC 1996, Lewis et al. 2001), but the number and geographical scope of these studies is limited. In addition, variations in growth as a function of environmental change remain undescribed for this species in the northwest Atlantic, though one anticipates that such variations should exist, as the species is found at latitudes farther south off the U.S. coastline than elsewhere in its boreal circumambience (Merrill & Ropes 1969, Dahlgren et al. 2000, for further documentation of the North Atlantic range, see Brey et al. 1990, Rowell et al. 1990, Witbaard et al. 1999, Ragnarsson & Thórarinsdóttir 2002, Butler et al. 2009). Thus a need for understanding the length-at-age relationships throughout the range of the U.S. stock exists to inform fishery management, provide a basis for age-structured stock assessment models, and also to elucidate regional shifts in ocean climate over the last few centuries. The objective of this study was to investigate growth rates of selected individuals from four ocean quahog populations covering much of the mid-Atlantic range of the stock through the analysis of annual growth increments. To do this, growth increment time series for animals covering the age range observed in the four populations were used to determine the age at 60, 80, and 90 mm, the average growth rates from birth to 60 mm, 60 to 80 mm, 80 to 90 mm, and post-90 mm. These data were evaluated as a function of birth year, within and between populations to elucidate regional trends in growth and uncover time dependent trends in growth, should they exist.

Methods

Sample collection and preparation

Ocean quahog samples were collected from New Jersey and Long Island from the *F/V Christie* in March 2015 and from Southern New England and Georges Bank from the *F/V Pursuit* in May 2015 using hydraulic dredges (Figure 8). Clams were arbitrarily selected from each 5-mm size bin starting with 80 mm through the maximum shell length (anterior-posterior) collected at each site. Clams were sectioned along the height axis (dorsal-ventral) using a modified commercial tile saw. Sectioned clams were ground and polished on a wet polishing wheel on 400-µm and 600-µm sandpaper grit, followed by 6-µm and 1-µm diamond suspensions on polishing pads. Additional details are provided in Chapter II.

Images of the hinge region of all sectioned clams were captured using either a high definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software or a high definition Olympus America microscope camera using Olympus MicroSuite software. Many photographs of the hinge region were required to produce a continuous image of the hinge at high magnification. Each individual image was automatically stitched together by the cellSens microscope imaging software. Hinge photographs taken using the Olympus MicroSuite software were stitched together using the open source software ImageJ (FIJI) to create a complete image of the hinge section. Through the use of the Object J plugin in ImageJ, annual growth lines in the hinge region of each individual were annotated (Figure 9) and the growth increment widths (distance between consecutive annual growth lines) measured in units of pixels.

The total shell length (mm) of an individual divided by the cumulative sum of all growth increment widths (pixels) provided a conversion of pixels into mm.

Correlation analysis

Age estimates and measurements of growth increment widths were recorded for 205 individuals throughout the Mid-Atlantic [New Jersey (80), Long Island (65), Georges Bank (35), southern New England (25)]. Using this growth increment information, the age at which individuals reached 80 mm was compared to the year each individual was born. This shell length was initially selected because 80 mm is the size at which animals are nearly fully selected to the commercial dredge (NEFSC 2017a); thus it is a size of interest to the fishery and management of the species. To investigate whether any trends relating to birth year were specific to 80 mm, or if they held true throughout a larger size range, the ages at which animals reached 60- and 90-mm in shell length were also compared to the birth year of each individual. The 60-mm size was chosen because in approximates size a maturity (Rowell et al. 1990, Thórarinsdóttir and Jacobson 2005, NEFSC 2017a). The 90-mm size is a convenient size well within the adult age span, but under the maximum size obtained at each of the four sites. A Pearson's correlation test was used to test the strength of correlations between birth year and these variables at each site. Additional Pearson's correlation tests were used to test for correlations between birth year and shell length. Specifically, the variables examined were the average growth rate from birth to 60 mm, from 60 to 80 mm, from 80 to 90 mm, and the average growth rate from 90 mm to size at time of collection (Equations 1-4) at each of the four sites. Hereafter, the former three average growth rates will be referenced by the upper size boundary, e.g., average growth rate from birth to 60 mm will be referred to as growth rate to 60 mm. The final growth increment from 90 mm to size at time of collection will be referred to as post-90 mm.

$$\text{average growth rate to 60 mm} = \frac{\text{age at 60 mm}}{\text{60 mm}} \tag{5}$$

$$\text{average growth rate to 80 mm} = \frac{\text{age at 80 mm} - \text{age at 60 mm}}{\text{20 mm}} \tag{6}$$

$$\text{average growth rate to 90 mm} = \frac{\text{age at 90 mm} - \text{age at 80 mm}}{\text{10 mm}} \tag{7}$$

$$\text{average growth rate post} - \text{90 mm} = \frac{\text{terminal age} - \text{age at 90 mm}}{\text{total shell length} - \text{90 mm}} \tag{8}$$

ANCOVA and regression analysis

Analyses of covariance and post-hoc least squares means tests were used to identify the relationship between the age at which animals reached each size (60, 80, 90 mm) and the intervening growth rates as a function of birth year and location. Each ANCOVA retained the interaction term if significant ($\alpha \leq 0.05$). We use the term ANCOVA because birth year is a discrete variable in this analysis rather than a main effect and thus serves as a covariate.

Multiple linear regression using the maximum R-square improvement method (Freund and Littell 2000) was used to examine the ability of growth-dependent variables to predict the birth year of an individual at each site. Shell length and average growth rate to 60 mm, 80 mm, 90 mm, and post-90 mm were used as independent variables. Significant regression models indicate that the growth process has varied over time at a site with sufficient directionality that the growth dynamics of an individual are in part determined by the year of birth. For a given age, the size at time of collection for an ocean quahog will be determined by the time required to reach maturity and the rate of growth as an adult. To further assess the importance of birth year, and to evaluate the relative importance of growth rate to maturity relative to adult growth, two additional regression models were investigated. The first limited the independent variables to those associated only with early growth rates, namely the average growth rate to 60 mm and to 80 mm. A second employed growth rates to 60 mm, 80 mm, and 90 mm. Animals that were less than 90 mm at time of collection perforce were omitted from this model. Many, but not all, of these animals were relatively young. Thus, this last regression model was biased in favor of animals born earlier in the time history of the population

Results

Correlation analysis

Plots of age at 60, 80, and 90 mm versus birth year are shown in Figures 14-16. A significant negative Pearson's correlation exists between birth year and age at 60 mm ($r = -0.567$, $p < 0.0001$), 80 mm ($r = 0.592$, $p < 0.0001$), and 90 mm ($r = -0.396$, $p = 0.0003$) at the New Jersey site. The same was true at the Long Island site [60 mm ($r = -0.745$, $p < 0.0001$); 80 mm ($r = -0.799$, $p < 0.0001$); 90 mm ($r = -0.634$, $p < 0.0001$)]; that is, at the two southern sites, as birth year increased, the age at which individuals reached 60, 80, and 90 mm decreased. Thus older animals were characterized by slower growth rates to an equivalent size, including juvenile and adult growth. In addition, the correlations were consistently strongest at the Long Island site.

In contrast, at the Georges Bank site, the correlation between birth year and age at 60 mm or 80 mm was not significant, but a significant negative correlation existed between birth year and age at 90 mm ($r = -0.429$, $p = 0.0102$). Similarly, at the Southern New England site, the correlation between birth year and age at 60 mm or 80 mm was not significant, whereas a significant negative correlation was observed at 90 mm ($r = -0.496$,

$p = 0.0116$). Results of these correlation tests suggest that ocean quahogs born more recently grew at a faster rate than older clams at the two southern sites, whereas at the two northern sites, the year that individuals were born had little effect on early growth rates and thus little effect on the age at which animals reached 60 or 80 mm. Growth rates of older adults, however, had a significant correlation with birth year, as shown by the growth rate between 80 and 90 mm and the correlation coefficients were stronger for the two northeastern sites than for the most southern site off New Jersey, but still lower than for the Long Island site.

At all four sites, a significant correlation existed between birth year and total shell length [New Jersey ($r = -0.790$, $p < 0.0001$, Long Island ($r= -0.789$, $p < 0.0001$), Georges Bank ($r = -0.789$, $p = 0.601$, $p = 0.0001$), Southern New England ($r = -0.613$, $p = 0.001$)], indicating that, in general, larger clams tended to be older. That is, the change in growth rates observed with birth year were not sufficiently intense that the younger clams, born more recently and growing at higher rates, were not larger at the time of collection than the older clams, born earlier and growing at slower rates at the same time in their life history.

Plots of average growth rate to 60, 80, 90, and post-90 mm versus birth year are shown in Figures 17-20. At the New Jersey site, significant positive correlations exist between birth year and growth rates to 60 mm ($r = 0.539$, $p < 0.0001$), 80 mm ($r = 0.602$, $p < 0.0001$), and 90 mm ($r = 0.401$, $p = 0.0002$), and post-90 mm ($r = 0.500$, $p < 0.0001$). The same was true at the Long Island site [growth rate to 60 mm ($r = 0.768$, $p <0.0001$); 80 mm ($r = 0.516$, $p <0.0001$); 90 mm ($r = .522$, $p <0.0001$); and post-90 mm ($r = 0.516$, $p <0.0001$)], thus, at these two sites animals born more recently were growing at faster rates in each of these phases of growth compared to animals born many decades previously, explaining the presence of a decreasing age at 60-90 mm as birth year increased. The trend is a product of lifetime growth at these two southern sites rather than, for example, differential growth rate at one specific life stage.

At the Georges Bank site, the only growth phase with a growth rate correlated with birth year was growth rate post-90 mm (r = 0.562, p = 0.0004). At the Southern New England site, whereas average growth rates to 60 and 80 mm were not significantly correlated with birth year, the growth rate to 90 mm (r = 0.490, p = 0.0129) and post-90 mm (r = 0.561, p = 0.0035) were both significantly correlated with birth year. These correlations explain earlier results in the comparison of birth year to age at which animals reach 90 mm, in that growth rates only appear to increase with more recent birth years after animals reach 90 mm in size at the Georges Bank site, whereas growth rates began to increase after animals reached >80 mm in length at the Southern New England site, resulting in the significant negative correlation between age at 90 mm and birth year at the two northern sites. Of note is the strong tendency for early growth rates to be less affected by birth year at higher latitudes, with an increasing restriction of this differential to increasingly older animals at progressively more northeastern locations.

ANCOVA

For age at 60 mm, the main effect of location (F = 5.87, p = 0.0007), the covariate birth year (F = 16.65, p < 0.0001), and the interaction term (F = 5.71, p = 0.0009) were all significant. Results of pairwise post-hoc comparisons indicate that clams from New Jersey were significantly younger at 60 mm than clams from the other three sites which were not significantly different. For age at 80 mm, the main effect of location (F = 5.87, p

= 0.0020), covariate birth year (F = 16.65, p < 0.0001), and the interaction term (F = 5.71, p = 0.0024) also were all significant. At 80 mm, clams from New Jersey were significantly younger than clams from all other sites, and clams from Southern New England were significantly older than clams from the three other sites. For age at 90 mm, the main effect of location (F = 25.71, p < 0.0001) and the covariate birth year (F = 77.83 p < 0.0001) remained significant, but the interaction term was no longer so. *A posteriori* comparisons indicate that animals from New Jersey and Georges Bank were significantly younger at 90 mm than clams at the Long Island and Southern New England sites, but no significant differences in age at 90 mm existed between New Jersey and Georges Bank clams, nor did a significant difference exist between Long Island and Southern New England clams. Plots of the least squares means values and associated 95% confidence intervals for each site are shown in Figure 21.

ANCOVAs using average growth rate to 60 mm and from 60 to 80 mm as dependent variables corroborate the results of the ANCOVAs with dependent variables of age at 60 mm and 80 mm. Results of the ANCOVA using growth rate from 80 to 90 mm as the dependent variable indicate show a significant main effect of location and a significant birth year covariate [location (F= 22.80, p < 0.0001); birth year (F = 39.54, p < 0.0001)]. *A posteriori* comparisons indicate that ocean quahogs from New Jersey grew significantly faster from 80 to 90 mm than the other three sites, and clams from Southern New England grew significantly slower than at all other sites. The average growth rate post-90 mm was also significantly influenced by location and birth year [location (F= 23.48, p < 0.0001); birth year (F = 39.54, p < 0.0001)]. The interaction term was not significant. Results of *a posteriori* comparisons suggest that clams from New Jersey had the fastest average growth rate at larger sizes than the three other sites, whereas clams from Southern New England grew significantly slower than clams from both New Jersey and Long Island. Plots of the least squares means values and associated 95% confidence intervals for growth rates to each size are shown in Figure 22.

Regression analysis

Multiple regression models for the New Jersey and Long Island sites suggest that the strongest predictors of birth year were length and average growth rate to 80 and 90 mm. These variables explained about 91% of the variation in predicting birth year at both sites (Table 21). At the Georges Bank and Southern New England sites, length, growth rate to 80 mm, and growth rate post-90 mm explained approximately 86% and 91% of the variability respectively. These results suggest that the ability to predict birth year at the two northern sites depends more on growth rates at larger sizes in addition to the total length of an individual, whereas the average growth rates from 60 to 90 mm in addition to the length are better predictors of birth year at the New Jersey and Long Island sites. These results recapitulate earlier trends exposed by Pearson correlations and ANCOVA. Figure 23 shows the observed versus predicted birth year generated by the best three-variable model at each site.

Table 22 shows the results of the regressions to predict birth year for each site using only average growth rates to 60 and 80 mm (Figure 24), and average growth rates to 60, 80, and 90 mm (Figure 25). In the former, using only growth rates to 60 and 80 mm to predict birth year, significant regressions were produced for the New Jersey and Long Island locations only. Although significant, early growth rates only accounted for about 39% of the variation at the New Jersey site, but a higher 58.6% of the variation at the Long Island site. Nevertheless, the regression analysis indicates that a significant relationship does exist between birth year and these early growth rates at these two sites. In contrast, the two-variable models for Georges Bank and Southern New England not only were non-significant, but also lacked any ability to accurately predict birth year, as indicated by the very low R-square values.

The addition of average growth rate from 80 to 90 mm somewhat improves the Long Island model, increasing the R-square by 0.13. In the New Jersey model, the inclusion of this variable marginally diminishes the total variance explaining birth year, though this is likely due to the removal of animals <90 mm in shell length from the model. The regressions for both the Long Island and New Jersey models remained significant, however. At the Southern New England site, the addition of this third variable results in a regression model accounting for about 51% of the variation in predicting birth year and a significant correlation, whereas the addition of this variable only modestly improves the R-square value for Georges Bank and the correlation remains non-significant. These analyses suggest that the inclusion of growth rate from 80 to 90 mm results in a reasonable ability to predict birth year at three of the four locations, excluding only Georges Bank, which is the most northern site.

Discussion

The relationship of growth rate and birth year

The variable growth rates of ocean quahogs to a shell length of 80-mm throughout the range of this commercially valuable species has important implications for fishery management, as this is the size at which clams are nearly fully selected to the commercial dredge. Based on Figure 15, clams in New Jersey and Long Island are reaching a size that is available to the commercial dredge typically between 10 to 20 years earlier than clams from the two more northeastern areas. Consider also that growth rates vary on decadal and longer time scales at the New Jersey and Long Island sites, with clams born more recently (e.g., 1960) reaching lengths of 80 mm at younger ages (e.g., average age of about 30 years in New Jersey and about 41 years in Long Island) than clams that recruited prior to 1900 (e.g., average age of about 49 years in New Jersey and 75 years in Long Island). As concerns exist about the ability of any long-lived species to recover in a reasonable amount of time should overfishing occur, this information suggests that the southern portion of the stock has higher resilience than the more northern portion and that this resiliency has increased substantively over time. Moreover, management based upon growth rates for the stock as a whole would gravely underestimate the dynamics of the population anticipated for future years at least at these two more southern sites.

At the two northern sites, the significant correlation between birth year and age at 90-mm, as well as the average growth rate for animals exceeding 90 mm (dlen in Table 21, Figure 20), is not entirely surprising, as a strong correlation exists between an individual's total shell length and the year the animal was born. The relationship between average growth rate for animals exceeding 90 mm and birth year would be anticipated, as ocean quahogs continue to grow as long as they are alive, so older animals should generally grow to a larger size than younger animals that have not had as much time to grow, and the amount of time that has passed between the time the animal reached 90 mm and the date of collection, being the denominator, will substantively influence the metric. This was supported in the regression analyses, as total shell length was the variable most strongly correlated with birth year at all four locations (Table 21). This likely explains why a significant relationship between birth year and average growth rate post-90 mm exists at the Southern New England and Georges Bank sites, but no relationship exists for the growth rates at 60 and 80 mm, as a multiple regression predicting birth year from just these two metrics has no predictive power (Table 22). However, one cannot discount that the existence of this relationship with birth year at larger sizes may also be due to increasing water temperatures, which may have resulted in increased growth rates at older ages for ocean quahogs born long ago that grew slower at younger ages while living in a cooler environment. The growth rate from 80 to 90 mm may be instructive in this case. The correlation is significant for Southern New England (Figure 19), and inclusion of the metric in a regression model provides considerably improved explanatory power, though still weak in comparison to that of the two southern sites (Table 22, Figure 25).

Despite relatively small R-square values, examination of the significant regression produced using only early growth rates (Figure 24) suggests that the two-parameter model provides a reasonably accurate prediction of birth year at the New Jersey and Long Island sites. If growth rates early in an individual's life had not varied over time, restriction of regression analysis to the use only of early growth rates should result in an inability to predict birth year. The converse being true validates the inference seen in the correlation test results that the signal of time-dependent changes in early growth rates at the two southern sites was sufficiently strong to provide a reasonable estimate of birth year just from these metrics. The lower R-square value at the New Jersey site in comparison to the Long Island site could be a consequence of the fact that this population is situated closest to the southern end of the species' range, where higher intra-decadal climate variability can be anticipated. Such variability would insert increased small-temporal-scale variation in growth rates, which would reduce the strength of the correlation while retaining a strong long-term temporal signal. The Long Island site, being north of Hudson Canyon, is in a distinctly different oceanographic regime less influenced by the vagaries of the Gulf Stream's influence on the continental shelf and the degree of southerly intrusion of the cold pool that permits ocean quahogs to survive at latitudes unusually far south for a boreal species (for more on the cold pool, see Bignami & Hopkins 2003, Castelao et al. 2010, Lentz 2017; for more on the Hudson Canyon as an oceanic barrier, compare NEFSC 2017a, b; see also Lucey & Nye 2010; Zhang et al. 2015). Lesser intra-decadal climate variability may explain why of the two southern sites, the Long Island site had a better model fit than New Jersey, when the population at both sites responded relatively similarly to longer-term changes in oceanic climate.

Conversely, the Georges Bank and Southern New England sites lack a significant regression predicting birth year from only early growth rate variables (Table 22); the regression fails to provide a discernable correlation between observed and predicted birth year (Figure 24). The modest predictive capacity introduced by adding the 90-mm growth rate variable to the regression for the Southern New England site emphasizes a strong southwest to northeast trend in the long-term influence of climate change on ocean quahog populations in this region earlier considered in Chapter III At the southern extreme, variation in growth rate over time exists in all phases of ocean quahog life, whereas on Georges Bank, little evidence exists for any differential in growth rate over the last ~200 years.

Results of the ANCOVAs and post-hoc least squares means tests indicate that clams from New Jersey were significantly younger than all other sites when they reached 60 and 80 mm, and significantly younger than clams from Long Island and Southern New England when they reached 90 mm. At 90 mm, clams from Georges Bank were also significantly younger than clams from Long Island and Southern New England. Additionally, ocean quahogs from Southern New England were significantly older than those from the other three sites at 80 mm. This is best seen in Figure 15 where clams born in New Jersey reached 80 mm at a younger age consistently across all birth years in comparison to the other sites.

Ocean quahogs from New Jersey also had significantly faster average growth rates to each size than all other sites. These tests included birth year as a covariate; that is, growth rates were inherently faster at the southern sites regardless of the effect of birth year on growth rate. This is best seen in Figure 18 where clams born in New Jersey grew at higher rates consistently across all birth years in comparison to the other sites. Clams from Southern New England grew significantly slower than those from the three other sites between 60 and 80 mm and 80 to 90 mm, whereas these animals only grew significantly slower than clams from New Jersey and Long Island post-90 mm.

Interestingly, Long Island and Georges Bank tend to be paired in the results of the post-hoc tests (Figures 21-22), as the only variable that clams from these two sites significantly differed in was age at 90 mm, yet these two sites displayed little difference in growth rate from 80 to 90 mm. Additionally, although ocean quahogs from Georges Bank were significantly older in age at 90 mm than those from Southern New England, clams post-90 mm exhibited no differences in growth rates at these two sites. Also of note is that no interaction effects between birth year and location were detected at either the age of 90 mm, growth rates from 80 to 90 mm or growth rates post-90 mm, suggesting that at larger sizes, the effect of birth year was similar across all locations. Perhaps the strong correlation between shell length and birth year evident at all sites overrode the regional changes in growth rate with birth year noted at earlier life stages; alternatively, the inherently more modest growth rates of the adults may have limited the influence of changing environmental conditions at the southern sites.

Origin of growth rate variation

Growth rates of ocean quahogs are known to be variable throughout the species range. Table 23 reports the parameters of the von Bertalanffy growth model for ocean quahogs from various studies, including parameters from the five oldest clams from the New Jersey, Long Island, and Southern New England sites in this study. Although this growth model has important weaknesses for this species as described in Chapter II, its common use provides an opportunity for comparison. Evidence presented in this study, however, constrains comparisons on geographic scales or even site to site. Growth rates vary between animals born at different times and, thus, parameter values for growth models, such as Brody’s k, will also vary. Hence, the variation in growth rates between the populations summarized in Table 23 may be a result of the limited size and age ranges of the sampled animals, and not necessarily representative of the larger age range of the species at the various sites. For example, at Georges Bank, Lewis et al. (2001) estimated the age of only seven animals to be >40 years, whereas no animals younger than 54 years were sampled by for the Georges Bank population in Chapter II. Almost no overlap exists in the estimated ages of sampled individuals in these two studies. Whether this is the cause of the difference between the estimated growth parameters for Georges Bank between the two studies is unclear, but considering the rapid, essentially exponential growth of juvenile ocean quahogs compared to the very slow, continuous growth of older individuals, such a possibility cannot be excluded.

Differences in the size of ocean quahogs that were aged also likely had an influence on the varying growth rates throughout the species range. Murawski et al. (1982) sampled animals <60 mm from Long Island. Kilda et al. (2007) estimated the age of animals <86 mm. The Georges Bank population from Chapter II focused only on animals ≥80 mm. In our study, substantive variation in growth model parameters can be anticipated depending on the birth year of the animal at the New Jersey and Long Island sites, and perhaps also at the Southern New England site. For the purpose of comparison to the study using ocean quahogs from Georges Bank in Chapter II, the growth of the five oldest clams from each site was modeled using the von Bertalanffy growth equation. Had the growth of younger clams been modeled instead, parameter values likely would have differed substantially.

Additionally, various methods were used to age the animals in the studies summarized in Table 23, some of which can produce less accurate age estimates than other methods, which would affect the resulting growth curves. In general then, the uniqueness of ocean quahog growth and the sensitivity to climate change due to the long life span of the species, which exceeds the cycle period of commonly studied climate cycles (e.g., ENSO, NAO, AMO – Sutton & Hodson 2003, Soniat et al. 2009, Nye et al. 2014) limits comparability of growth parameters. In fact, determining a population-level growth model depends upon variation in growth being a product of random variation between growth rates within and between cohorts, rather than directional change. That changing environmental conditions can modify growth model parameters within the time span of the life of a long-lived species is already well described for Atlantic surfclams, *Spisula solidissima* (Munroe et al. 2016, Chute et al. 2016) and other bivalve species (Brey et al. 2011). The much longer life span for ocean quahogs assures that any population with animals living through periods of climate change will be composed of animals with varying growth parameters, making a population estimate potentially illusory and certainly limiting between-population comparisons.

Temperature is a primary determinant of growth in bivalves, being a strong effector of filtration and ingestion rate, respiration rate, and gametogenesis (e.g., Hofmann et al. 2006, Flye-Sainte-Marie et al. 2007, Munroe et al. 2013). Environmental factors such as mean annual temperature and food availability (e.g., Taylor & Brand 1975b, Witbaard 1996, Begum et al. 2009, Ballesta-Artero et al. 2017) likely have an effect on growth rates throughout the range of this species. These factors may also explain the large disparity in maximum size of individuals at different sites; for example, the largest ocean quahog retrieved from New Jersey was 125-mm in shell length, whereas at the Southern New England site, the largest clam observed was only 108-mm, with only six individuals larger ≥105-mm encountered in the population sample. Furthermore, the age of animals at various sizes differed between sites, with the youngest ocean quahogs at each length typically from the New Jersey site, and the oldest typically belonging to Southern New England. These differences were evident in the correlation tests and confirmed in regression and ANCOVA analysis. As the most southern sampling site, the

New Jersey site probably has had the warmest mean annual bottom temperatures, which could facilitate rapid growth, as well as growth to larger size maxima.

However, studies at different locations throughout the species range suggest that local temperature typically explains only about 10-30% of interannual shell growth variability (Schöne et al. 2003, Butler et al. 2010, Butler et al. 2013, but see evidence for even higher explanatory power provided by Marali & Schöne 2015, Reynolds et al. 2017). Although this degree of explanatory power seems small, in all likelihood it identifies the key parameter leading to differential growth rates observed by these authors and identified in this study. The afore-referenced studies have used a variety of sea water temperatures as a proxy, including sea surface temperature, mean seawater temperature taken from a range of depths, and bottom water temperature. Bottom water temperature is the proximal temperature signal and the role of temperature in yearly growth is a complex interplay between age, size, and the seasonal temperature signal. Moreover, temperature also has an effect on the length of the growing season (Schöne et al. 2005a) and on food supply, both of which can influence temporal trajectories of population metrics (system memories - see Soniat et al. 1998) on as yet indeterminate, but multi-year, time scales. Accordingly, temperature can directly and indirectly result in differences in growth rates throughout the species range. Such variations would reduce the explanatory value of any single temperature proxy, even though much of the differentials in growth were ultimately a product of differences in the local temperature time series.

Furthermore, the northwest Atlantic continental shelf, in particular the New York Bight and Georges Bank, are among the most productive regions in the world (O’Reilly & Busch 1984); accordingly, differences in primary production throughout the Mid-

Atlantic may help explain the differences in growth between the four sample populations in this study. According to a report by Witbaard et al. (1999) in a study in the North Sea, primary productivity was considered to be the most important determinant of growth rate. Similarly, Lewis et al. (2001) suggested that the fast growth of ocean quahogs from Georges Bank was likely a result of the high productivity in the Georges Bank region. Perhaps this may help elucidate why in this study, animals from Georges Bank had similar ages-at-size, growth rates, and maximum observed shell length as animals from Long Island. Possibly, changes in temperature have resulted in the changing relationship between birth year and age-at-size and growth rate at the Long Island site, whereas at Georges Bank, the growth rates similar to those observed in Long Island may be a due to the fact that Georges Bank is and has likely been a more productive region over the histories of these populations. What is clear is that, despite a range of studies on the physiology and behavior of this species (e.g., Taylor & Brand 1975b, Mann 1982, Oeschger & Storey 1993, Begum et al. 2009), we still do not have a physiological model that can accurately recapitulate the growth trajectory of this species in the way that is feasible for many other bivalves (see earlier references).

One important unknown is the influence of ocean quahog density on growth rate. Dense populations of bivalves are known to compete for food, thereby limiting growth rate (Powell et al. 1995, Fréchette & Daigle 2002, Freitas et al. 2009). Ocean quahogs are considered to be near carrying capacity throughout their U.S. range today (NEFSC 2017a) and this has likely been true through over half of the population’s history since initial colonization (Chapter II). Thus, some influence of population density on growth rates might be anticipated. Evidence does not support such an influence, however.

Lowest growth rates are recorded from New Jersey and Long Island early in the population's history when population densities were likely much lower (Chapter II) and increasing population density on Georges Bank over the last 100+ years has not had any discernable influence on growth rates early or late in life. The fishing mortality rate has been well below the natural mortality rate over the history of the fishery (NEFSC 2017a) and the animals supporting the correlations between birth year and growth rate were nearly all born and grow to market size prior to the inception of the fishery, accordingly, the influence of changes in population density is an unlikely factor influencing the variations in growth rate as a function of birth year reported here.

Conclusions

Interpreting temperature effects on growth rates of ocean quahogs throughout the history of the population is infeasible, as bottom water temperature records do not extend back to the time when colonization by this species began in the northwest Atlantic (Hulme & Jones 1994, Hanna et al. 2004). Chapter II suggested that initial ocean quahog colonization on the continental shelf of the U.S. east coast co-occurred with the ending of the Little Ice Age, as warming bottom water temperatures would have permitted colonization by ocean quahogs in areas previously unsuitable for survival due to colder temperatures. The timing of this colonization coincides with a report by Moore et al. (2017), which presented evidence of significant a warming trend in the northwest Atlantic Ocean beginning during the middle of the 19th century, the time period concurrent with the end of the Little Ice Age (Schöne et al. 2005b, Mann et al. 2009, Cronin et al. 2010). Moore et al. (2017) show this warming trend continuing through to the present time. The warming of the northwest Atlantic may explain the significant correlation between birth year and the age at which individuals reach 60, 80, and 90 mm in shell length at the New Jersey and Long Island sites, as these two sites are closer to the southern end of the species range than the Georges Bank and Southern New England populations. Increased bottom water temperatures could facilitate faster growth directly through higher filtration rates or indirectly through increased food supply, which may explain why ocean quahogs born more recently are growing faster than those born long ago. Birth year had little influence on the age-at-size at the two northern sites, however, with the modest exception of clams 90 mm in length. As water temperatures continue to increase, it is possible that changing growth rates will become evident at smaller sizes in future decades within the Georges Bank and Southern New England populations. Nevertheless, the Moore et al. (2017) temperature proxy comes from the Labrador Sea, well north of Georges Bank, so the minor or absent temperature signal in the Southern New England and Georges Bank populations would seem to be unexpected. Reconstructed bottom water temperatures from 1875-1983 using *A. islandica* specimens from Georges Bank (Marsh et al. 1999) confirm the absence of a signal of increasing temperatures on Georges Bank.

Regardless of the mechanism, growth rates of ocean quahogs from the New Jersey and Long Island sites have clearly increased through time, with the age at which animals reaching 60, 80, and 90 mm decreasing as birth years advanced to recent years. Correspondingly, the growth rates to 60, 80, 90, and post-90 mm were all negatively correlated with birth year; that is, younger clams grew significantly faster than older clams at a comparable size born decades previously. This relationship was only evident at the age at which animals reached 90 mm at the Georges Bank and Southern New England site. This has important implications for fishery management, as ocean quahogs are becoming available to the commercial dredge in the southwestern region of the Mid-Atlantic Bight faster than they have in the past. These results also pose interesting questions on the mechanism behind the spatially and temporally variable growth rates of ocean quahogs throughout the range of this species. In particular, ocean quahogs record the rise in ocean temperatures after the Little Ice Age in the Mid-Atlantic Bight southeast of southern New England, yet demonstrate no evidence of such a rise in the Southern New England and Georges Bank region, which would suggest a differential response of ocean circulation and its control of bottom water temperature in this region over the last 200+ years.

CHAPTER V – CONCLUSIONS

Parts of the information from this chapter have been published in the Journal of Shellfish Research or have been submitted for publication to the Marine Ecology Progress Series or the Journal of Experimental Marine Biology and Ecology.

Pace, S. M., E. N. Powell, R. Mann, C. M. Long, & J. M. Klinck. 2017. Development of an age-frequency distribution for ocean quahogs (Arctica islandica) on Georges Bank. J. Shellfish Res. 36:41-53.

Pace, S. M., E. N. Powell, R. Mann & C. M. Long. Submitted. Comparison of Age-Frequency Distributions for Ocean Quahogs (*Arctica islandica*) on the Western Atlantic US Continental Shelf. Mar. Eco. Prog. Ser.

Pace, S. M., E. N. Powell & R. Mann. Submitted. Two-hundred year record of increasing growth rates in the ocean quahog (*Arctica islandica*) in the western Atlantic Ocean. J. Exp. Mar. Biol. Ecol.

While considerable research has been done on the biology of ocean quahogs as well as the age structure of various populations, limited information is available on the historic recruitment patterns of ocean quahogs and the uncertainty of the response of these animals as the stock is fished down has led to concerns about the sustainability of managing these long-lived animals. The variable growth rates of these clams result in geographical differences in the age structure of ocean quahog population throughout the range of the stock. The amount of time and resources required to age a sufficient number of ocean quahogs to develop age-length keys often limits studies to a single population. Additionally, the sample size used to assess a population will almost always underrepresent the entire age range present in a population as ocean quahogs commonly exceed 200 years in age. Thus, a sample size of 200 animals assigns on average approximately one individual per year assuming no duplicates in age. It is also rare for a study to assess the age of animals from all sizes present in a population, e.g. from young of the year to the largest size observed, which limits the information about the population that can be drawn from the results. Furthermore, an age-length key produced for a specific population will not produce accurate age estimates due to the variable growth rates of these animals throughout the Atlantic Ocean. By investigating long-term recruitment trends for four populations throughout the range of the U.S. stock, this study contributes valuable information that can be used to inform stock assessments and to improve management of ocean quahogs.

In Chapter II, the long-term recruitment trends for a Georges Bank population were investigated through the analysis of annual growth lines in the hinge plate. Ages of animals representing the fully recruited size range were used to develop an age-length key, enabling reconstruction of the population age frequency. The population age frequency showed that the Georges Bank population experienced an increase in recruitment beginning in the late 1890’s. Initial settlement, documented by a few ocean quahogs that were much older, occurred much earlier, in the early 1800s. Following the late 1890s increase in recruitment, the population expanded rapidly reaching carrying capacity in 20 to 30 years. Recruitment was more or less continuous after this expansion, consistent with maintenance of a population at carrying capacity. Unusually large year classes were not observed, nor were significant periods of high recruitment interspersed with periods of low recruitment. One would expect to see large year classes if recruitment occurred only once or twice every several decades as previously thought. Finally, the relationship of growth rate with age for the oldest clams was assessed using the time series of yearly growth increments and the resulting relationship fitted to three models (von Bertalanffy, Gompertz, and Tanaka's ALOG curve). The ALOG model was clearly superior because it allows for persistent indeterminate growth at old age, rather than the asymptotic behavior of the other two, and because it allows for a rapid change in growth rate at what is presumed to be maturity.

In Chapter III, geographic differences in the age structure of three additional populations of ocean quahogs throughout the range of the U.S. stock were examined. The ages of animals ≥80-mm shell length were estimated. The observed age frequency from each site was used to develop an age-length key enabling reconstruction of the population age frequency for the site. Within-site variability was high for both age at length and length at age; a single age-length key could not be applied and would not result in accurate age estimates for populations throughout the northwestern Atlantic. For most sites, initial colonization began 200-250 years BP, coincident with the ending of the Little Ice Age, with the southern populations being established first, consistent with a presumed warming from the south. All sites experienced an increase in recruitment beginning in the late 1800's to early 1900's, depending upon site, whereupon the populations reached carrying capacity and remained so characterized subsequently through more or less continuous low-level recruitment. The lag in population expansion following initial colonization is consistent with the extended time to maturity in this species. Major year classes and periods of curtailed recruitment were rare. All four populations, including the Georges Bank population, show evidence of high recruitment capacity when below carrying capacity and relatively continuous recruitment when at carrying capacity.

In Chapter IV, the growth rates of ocean quahogs from the four populations throughout the range of the U.S. stock were examined. Both geographic and temporal differences (on a scale of decadal or longer) in growth rates exist throughout the range of the stock. The age at which animals reached 60, 80, and 90 mm decreased significantly, and average growth rates to 60, 80, and 90 mm increased significantly with birth year at a New Jersey and a Long Island site, both located in the southwestern portion of the stock, since initial colonization, likely in response to increasing bottom water temperatures. That is, growth rates vary temporally with birth date at the southwestern sites, with younger animals growing at a much faster rate in recent decades than those born many decades previously, whereas at the northern sites off southern New England and on Georges Bank, changes in growth rates through time are limited to older adult animals or absent altogether. Thus, at the southern portion of the range, variation in growth rate over time exists in all phases of ocean quahog life, whereas on Georges Bank, little evidence exists for any differential in growth rate over the last ~200 years. The fact that ocean quahogs record the rise in ocean temperatures after the Little Ice Age in the Mid-Atlantic Bight southeast of southern New England, yet demonstrate no evidence of such a rise in the southern New England and Georges Bank region, would suggest a differential response of ocean circulation and its control of bottom water temperature between the northern and southern portions of the Mid-Atlantic Bight over the last 200+ years.

The research in this thesis provides substantial information about ocean quahog population dynamics that is essential to the management of this species. By describing the age, growth, and recruitment dynamics of this commercially important species, this thesis provides the first comprehensive population age frequencies for ocean quahogs in the mid-Atlantic, which lend insight on long-term recruitment dynamics necessary to improve fishery management. Some of the most important knowledge gained from this research is that recruitment of ocean quahogs throughout the mid-Atlantic has been effectively continuous since the 1800s, alleviating concerns that recruitment is infrequent, occurring only a few times in several decades. These results have contributed to a successful benchmark assessment in 2017 by the NEFSC, and have subsequently be used to inform fishery management decisions by the Mid-Atlantic Fisheries Management Council’s Scientific and Statistical Committee

APPENDIX A

Tables

Table 1

Parameter estimates of von Bertalanffy and Gompertz models.

	Von Bertalanffy Estimate	**Von Bertalanffy Std. Error**	**Gompertz Estimate**	**Gompertz Std. Error**
Linf	101.9000	0.4223	100.6000	0.4086
K	0.0225	0.0005	0.0285	0.0007
t0	-12.3400	0.6254	5.6510	0.5057

Table 2

Test statistics for each metric.

	80 mm	**85 mm**	**90 mm**	**95 mm**	**100 mm**	**105 mm**	**110 mm**
$\bar{x}$	0.1 < P < 0.2	0.1 < P < 0.2	0.05 < P < 0.1	0.1 < P < 0.2	P = 0.005	0.6 < P < 0.7	0.3 < P < 0.4
var	0.2 < P < 0.3	0.1 < P < 0.2	0.6 < P < 0.7	0.2 < P < 0.3	P < 0.005	0.05 < P < 0.1	0.05 < P < 0.1
d $\bar{x}$	P = 0.4	P = 0.4	P = 0.4	0.4 < P < 0.5	P = 0.4	0.4 < P < 0.5	P = 04
d var	0.7 < P < 0.8	0.05 < P < 0.1	0.6 < P < 0.7	0.95 < P < 0.99	0.95 < P < 0.99	0.5 < P < 0.6	0.05 < P < 0.1

Non-random statistics are shaded for each observed mean ($\bar{x}$), observed variance (var), observed mean of the difference in ages of animals ordered by their age (d $\bar{x}$), and the observed variance of these differences (d var) in each size class. The difference mean and variance are obtained from the difference between consecutive ages ordered by age.

Table 3

Age data from the original 20 clams sampled and the resample of 20 additional individuals in the 100-<105 mm size class.

Original ages	**Resample ages**
73	81
75	82
79	86
99	90
101	104
103	107
106	109
106	113
107	117
110	122
112	122
114	123
114	125
115	128
118	131
121	135
134	139
165	152
182	166
198	198

Table 4

Results of permutation tests comparing the first set of aged animals in the 100-<105 mm size class to the second.

	With replacement: F	**Without replacement: T**
$\bar{x}$	P = 0.219	P = 0.320
var	P = 0.832	P = 0.694
d $\bar{x}$	-	P = 0.622
d var	-	P = 0.657

For the left column, the observed mean ($\bar{x}$), observed variance (var), observed mean of the difference in ages of animals ordered by their age ($d\ \bar{x}$), and the observed variance of these differences (d var) in each size class for the two datasets were directly compared. Only the first two metrics can be evaluated as any test using a 'with replacement' option produces biased results for a set of differences between consecutive ages ordered by age. The second test, using a 'without replacement' option investigated the likelihood that the second set of ages represented a random draw from the combined dataset.

Table 5

Age-length key: probability of each decadal age group occurring within each 5-mm size class.

	50	**60**	**70**	**80**	**90**	**100**	**110**	**120**	**130**	**140**	**150**	**160**	**170**	**180**	**190**
80 mm	0.138	0.184	0.161	0.204	0.168	0.066	0.079	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
85 mm	0.000	0.089	0.165	0.231	0.200	0.139	0.100	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.000
90 mm	0.000	0.238	0.175	0.108	0.150	0.113	0.121	0.096	0.000	0.000	0.000	0.000	0.000	0.000	0.000
95 mm	0.000	0.127	0.140	0.079	0.132	0.233	0.097	0.061	0.040	0.070	0.022	0.000	0.000	0.000	0.000
100 mm	0.000	0.000	0.065	0.085	0.115	0.145	0.180	0.135	0.065	0.075	0.015	0.055	0.025	0.010	0.030
105 mm	0.000	0.013	0.048	0.083	0.075	0.162	0.136	0.167	0.149	0.092	0.061	0.013	0.000	0.000	0.000
110 mm	0.000	0.000	0.000	0.000	0.057	0.077	0.144	0.172	0.191	0.148	0.091	0.077	0.043	0.000	0.000

Zero probabilities indicate the absence of animals at that size and age given the sampling constraints as discussed in the text.

Table 6

Generated age frequency; number of individuals per tow at each age. Shaded boxes represent ages with the highest probability of occurring.

Age	N	Age	N	Age	N	Age	N	Age	N
51	6.86	**81**	44.99	**111**	23.57	**141**	2.43	**171**	0.03
52	0.00	**82**	41.51	**112**	37.53	**142**	4.31	**172**	0.03
53	6.86	**83**	41.10	**113**	20.95	**143**	3.39	**173**	0.72
54	13.71	**84**	39.30	**114**	37.18	**144**	9.40	**174**	0.03
55	9.14	**85**	44.16	**115**	41.83	**145**	1.93	**175**	0.03
56	18.28	**86**	46.41	**116**	19.21	**146**	4.81	**176**	0.00
57	15.99	**87**	40.20	**117**	26.94	**147**	5.11	**177**	0.00
58	6.86	**88**	58.17	**118**	28.91	**148**	7.79	**178**	0.00
59	13.71	**89**	50.44	**119**	21.28	**149**	0.44	**179**	0.00
60	16.56	**90**	43.72	**120**	19.04	**150**	4.83	**180**	0.00
61	6.86	**91**	45.63	**121**	17.08	**151**	2.43	**181**	0.00
62	18.90	**92**	32.23	**122**	25.29	**152**	2.67	**182**	0.66
63	32.48	**93**	74.74	**123**	38.60	**153**	0.91	**183**	0.00
64	31.01	**94**	38.94	**124**	19.22	**154**	1.71	**184**	0.00
65	47.49	**95**	44.78	**125**	11.54	**155**	0.74	**185**	0.00
66	54.46	**96**	38.97	**126**	20.53	**156**	0.91	**186**	0.00
67	58.84	**97**	29.74	**127**	9.15	**157**	1.52	**187**	0.00
68	43.92	**98**	43.19	**128**	9.19	**158**	0.44	**188**	0.00
69	45.15	**99**	28.57	**129**	0.91	**159**	1.66	**189**	0.00
70	35.39	**100**	26.44	**130**	2.36	**160**	1.03	**190**	0.00
71	61.24	**101**	20.67	**131**	2.52	**161**	0.88	**191**	0.00
72	24.99	**102**	37.16	**132**	0.61	**162**	0.17	**192**	0.00
73	32.99	**103**	40.78	**133**	6.66	**163**	0.13	**193**	1.33
74	51.51	**104**	21.04	**134**	2.73	**164**	0.00	**194**	1.33
75	31.10	**105**	18.99	**135**	2.24	**165**	0.74	**195**	1.33
76	36.93	**106**	18.76	**136**	3.79	**166**	0.69	**196**	1.33
77	49.56	**107**	30.58	**137**	4.97	**167**	1.35	**197**	0.66
78	42.21	**108**	35.73	**138**	5.13	**168**	0.00	**198**	0.66
79	26.22	**109**	42.49	**139**	5.52	**169**	0.08	**199**	0.66
80	53.36	**110**	24.53	**140**	1.91	**170**	0.74	**200**	0.00

Table 7

Observed age frequency; number of individuals per tow at each age.

Age	N	Age	N	Age	N	Age	N	Age	N
51	0.00	**81**	56.99	**111**	37.68	**141**	0.00	**171**	0.00
52	0.00	**82**	0.00	**112**	45.45	**142**	0.00	**172**	0.00
53	0.00	**83**	37.30	**113**	38.47	**143**	0.00	**173**	0.32
54	54.84	**84**	65.57	**114**	92.52	**144**	0.00	**174**	0.00
55	0.00	**85**	56.99	**115**	7.30	**145**	0.00	**175**	0.00
56	0.00	**86**	74.60	**116**	46.26	**146**	0.00	**176**	0.00
57	27.42	**87**	54.84	**117**	20.68	**147**	1.84	**177**	0.00
58	0.00	**88**	37.30	**118**	7.30	**148**	19.16	**178**	0.00
59	27.42	**89**	77.29	**119**	37.30	**149**	0.00	**179**	0.00
60	0.00	**90**	1.84	**120**	77.68	**150**	0.00	**180**	0.00
61	0.00	**91**	27.42	**121**	7.62	**151**	0.32	**181**	0.00
62	0.00	**92**	0.00	**122**	1.84	**152**	0.00	**182**	7.30
63	0.00	**93**	130.29	**123**	37.68	**153**	0.00	**183**	0.00
64	18.84	**94**	0.00	**124**	0.00	**154**	0.00	**184**	0.00
65	114.45	**95**	74.60	**125**	0.32	**155**	0.00	**185**	0.00
66	65.57	**96**	102.87	**126**	75.77	**156**	0.00	**186**	0.00
67	92.14	**97**	0.32	**127**	1.84	**157**	0.00	**187**	0.00
68	56.99	**98**	0.00	**128**	0.00	**158**	2.16	**188**	0.00
69	65.57	**99**	46.44	**129**	0.00	**159**	0.00	**189**	0.00
70	18.84	**100**	0.00	**130**	0.32	**160**	0.00	**190**	0.00
71	76.44	**101**	7.30	**131**	3.68	**161**	0.00	**191**	0.00
72	18.84	**102**	0.00	**132**	0.00	**162**	0.00	**192**	0.00
73	44.60	**103**	26.14	**133**	0.00	**163**	0.32	**193**	0.00
74	18.84	**104**	4.00	**134**	7.30	**164**	0.00	**194**	0.00
75	64.29	**105**	0.00	**135**	0.32	**165**	7.30	**195**	0.00
76	0.00	**106**	33.44	**136**	0.00	**166**	0.00	**196**	0.00
77	0.00	**107**	36.88	**137**	2.47	**167**	0.00	**197**	0.00
78	0.00	**108**	37.30	**138**	0.00	**168**	0.00	**198**	7.30
79	7.30	**109**	39.99	**139**	0.00	**169**	0.00	**199**	0.00
80	130.29	**110**	44.60	**140**	2.16	**170**	0.00	**200**	0.00

Table 8

Test statistics comparing the observed distribution of ages to that expected from a random draw of ages from the age range recorded in the size class.

	80 mm	**85 mm**	**90 mm**	**95 mm**	**100 mm**	**105 mm**	**110 mm**	**115 mm**	**120 mm**
NJ $\bar{x}$	$P < 0.005$	$P < 0.05$	$P < 0.005$	$P < 0.1$	$P > 0.05$	$P > 0.9$	$P > 0.05$	$P < 0.005$	$P > 0.05$
NJ var	$P > 0.05$	$P > 0.05$	$P < 0.05$	$P = 0.6$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P < 0.05$	$P > 0.05$
NJ d $\bar{x}$	$P = 0.4$	$P = 0.4$	$P = 0.4$	$P > 0.05$	$P > 0.05$	$P = 0.4$	$P = 0.4$	$P > 0.05$	$P > 0.05$
NJ d var	$P > 0.05$	$P > 0.05$	$P > 0.9$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.99$	$P > 0.05$
LI $\bar{x}$	$P < 0.005$	$P < 0.005$	$P < 0.005$	$P < 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$		
LI var	$P < 0.05$	$P < 0.05$	$P < 0.1$	$P > 0.05$	$P < 0.05$	$P > 0.05$	$P > 0.05$		
LI d $\bar{x}$	$P = 0.4$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.95$	$P = 0.4$	$P > 0.05$		
LI d var	$P > 0.99$	$P > 0.99$	$P > 0.99$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$		
SNE $\bar{x}$	$P < 0.005$	$P > 0.05$	$P < 0.005$	$P > 0.05$	$P > 0.05$				
SNE var	$P = 0.3$	$P > 0.05$	$P < 0.005$	$P > 0.05$	$P < 0.1$				
SNE d $\bar{x}$	$P = 0.6$	$P = 0.6$	$P = 0.4$	$P > 0.05$	$P = 0.4$				
SNE d var	$P > 0.05$	$P > 0.05$	$P > 0.99$	$P > 0.05$	$P > 0.05$				

The observed mean ($\bar{x}$), the observed variance (var), the observed mean of the differences of consecutive pairs of animals ordered by their age ($d\ \bar{x}$), and the observed variance of these differences (d var) within each size class for each site are shown for each site. Sizes are the lower size boundary of the size class. Cases where the observed distribution of ages were unlikely to be obtained by a random draw of ages in the observed age range are shaded.

Table 9

Age data from the (1) original 20 clams chosen to be aged and (2) the resample of 20 additional individuals for each site.

NJ1	NJ2	LI1	LI2	SN1	SN2	GB1	GB2
65	73	57	76	79	80	73	81
69	81	60	82	81	87	75	82
70	84	70	84	84	88	79	86
73	89	71	87	84	91	99	90
74	90	72	96	85	92	101	104
75	104	77	99	90	93	103	107
77	116	79	99	91	93	106	109
79	131	94	100	91	93	106	113
81	134	96	115	95	99	107	117
86	134	98	127	103	100	110	122
89	138	117	141	104	102	112	122
90	140	131	156	106	103	114	123
92	141	137	163	114	103	114	125
105	143	145	168	118	103	115	128
105	146	169	183	120	106	118	131
109	146	177	189	128	106	121	135
112	165	221	219	129	110	134	139
113	169	227	222	132	112	165	152
116	171	233	225	162	140	182	166
153	173	240	243	172	141	198	198

New Jersey (NJ) 95-mm size class, the Long Island (LI) 90-mm size class, the Southern New England (SN) 90-mm size class, and the Georges Bank (GB) 100-mm size class. Shaded boxes highlight ages present in the first set of 20 that were also observed in the second set of 20. Note the selected size classes correspond to those classes with outliers and extended age ranges (Figure 12).

Table 10

Permutation test statistics for each test metric.

	NJ	**LI**	**SNE**
$\bar{x}$	P = 0.001	P = 0.210	P = 0.201
var	P = 0.011	P = 0.814	P = 0.097
d $\bar{x}$	P = 0.126	P = 0.501	P = 0.196
d var	P = 0.995	P = 0.706	P = 0.601

Statics are shown for the observed mean ($\bar{x}$), observed variance (var), observed mean of the difference in ages of animals ordered by their age (d $\bar{x}$), and the observed variance of these differences (d var).

Table 11

New Jersey age-length key.

	80 mm	85 mm	90 mm	95 mm	100 mm	105 mm	110 mm	115 mm	120 mm
20	0.335	0.167	0.000	0.000	0.000	0.000	0.000	0.000	0.000
30	0.421	0.179	0.025	0.000	0.000	0.000	0.000	0.000	0.000
40	0.182	0.159	0.108	0.000	0.000	0.000	0.000	0.000	0.000
50	0.062	0.115	0.104	0.000	0.000	0.000	0.000	0.000	0.000
60	0.000	0.083	0.125	0.087	0.083	0.000	0.000	0.000	0.000
70	0.000	0.103	0.179	0.129	0.079	0.017	0.000	0.000	0.000
80	0.000	0.068	0.192	0.122	0.116	0.100	0.004	0.061	0.000
90	0.000	0.036	0.108	0.109	0.139	0.144	0.061	0.147	0.000
100	0.000	0.091	0.050	0.078	0.130	0.194	0.082	0.113	0.000
110	0.000	0.000	0.038	0.073	0.176	0.181	0.126	0.130	0.000
120	0.000	0.000	0.021	0.058	0.125	0.207	0.165	0.108	0.100
130	0.000	0.000	0.004	0.087	0.065	0.157	0.095	0.134	0.290
140	0.000	0.000	0.042	0.087	0.088	0.000	0.165	0.100	0.080
150	0.000	0.000	0.004	0.067	0.000	0.000	0.134	0.069	0.140
160	0.000	0.000	0.000	0.062	0.000	0.000	0.074	0.069	0.260
170	0.000	0.000	0.000	0.044	0.000	0.000	0.091	0.022	0.130
180	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000
190	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
200	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
210	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000
220	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.000

For convenience, the probability of each decadal age group occurring within each 5-mm size class is provided. Population age frequencies derived in this study used the probability at each age rather than decadal age groups.

Table 12

Long Island age-length key.

	80 mm	85 mm	90 mm	95 mm	100 mm	105 mm	110 mm
40	0.154	0.154	0.118	0.000	0.000	0.000	0.000
50	0.245	0.231	0.140	0.069	0.000	0.000	0.000
60	0.146	0.159	0.127	0.092	0.000	0.000	0.000
70	0.146	0.163	0.127	0.055	0.000	0.000	0.000
80	0.110	0.140	0.086	0.062	0.016	0.000	0.000
90	0.075	0.077	0.100	0.069	0.041	0.000	0.000
100	0.059	0.022	0.031	0.069	0.012	0.000	0.000
110	0.015	0.000	0.072	0.067	0.008	0.007	0.048
120	0.000	0.000	0.050	0.057	0.020	0.059	0.138
130	0.027	0.050	0.040	0.051	0.090	0.027	0.229
140	0.019	0.000	0.027	0.042	0.119	0.035	0.138
150	0.000	0.000	0.004	0.021	0.107	0.087	0.131
160	0.000	0.000	0.004	0.046	0.144	0.099	0.138
170	0.000	0.000	0.004	0.037	0.107	0.115	0.159
180	0.000	0.000	0.009	0.032	0.078	0.131	0.013
190	0.000	0.000	0.050	0.032	0.099	0.091	0.000
200	0.000	0.000	0.004	0.041	0.028	0.087	0.000
210	0.000	0.000	0.000	0.042	0.028	0.067	0.000
220	0.000	0.000	0.000	0.028	0.041	0.059	0.000
230	0.000	0.000	0.000	0.032	0.049	0.051	0.000
240	0.000	0.000	0.000	0.046	0.004	0.067	0.000
250	0.000	0.000	0.000	0.000	0.000	0.011	0.000

For convenience, the probability of each decadal age group occurring within each 5-mm size class is provided. Population age frequencies derived in this study used the probability at each age rather than the decadal age group.

Table 13

Southern New England age-length key.

	80 mm	**85 mm**	**90 mm**	**95 mm**	**100 mm**
70	0.190	0.116	0.059	0.031	0.033
80	0.372	0.238	0.131	0.095	0.042
90	0.295	0.333	0.154	0.090	0.084
100	0.140	0.216	0.181	0.150	0.096
110	0.000	0.095	0.154	0.072	0.180
120	0.000	0.000	0.125	0.100	0.197
130	0.000	0.000	0.086	0.040	0.100
140	0.000	0.000	0.063	0.113	0.138
150	0.000	0.000	0.013	0.118	0.046
160	0.000	0.000	0.009	0.168	0.071
170	0.000	0.000	0.020	0.018	0.004

For convenience, the probability of each decadal age group occurring within each 5-mm size class is provided. Population age frequencies derived in this study used the probability at each age rather than the decadal age group.

Table 14

Generated age frequency for New Jersey.

Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N
20	5.77	**50**	19.95	**80**	20.49	**110**	17.53	**140**	15.19	**170**	2.3	**200**	0
21	4.62	**51**	13.96	**81**	25.78	**111**	19.94	**141**	8.2	**171**	5.35	**201**	0
22	6.93	**52**	2.31	**82**	22.29	**112**	9.88	**142**	9.62	**172**	4.97	**202**	0
23	4.62	**53**	18.54	**83**	23.77	**113**	16.22	**143**	12.06	**173**	5.31	**203**	0
24	5.77	**54**	10.42	**84**	25.28	**114**	9.63	**144**	20.55	**174**	2.73	**204**	0
25	15.88	**55**	5.78	**85**	32.19	**115**	9.08	**145**	6.33	**175**	3.33	**205**	0
26	23.81	**56**	10.45	**86**	18.93	**116**	17.84	**146**	5.92	**176**	0.21	**206**	0
27	18.09	**57**	5.83	**87**	16.12	**117**	14.9	**147**	7.82	**177**	0.21	**207**	0
28	22.74	**58**	11.76	**88**	23.78	**118**	12.81	**148**	14.73	**178**	0.43	**208**	0
29	19.3	**59**	8.24	**89**	32.29	**119**	22.84	**149**	3.73	**179**	0.23	**209**	0
30	14.68	**60**	21.21	**90**	15.6	**120**	15.47	**150**	4.38	**180**	0.21	**210**	0
31	20.45	**61**	6.9	**91**	23.1	**121**	14.24	**151**	7.08	**181**	0	**211**	0
32	23.89	**62**	15.14	**92**	16.34	**122**	13.18	**152**	5.01	**182**	0	**212**	0
33	8.03	**63**	14.68	**93**	34.16	**123**	6.41	**153**	5.79	**183**	0	**213**	0
34	13.68	**64**	9.42	**94**	21.43	**124**	10.24	**154**	2.89	**184**	0	**214**	0
35	21.66	**65**	11.47	**95**	13.21	**125**	11.33	**155**	2.97	**185**	0	**215**	0.04
36	15.88	**66**	15.11	**96**	19.44	**126**	17.62	**156**	3.52	**186**	0	**216**	0.04
37	20.69	**67**	30.2	**97**	2.53	**127**	13.27	**157**	5.16	**187**	0	**217**	0.02
38	11.5	**68**	17.55	**98**	18.92	**128**	12.27	**158**	1.51	**188**	0	**218**	0.02
39	15.04	**69**	23.65	**99**	31.17	**129**	7.05	**159**	1.72	**189**	0	**219**	0.02

Table 14 (continued)

40	12.65	**70**	21.58	**100**	14	**130**	9.29	**160**	2.7	**190**	0	**220**	0.04
41	13.76	**71**	22.15	**101**	13.58	**131**	21.63	**161**	3.34	**191**	0	**221**	0.02
42	24.33	**72**	22.6	**102**	17.94	**132**	8.56	**162**	2.12	**192**	0	**222**	0.02
43	11.68	**73**	26.71	**103**	16.65	**133**	7.81	**163**	1.5	**193**	0		
44	18.48	**74**	17.4	**104**	20.02	**134**	13.21	**164**	1.05	**194**	0		
45	15.15	**75**	23.09	**105**	16.1	**135**	10.04	**165**	5.33	**195**	0		
46	14.02	**76**	20.53	**106**	24.8	**136**	7.26	**166**	2.71	**196**	0		
47	19.58	**77**	21.15	**107**	15.53	**137**	1.78	**167**	5.87	**197**	0		
48	12.73	**78**	20.16	**108**	15.39	**138**	6.41	**168**	0.31	**198**	0		
49	8.14	**79**	26.42	**109**	15.09	**139**	6.98	**169**	7.85	**199**	0		

Standardized to the number of individuals per tow at each age. Percentages can be obtained by dividing by 2111, the total number of animals measured ≥80-mm in shell length.

Table 15

Generated age frequency for Long Island.

Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N
40	6.62	**70**	15.64	**100**	8.89	**130**	6.24	**160**	1.82	**190**	2.1	**220**	1.52	**250**	0
41	17.88	**71**	17.44	**101**	8.03	**131**	10.37	**161**	2.91	**191**	7.31	**221**	1.79	**251**	0.1
42	13.41	**72**	20.12	**102**	5.83	**132**	4.24	**162**	2.61	**192**	4.33	**222**	2.13	**252**	0.1
43	13.4	**73**	32.52	**103**	14.57	**133**	7.12	**163**	4.15	**193**	5.6	**223**	0.56	**253**	0
44	20.13	**74**	25.39	**104**	9.76	**134**	10.57	**164**	4.28	**194**	3.97	**224**	1.1	**254**	0.1
45	37.88	**75**	24.94	**105**	9.24	**135**	13.89	**165**	2.16	**195**	2.88	**225**	0.88		
46	33.54	**76**	35.24	**106**	3.53	**136**	20.96	**166**	2.94	**196**	3.93	**226**	0.76		
47	22.45	**77**	19.11	**107**	9.32	**137**	4.56	**167**	3.59	**197**	5.44	**227**	1.81		
48	24.46	**78**	25.6	**108**	4.47	**138**	2.99	**168**	3.09	**198**	1.85	**228**	0.44		
49	31.18	**79**	23.22	**109**	4.77	**139**	1.21	**169**	1.54	**199**	6.4	**229**	1.19		
50	26.79	**80**	17.88	**110**	10.26	**140**	9.97	**170**	4.35	**200**	1.81	**230**	2.15		
51	26.66	**81**	18.67	**111**	3.95	**141**	8.81	**171**	1.49	**201**	1.1	**231**	0.9		
52	33.51	**82**	21.93	**112**	4.91	**142**	2.29	**172**	1.83	**202**	1	**232**	0.98		
53	37.97	**83**	34.78	**113**	6.72	**143**	7.16	**173**	3.41	**203**	4.41	**233**	1.42		
54	15.09	**84**	14.57	**114**	3.53	**144**	2.81	**174**	2.19	**204**	0.98	**234**	1.17		
55	34.73	**85**	19.09	**115**	6.15	**145**	2.91	**175**	1.37	**205**	1.42	**235**	1.44		
56	45.07	**86**	16.5	**116**	8.12	**146**	6.5	**176**	2.18	**206**	3.04	**236**	2.05		
57	30.24	**87**	16.05	**117**	6.05	**147**	0.81	**177**	2.63	**207**	1.1	**237**	1.54		

Table 15 (continued)

58	39.68	**88**	16.06	**118**	3.16	**148**	2.7	**178**	1.57	**208**	0.98	**238**	0.9
59	48.52	**89**	15.54	**119**	9.88	**149**	2.8	**179**	3	**209**	1.28	**239**	1.02
60	20.93	**90**	19.03	**120**	1.56	**150**	1.37	**180**	1.62	**210**	0.84	**240**	3.21
61	24.67	**91**	14.14	**121**	3.8	**151**	4.55	**181**	2.29	**211**	1	**241**	2.4
62	24.07	**92**	19.42	**122**	8.41	**152**	1.18	**182**	4.19	**212**	1.52	**242**	2.6
63	24.6	**93**	15.9	**123**	3.48	**153**	0.68	**183**	3.06	**213**	1.76	**243**	2.21
64	16.06	**94**	11.51	**124**	4.48	**154**	0.85	**184**	4.07	**214**	1.89	**244**	0.54
65	12.95	**95**	8.9	**125**	5.07	**155**	2.46	**185**	1.38	**215**	2.23	**245**	1.72
66	36.58	**96**	8.89	**126**	5.01	**156**	2.79	**186**	1.37	**216**	0.83	**246**	0.2
67	20.43	**97**	15.64	**127**	2.26	**157**	1.69	**187**	0.5	**217**	0.54	**247**	0.44
68	33.4	**98**	21.5	**128**	3.6	**158**	1.2	**188**	3.35	**218**	1.44	**248**	0.2
69	32.54	**99**	15.64	**129**	4.76	**159**	2.57	**189**	0.84	**219**	2.77	**249**	0

Standardized to the number of individuals per tow at each age. Percentages can be obtained by dividing by 1910, the total number of animals measured ≥ 80-mm in shell length.

Table 16

Generated age frequency for Southern New England.

Age	N	Age	N	Age	N	Age	N
72	10.71	**98**	59.17	**124**	6.48	**150**	3.52
73	10.71	**99**	46.61	**125**	6.10	**151**	1.92
74	24.98	**100**	46.12	**126**	6.39	**152**	2.25
75	31.56	**101**	26.94	**127**	5.32	**153**	0.74
76	45.45	**102**	26.69	**128**	5.11	**154**	0.40
77	37.34	**103**	43.85	**129**	4.66	**155**	0.81
78	58.52	**104**	47.29	**130**	4.04	**156**	0.47
79	22.28	**105**	29.27	**131**	6.08	**157**	2.32
80	25.22	**106**	37.02	**132**	6.97	**158**	1.00
81	44.96	**107**	26.39	**133**	3.66	**159**	0.66
82	49.26	**108**	18.44	**134**	3.88	**160**	1.80
83	57.90	**109**	10.40	**135**	1.78	**161**	1.21
84	69.21	**110**	23.20	**136**	2.04	**162**	1.99
85	41.92	**111**	14.36	**137**	4.00	**163**	1.66
86	38.32	**112**	22.38	**138**	1.96	**164**	2.54
87	39.31	**113**	19.99	**139**	0.00	**165**	1.47
88	47.16	**114**	7.70	**140**	2.44	**166**	0.78
89	71.76	**115**	4.80	**141**	4.59	**167**	1.54
90	36.64	**116**	10.16	**142**	3.22	**168**	1.40
91	63.03	**117**	3.59	**143**	4.59	**169**	2.22
92	48.74	**118**	4.77	**144**	4.44	**170**	4.11
93	45.53	**119**	6.25	**145**	3.69	**171**	1.89
94	53.87	**120**	5.30	**146**	1.92	**172**	2.41
95	46.80	**121**	8.27	**147**	1.85		
96	44.34	**122**	3.29	**148**	2.70		
97	43.62	**123**	2.63	**149**	3.06		

Standardized to the number of individuals per tow at each age. Percentages can be obtained by dividing by 1805, the total number of animals measured ≥80-mm in shell length.

Table 17

New Jersey age frequency based solely on the animals aged and standardized to the number of individuals per tow at each age.

Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N
20	0.00	**50**	0.00	**80**	26.24	**110**	6.19	**140**	11.22	**170**	2.33	**200**	0.00
21	0.00	**51**	0.00	**81**	42.72	**111**	0.00	**141**	11.22	**171**	11.22	**201**	0.00
22	0.00	**52**	13.86	**82**	48.63	**112**	11.22	**142**	0.00	**172**	0.00	**202**	0.00
23	0.00	**53**	0.00	**83**	0.00	**113**	11.46	**143**	11.46	**173**	11.22	**203**	0.00
24	13.86	**54**	0.00	**84**	31.03	**114**	0.00	**144**	42.89	**174**	0.00	**204**	0.00
25	27.71	**55**	12.42	**85**	56.70	**115**	0.00	**145**	0.00	**175**	0.00	**205**	0.00
26	26.28	**56**	0.00	**86**	11.22	**116**	54.87	**146**	51.03	**176**	0.00	**206**	0.00
27	12.42	**57**	13.86	**87**	5.96	**117**	22.61	**147**	0.00	**177**	2.33	**207**	0.00
28	24.84	**58**	0.00	**88**	48.63	**118**	0.00	**148**	0.00	**178**	0.00	**208**	0.00
29	37.26	**59**	0.00	**89**	64.88	**119**	28.35	**149**	0.24	**179**	0.00	**209**	0.00
30	12.42	**60**	28.35	**90**	36.30	**120**	16.82	**150**	2.33	**180**	0.00	**210**	0.00
31	24.84	**61**	0.00	**91**	0.00	**121**	46.75	**151**	0.00	**181**	0.00	**211**	0.00
32	52.56	**62**	0.00	**92**	11.22	**122**	0.00	**152**	4.87	**182**	0.00	**212**	0.00
33	0.00	**63**	0.00	**93**	2.33	**123**	0.00	**153**	11.22	**183**	0.00	**213**	0.00
34	0.00	**64**	20.28	**94**	34.54	**124**	2.33	**154**	0.00	**184**	0.00	**214**	0.00
35	0.00	**65**	39.57	**95**	2.33	**125**	10.62	**155**	0.00	**185**	0.00	**215**	0.00
36	12.42	**66**	0.00	**96**	40.56	**126**	26.24	**156**	2.33	**186**	0.00	**216**	0.00
37	12.42	**67**	13.86	**97**	0.24	**127**	22.81	**157**	0.00	**187**	0.00	**217**	0.00
38	13.86	**68**	0.00	**98**	28.35	**128**	0.00	**158**	0.24	**188**	0.00	**218**	0.00
39	13.86	**69**	11.22	**99**	0.00	**129**	2.33	**159**	2.33	**189**	0.00	**219**	0.00
40	12.42	**70**	11.22	**100**	20.52	**130**	0.00	**160**	0.00	**190**	0.00	**220**	0.24
41	12.42	**71**	42.21	**101**	0.00	**131**	29.33	**161**	0.00	**191**	0.00	**221**	0.00
42	42.21	**72**	0.00	**102**	0.00	**132**	0.00	**162**	0.00	**192**	0.00	**222**	0.00
43	0.00	**73**	50.79	**103**	5.96	**133**	5.96	**163**	11.22	**193**	0.00		
44	12.42	**74**	39.57	**104**	31.50	**134**	25.01	**164**	0.00	**194**	0.00		
45	0.00	**75**	39.57	**105**	22.68	**135**	0.24	**165**	11.22	**195**	0.00		
46	42.21	**76**	28.35	**106**	0.00	**136**	0.00	**166**	0.00	**196**	0.00		
47	13.86	**77**	53.43	**107**	5.96	**137**	0.20	**167**	0.00	**197**	0.00		
48	0.00	**78**	19.81	**108**	23.83	**138**	11.46	**168**	2.97	**198**	0.00		
49	40.77	**79**	31.50	**109**	27.41	**139**	0.24	**169**	11.22	**199**	0.00		

Table 18

Long Island age frequency based solely on the animals aged and standardized to the number of individuals per tow at each age.

Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N	Age	N
40	0.00	**70**	6.18	**100**	6.18	**130**	0.00	**160**	4.00	**190**	4.00	**220**	0.00	**250**	0.00
41	0.00	**71**	6.18	**101**	0.00	**131**	31.03	**161**	1.32	**191**	0.00	**221**	6.18	**251**	0.00
42	0.00	**72**	6.18	**102**	0.00	**132**	0.00	**162**	1.19	**192**	0.00	**222**	6.18	**252**	0.00
43	0.00	**73**	24.85	**103**	0.00	**133**	4.00	**163**	6.18	**193**	0.00	**223**	0.00	**253**	0.00
44	24.26	**74**	0.00	**104**	0.00	**134**	0.00	**164**	0.00	**194**	0.00	**224**	4.00	**254**	0.00
45	48.91	**75**	0.00	**105**	0.00	**135**	49.50	**165**	4.00	**195**	1.19	**225**	6.18		
46	0.00	**76**	6.18	**106**	0.00	**136**	0.00	**166**	8.13	**196**	0.00	**226**	0.00		
47	24.65	**77**	6.18	**107**	0.00	**137**	6.18	**167**	0.00	**197**	0.00	**227**	6.18		
48	49.11	**78**	24.85	**108**	0.00	**138**	4.00	**168**	7.37	**198**	0.00	**228**	0.00		
49	49.11	**79**	6.18	**109**	0.00	**139**	0.13	**169**	6.18	**199**	28.85	**229**	0.00		
50	72.78	**80**	0.00	**110**	24.26	**140**	24.26	**170**	4.00	**200**	0.00	**230**	0.00		
51	48.91	**81**	48.91	**111**	0.00	**141**	6.18	**171**	0.00	**201**	0.00	**231**	0.00		
52	0.00	**82**	55.48	**112**	0.00	**142**	0.25	**172**	0.00	**202**	0.00	**232**	0.00		
53	98.22	**83**	24.65	**113**	0.00	**143**	0.00	**173**	1.19	**203**	0.00	**233**	6.18		
54	24.26	**84**	30.44	**114**	0.00	**144**	5.19	**174**	0.00	**204**	0.00	**234**	0.00		
55	49.30	**85**	24.65	**115**	6.18	**145**	10.17	**175**	0.00	**205**	0.00	**235**	4.00		
56	98.21	**86**	0.00	**116**	0.00	**146**	4.00	**176**	0.00	**206**	0.00	**236**	0.00		
57	54.70	**87**	6.18	**117**	6.18	**147**	0.00	**177**	10.30	**207**	0.00	**237**	0.00		
58	99.00	**88**	24.85	**118**	0.00	**148**	0.00	**178**	1.19	**208**	1.19	**238**	0.00		
59	73.17	**89**	0.00	**119**	0.00	**149**	5.19	**179**	0.00	**209**	1.19	**239**	0.00		
60	6.18	**90**	28.85	**120**	0.00	**150**	0.00	**180**	0.00	**210**	0.00	**240**	6.18		

Table 18 (continued)

61	24.85	**91**	24.85	**121**	0	**151**	28.85	**181**	4	**211**	0	**241**	0
62	73.76	**92**	0	**122**	0	**152**	0	**182**	0	**212**	1.19	**242**	0
63	0	**93**	24.85	**123**	1.32	**153**	0	**183**	6.18	**213**	0	**243**	0
64	24.85	**94**	6.18	**124**	0	**154**	4	**184**	0	**214**	0	**244**	0
65	24.65	**95**	0	**125**	1.19	**155**	4	**185**	0	**215**	0	**245**	6.18
66	0	**96**	12.35	**126**	24.85	**156**	6.18	**186**	0	**216**	4	**246**	0
67	0	**97**	0	**127**	6.18	**157**	0	**187**	1.19	**217**	1.19	**247**	0
68	24.65	**98**	6.18	**128**	0.13	**158**	0	**188**	1.19	**218**	2.38	**248**	1.19
69	48.52	**99**	12.35	**129**	0	**159**	0	**189**	6.18	**219**	8.56	**249**	0

Table 19

Southern New England age frequency based solely on the animals aged and standardized to the number of individuals per tow at each age.

Age	N	Age	N	Age	N	Age	N
72	0.00	**98**	67.16	**124**	1.00	**150**	0.00
73	39.25	**99**	65.39	**125**	3.65	**151**	0.00
74	0.00	**100**	51.48	**126**	3.65	**152**	7.30
75	27.91	**101**	3.65	**127**	0.00	**153**	0.00
76	39.25	**102**	40.13	**128**	8.58	**154**	0.00
77	78.50	**103**	63.21	**129**	10.58	**155**	0.00
78	0.00	**104**	15.88	**130**	0.00	**156**	3.65
79	8.58	**105**	0.00	**131**	1.00	**157**	3.65
80	51.48	**106**	104.23	**132**	8.58	**158**	3.65
81	69.04	**107**	27.91	**133**	1.00	**159**	0.00
82	27.91	**108**	0.00	**134**	1.00	**160**	0.00
83	117.75	**109**	0.00	**135**	0.00	**161**	0.00
84	45.06	**110**	64.39	**136**	0.00	**162**	9.57
85	64.39	**111**	1.00	**137**	3.65	**163**	3.65
86	0.00	**112**	37.48	**138**	0.00	**164**	3.65
87	8.58	**113**	0.00	**139**	0.00	**165**	0.00
88	87.08	**114**	8.58	**140**	8.58	**166**	0.00
89	0.00	**115**	0.00	**141**	8.58	**167**	1.00
90	8.58	**116**	0.00	**142**	0.00	**168**	3.65
91	92.88	**117**	0.00	**143**	0.00	**169**	0.00
92	103.64	**118**	12.23	**144**	0.00	**170**	0.00
93	120.79	**119**	1.00	**145**	0.00	**171**	0.00
94	79.50	**120**	8.58	**146**	0.00	**172**	8.58
95	8.58	**121**	0.00	**147**	0.00		
96	39.25	**122**	1.00	**148**	1.00		
97	3.65	**123**	0.00	**149**	0.00		

Table 20

Summary of the age structure and period over which rapid recruitment occurred at each site, including Georges Bank (Chapter II).

Region	Oldest animal (observed)	Recruitment expansion start	Recruitment expansion end	Youngest animal (observed)	5th, 25th, 50th, 75th percentile age
NJ	220 (1795)	1855	1900	24 (1991)	30, 70, 121, 171
LI	248 (1767)	1895	1935	44 (1971)	50, 93, 147, 200
SNE	172 (1843)	1900	1915	73 (1942)	77, 97, 122, 147
GB	198 (1817)	1890	1920	54 (1961)	58, 88, 125, 162

Expansion years are visually approximated from Figure 13. Population age frequencies were used to determine age percentiles.

Table 21

Model selection results for each site using maximum R-squared selection to predict birth year.

Candidate model	R square	C_p	p-value
New Jersey			
Birth year ~ len	0.6241	377.2133	< 0.0001
Birth year ~ len + d80	0.8370	122.4907	< 0.0001
Birth year ~ len + d90 + d80	0.9153	30.0737	< 0.0001
Birth year ~ len + dlen + d90 + d80	0.9285	16.2522	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9386	6.0000	< 0.0001
Long Island			
Birth year ~ len	0.6228	244.2283	< 0.0001
Birth year ~ len + d80	0.8956	25.4769	< 0.0001
Birth year ~ len + d90 + d80	0.9137	12.8192	< 0.0001
Birth year ~ len + d90 + d80 + d60	0.9266	4.3747	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9271	6.0000	< 0.0001
Georges Bank			
Birth year ~ len	0.3609	166.5788	0.0001
Birth year ~ len + d80	0.7692	42.3623	< 0.0001
Birth year ~ len + dlen + d80	0.8594	16.4636	< 0.0001
Birth year ~ len + dlen + d90 + d60	0.8934	7.9490	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9062	6.0000	< 0.0001
Southern New England			
Birth year ~ len	0.3752	226.5912	0.0011
Birth year ~ len + d80	0.8066	57.6249	< 0.0001
Birth year ~ len + dlen + d80	0.9099	18.7007	< 0.0001
Birth year ~ len + dlen + d90 + d80	0.9343	11.0409	< 0.0001
Birth year ~ len + dlen + d90 + d80 + d60	0.9520	6.0000	< 0.0001

Birth year predicted using length (len), average growth rate birth to 60 mm (d60), 60-80 mm (d80), 80-90 mm (d90), and post-90 mm (dlen).

Table 22

Regression results for the two and three variable models to predict birth year.

Model	**R squared**	**C_p**	**p-value**
NJ			
Birth year ~ d60 + d80	0.3897	3.0000	< 0.0001
Birth year ~ d60 + d80 + d90	0.3798	4.0000	< 0.0001
LI			
Birth year ~ d60 + d80	0.5861	3.0000	< 0.0001
Birth year ~ d60 + d80 + d90	0.7189	4.0000	< 0.0001
GB			
Birth year ~ d60 + d80	0.0172	1.3022	0.6516
Birth year ~ d60 + d80 + d90	0.2800	4.0000	0.0702
SN			
Birth year ~ d60 + d80	0.0416	1.0008	0.6264
Birth year ~ d60 + d80 + d90	0.5058	4.0000	0.0446

The two-variable model uses the average growth rate birth to 60 mm (d60) and 60-80 mm (d80), and for the three-variable model, 80-90 mm (d90).

Table 23

Von Bertalanffy growth parameters for ocean quahogs from previously published studies and this study.

	L_∞ (mm)	**k**
Long Island (Murawaski 1982)	107.6	0.02
Kiel Bay (Brey et al. 1990)	93.6	0.07
Mid-Atlantic Bight (NEFSC 1995)	97.3	0.03
Georges Bank (Lewis et al. 2001)	97.6	0.06
Iceland (Thorarinsdottir and Jacobson 2005)	99.9	0.02
Iceland (Kilada et al. 2007)	92.5	0.03
St. Mary's Bay (Kilada et al. 2007)	87.6	0.05
Sable Bank (Kilada et al. 2007)	90.48	0.05
Belfast Lough (Ridgeway et al. 2012)	93.7	0.03
Georges Bank (Pace et al. 2017)	101.9	0.02
New Jersey (this study)	115.3	0.02
Long Island (this study)	104.73	0.01
Southern New England (this study)	94.62	0.03

Parameters from this study used only the five oldest animals at each site.

APPENDIX B

Figures

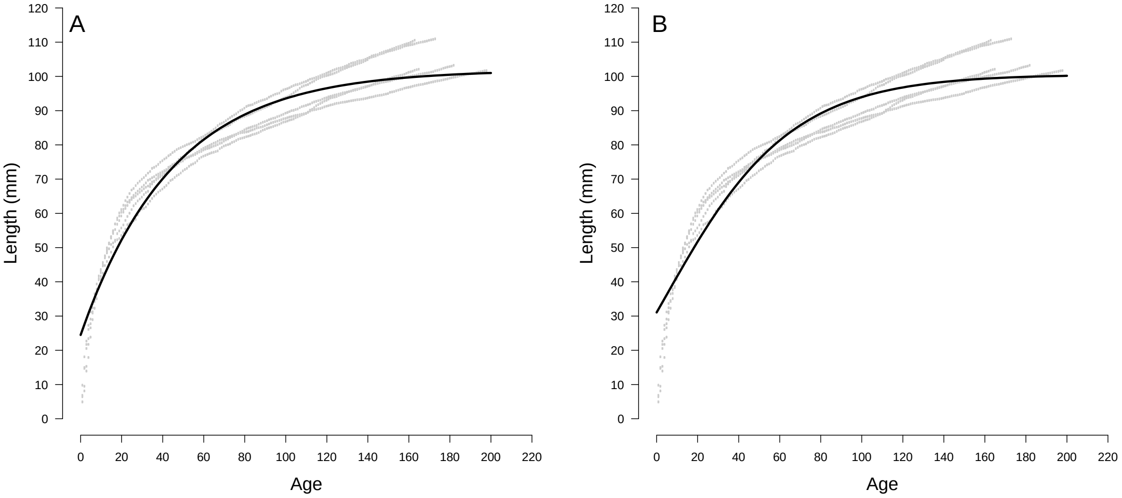

Figure 1. Length-at-age model fits using the von Bertalanffy relationship (A) and Gompertz relationship (B).

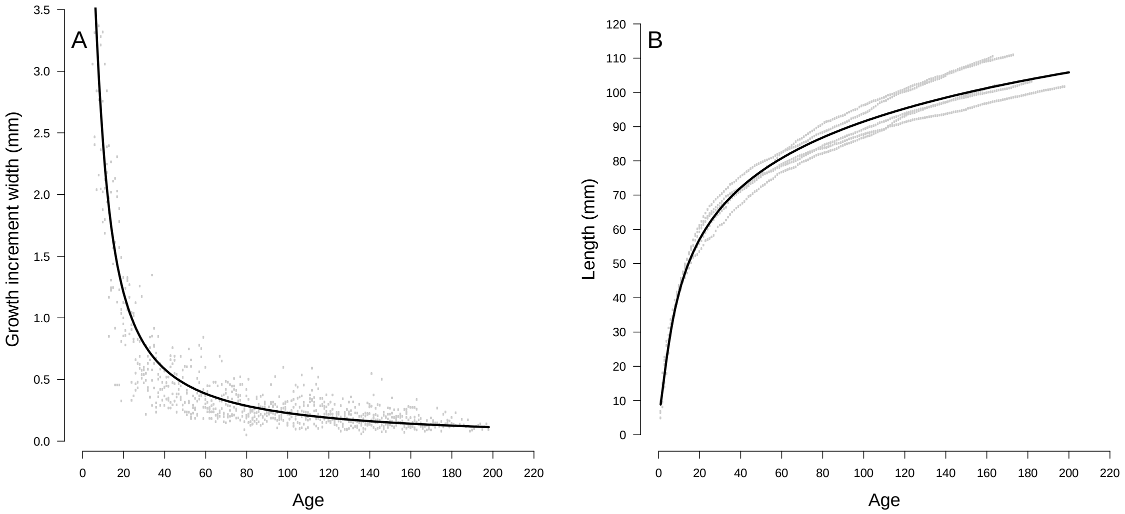

Figure 2. ALOG equation (Eq. 3) fit to age-at-growth increment width (A). Integrated 4-parameter ALOG equation (Eq. 4) fit to age-at-length (B).

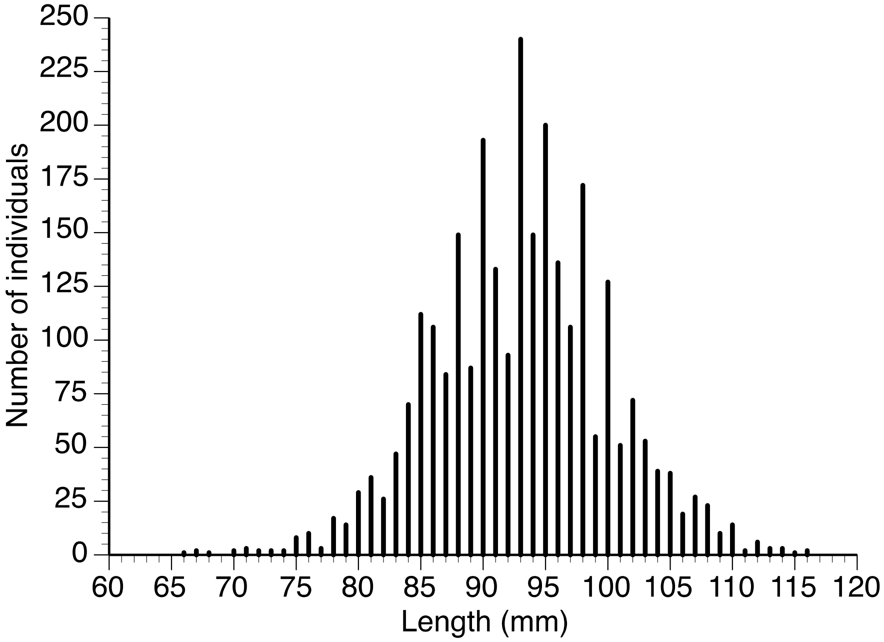

Figure 3. Length-frequency distribution for all animals collected and measured at the Georges Bank site.

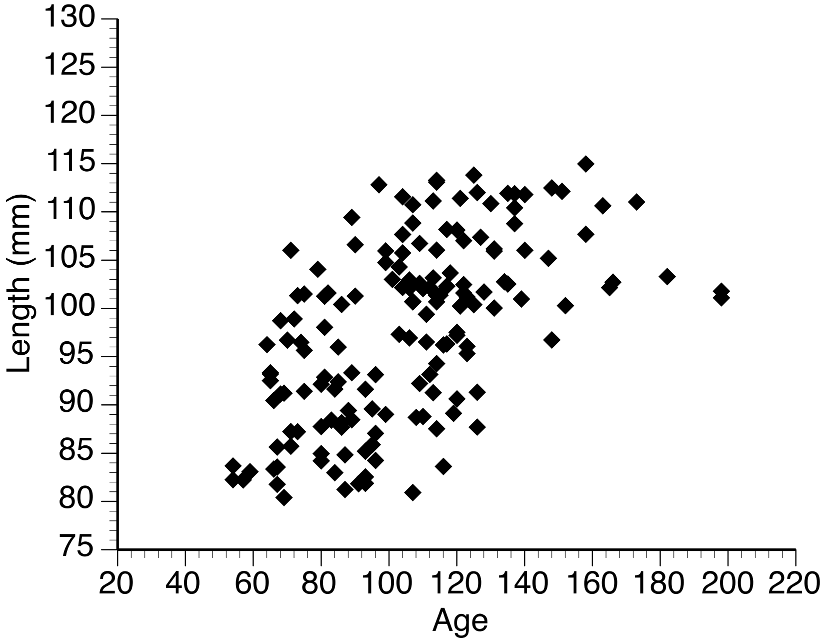

Figure 4. Observed age-at-length of 156 aged ocean quahogs.

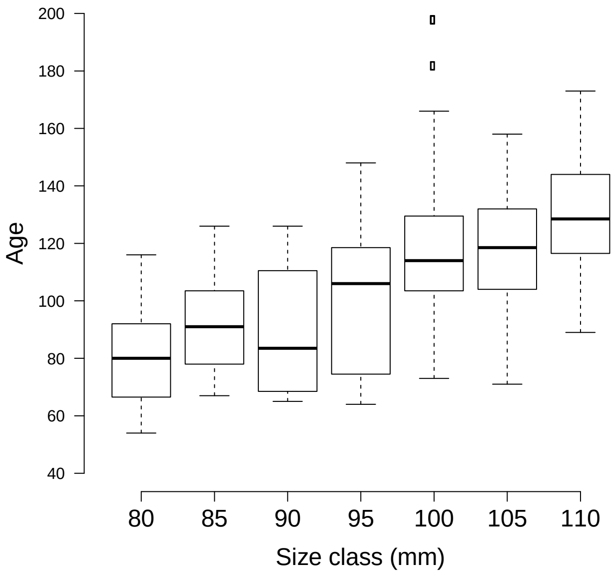

Figure 5. Observed age range within each 5-mm size class.

Dark horizontal lines are the medians, boxes show the interquartile range (IQR), error bars represent the full age range excluding outliers (circles) ±1.5IQR outside of the box.

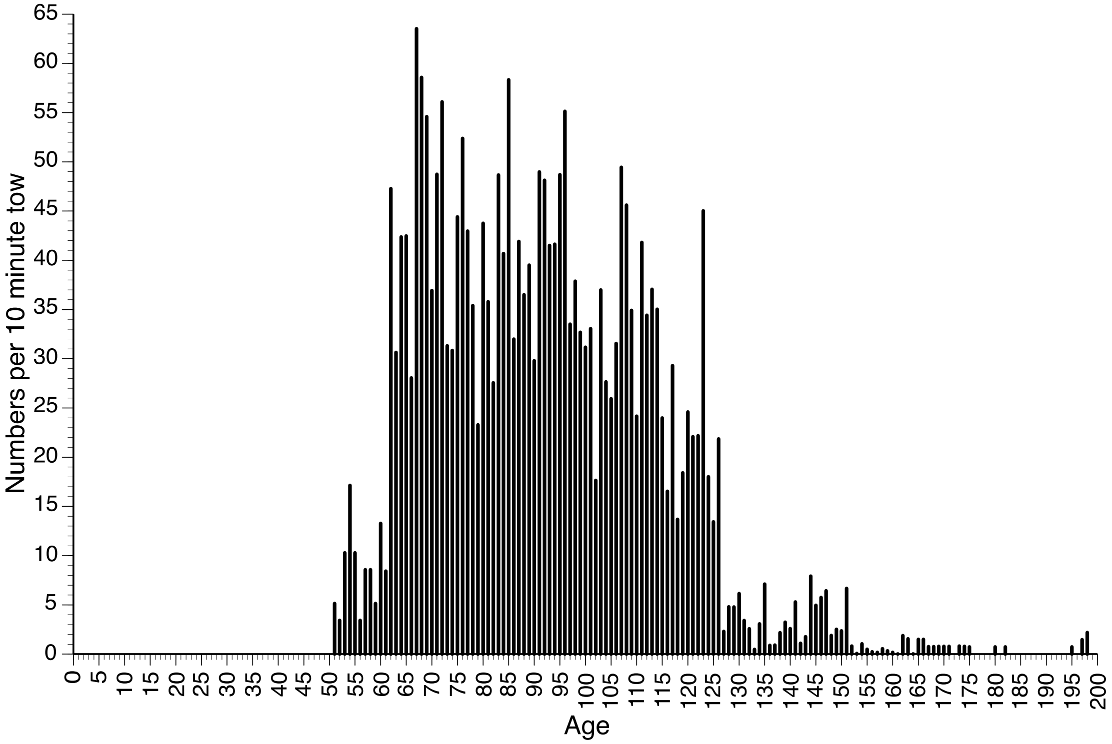

Figure 6. Age-frequency distribution of the Georges Bank population.

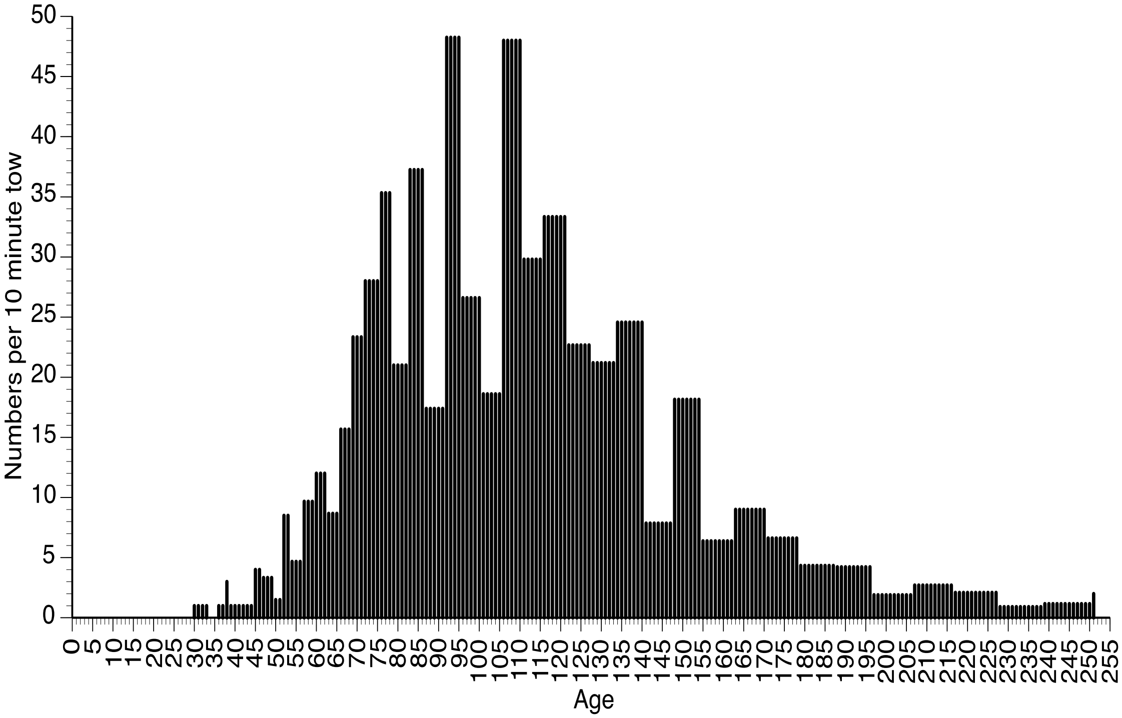

Figure 7. Age-frequency distribution generated from the Tanaka growth curve.

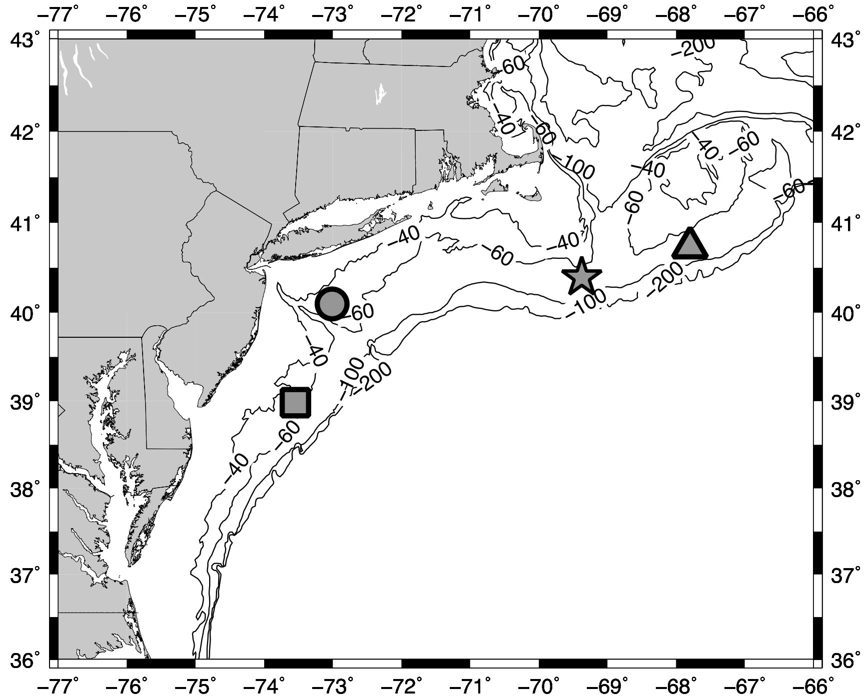

Figure 8. Map of sample collection sites: New Jersey (square), Long Island (circle), Southern New England (star), and Georges Bank (triangle).

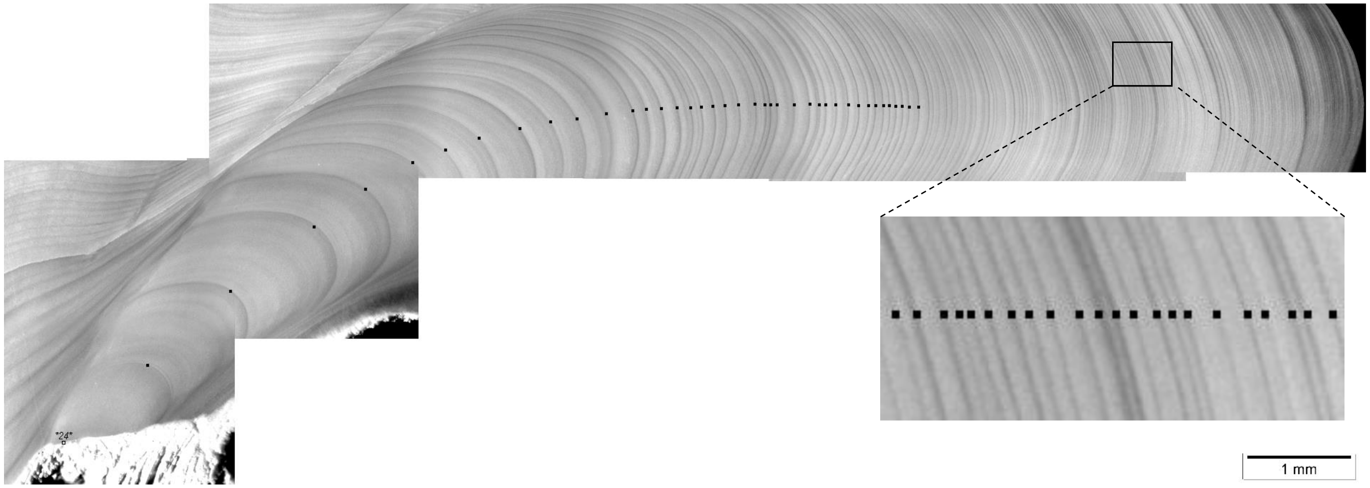

Figure 9. An example of a polished cross-section through the hinge plate of an ocean quahog.

The early-in-life annual growth lines are annotated (black dots) with markers using the Object J plugin for the software Image J.

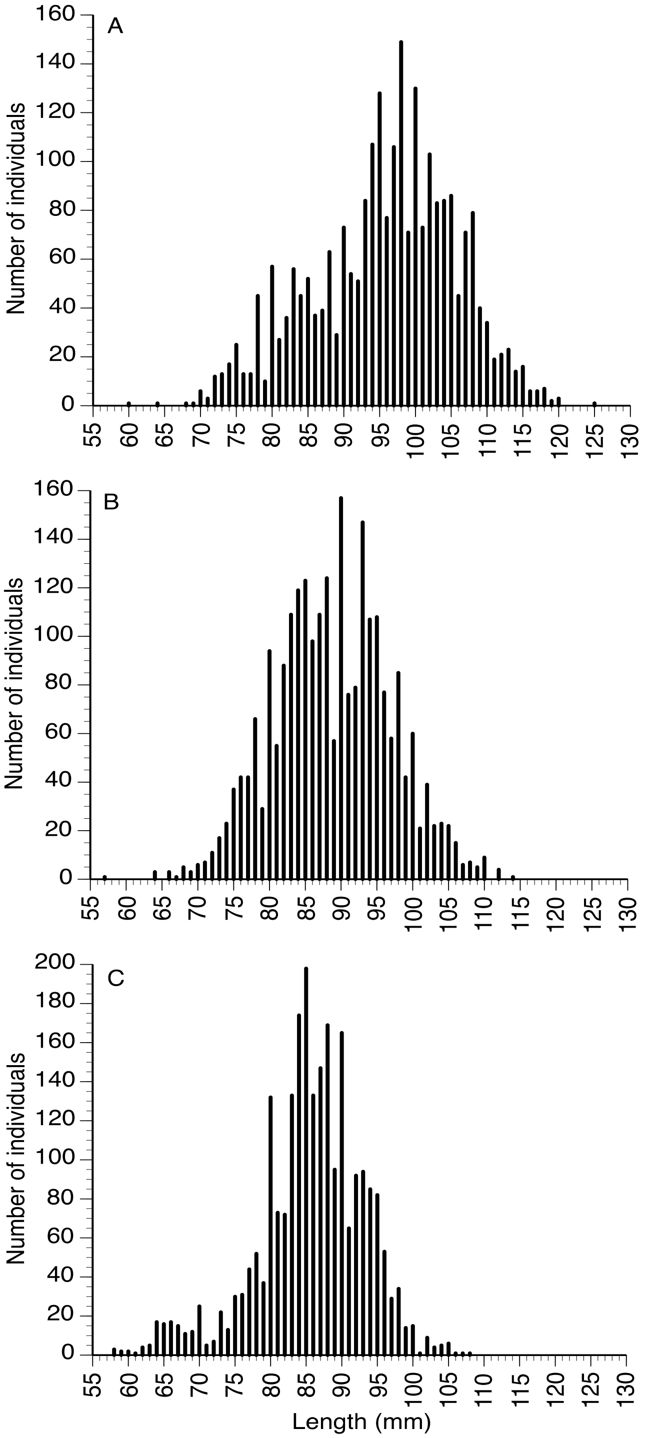

Figure 10. Size frequency distribution of all measured clams from (A) New Jersey, (B) Long Island, and (C) Southern New England.

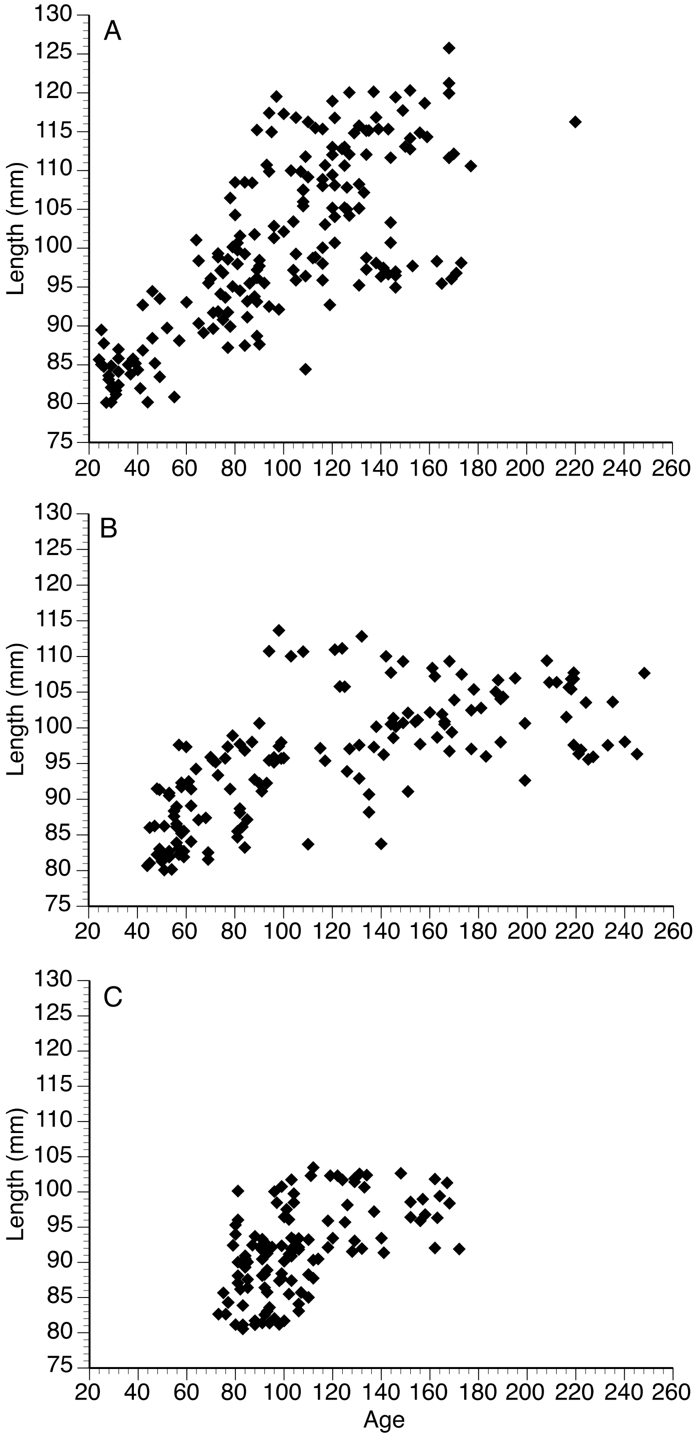

Figure 11. Age estimates for animals based on direct counts of hinge growth lines. (A) New Jersey, (B) Long Island, and (C) Southern New England.

See Figure 4 for Georges Bank.

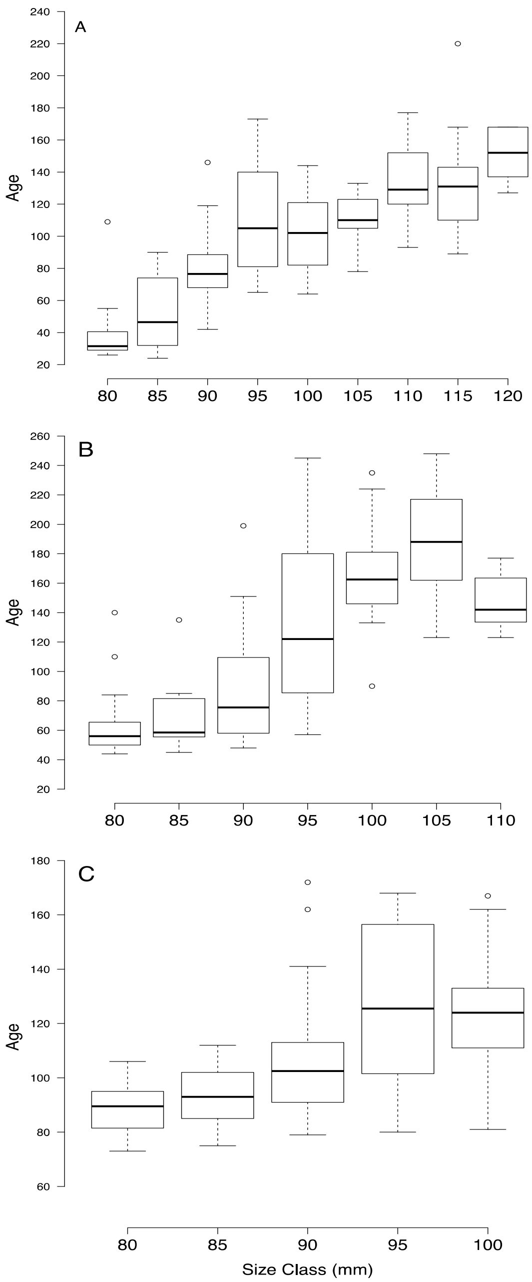

Figure 12. Observed age range for each size class for (A) New Jersey, (B) Long Island, and (C) Southern New England.

Size values represent the lower boundary of each size class. Dark horizontal lines are the median ages of animals plotted in Figure 4, boxes show the interquartile range (IQR) of these ages, error bars represent the full age range excluding outliers (circles) ±1.5 IQR outside of the box.

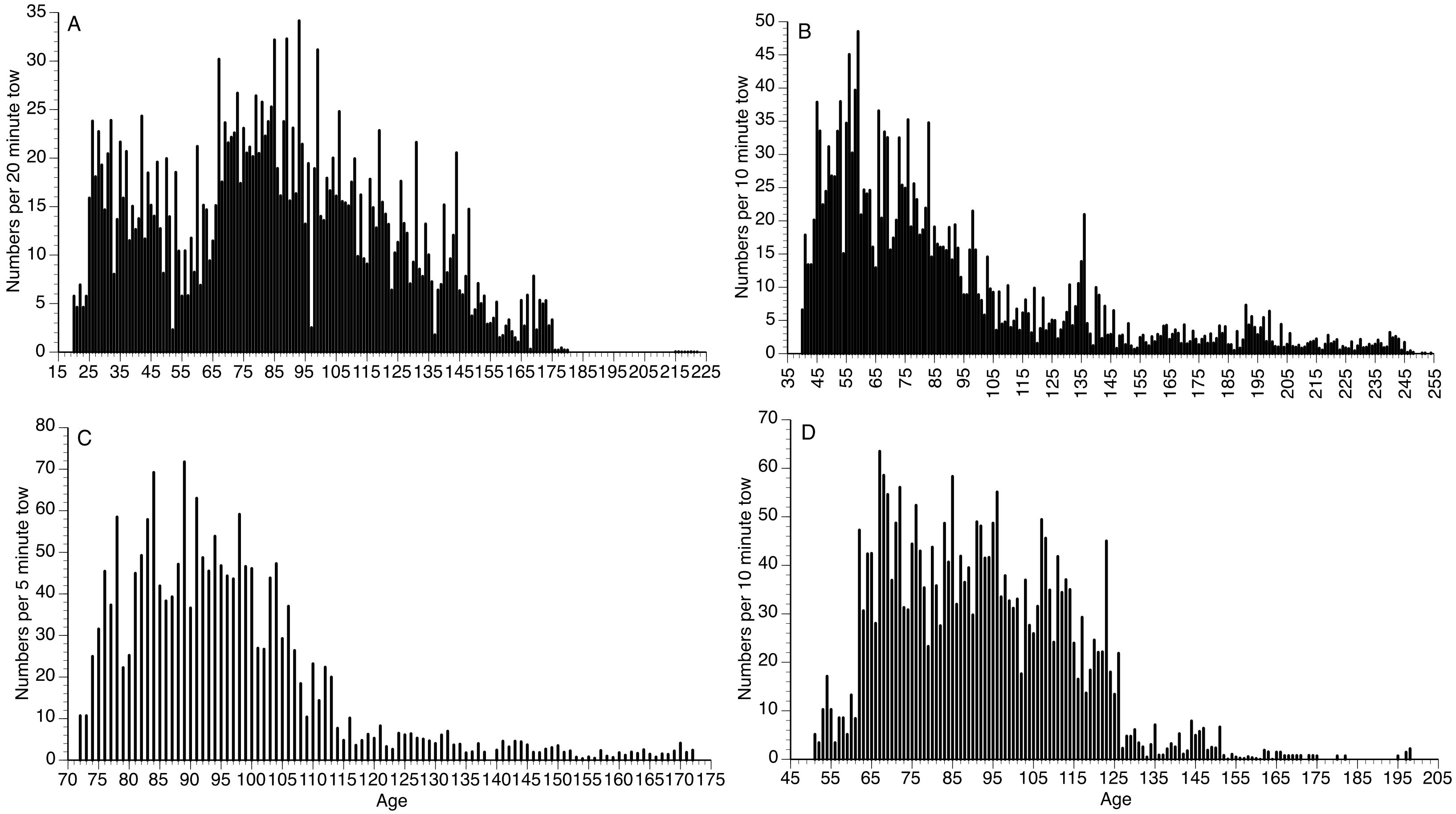

Figure 13. Age frequency distributions for (A) New Jersey, (B) Long Island, (C) Southern New England, and (D) Georges Bank (Chapter II).

Truncation at young ages is due to sample truncation at 80-mm; smaller and by inference mostly younger clams were not aged. Note that the x-axis and y-axis scales differ among plots.

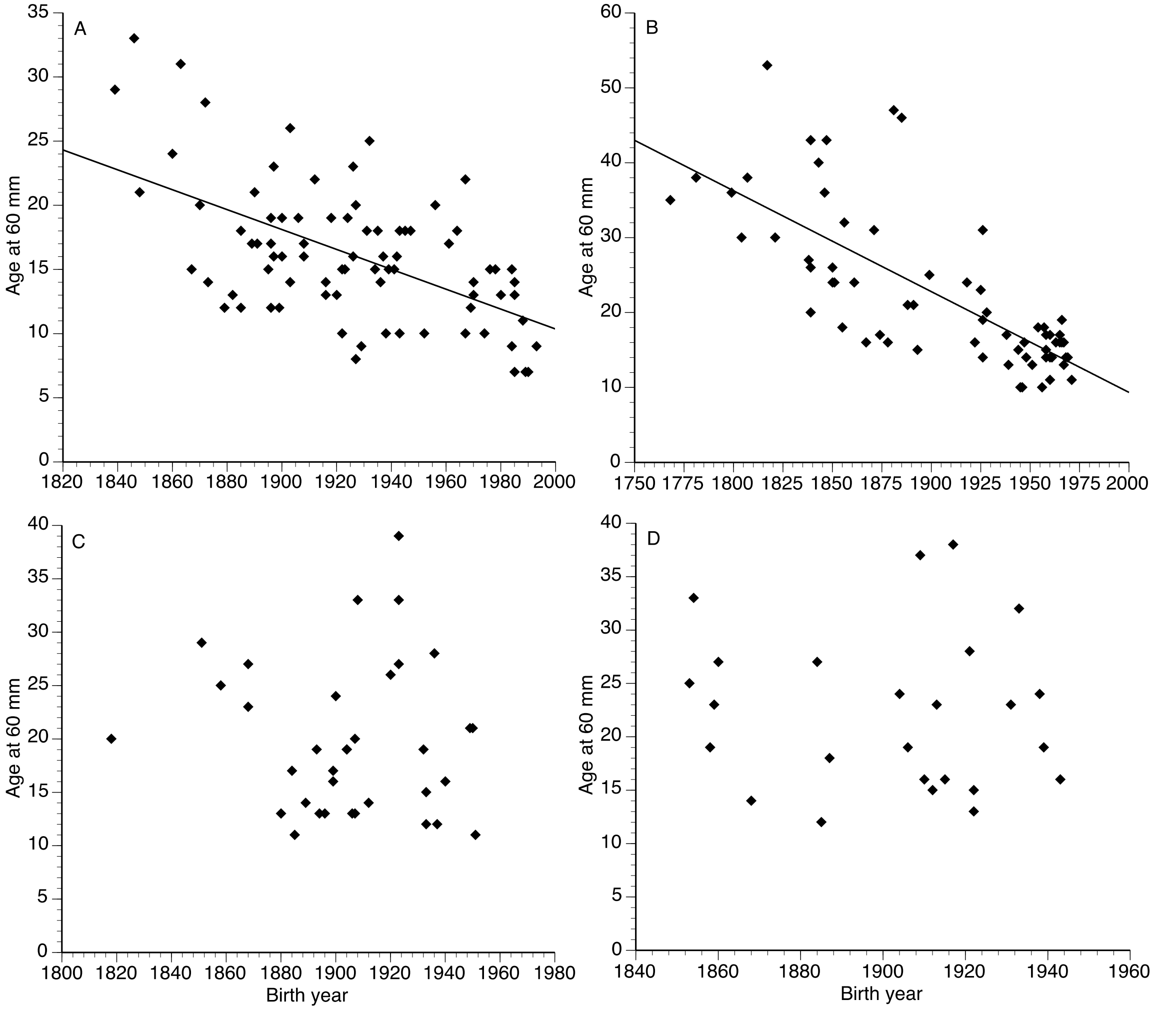

Figure 14. Birth year versus age at 60 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant regressions (P ≤ 0.05).

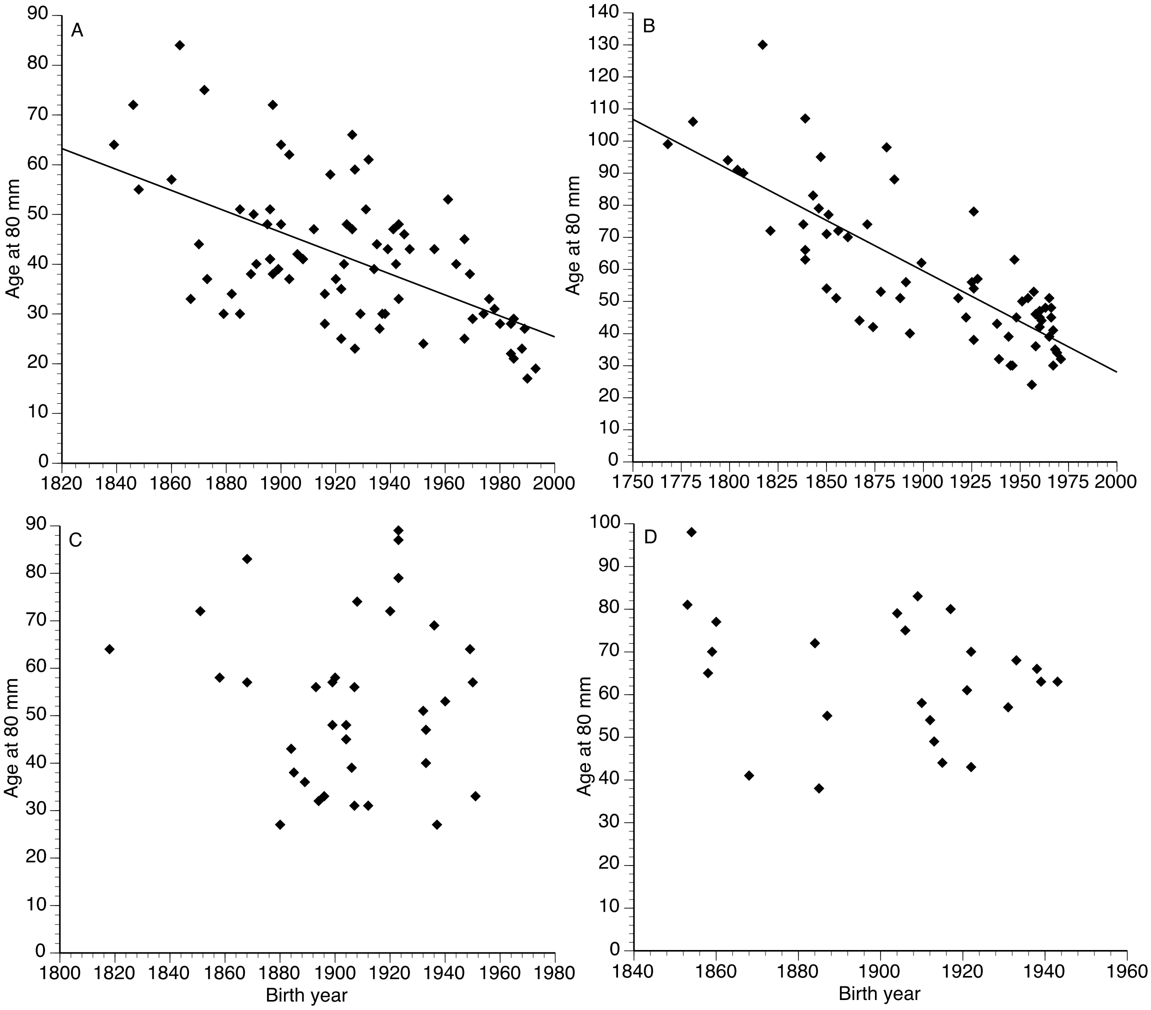

Figure 15. Birth year versus age at 80 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

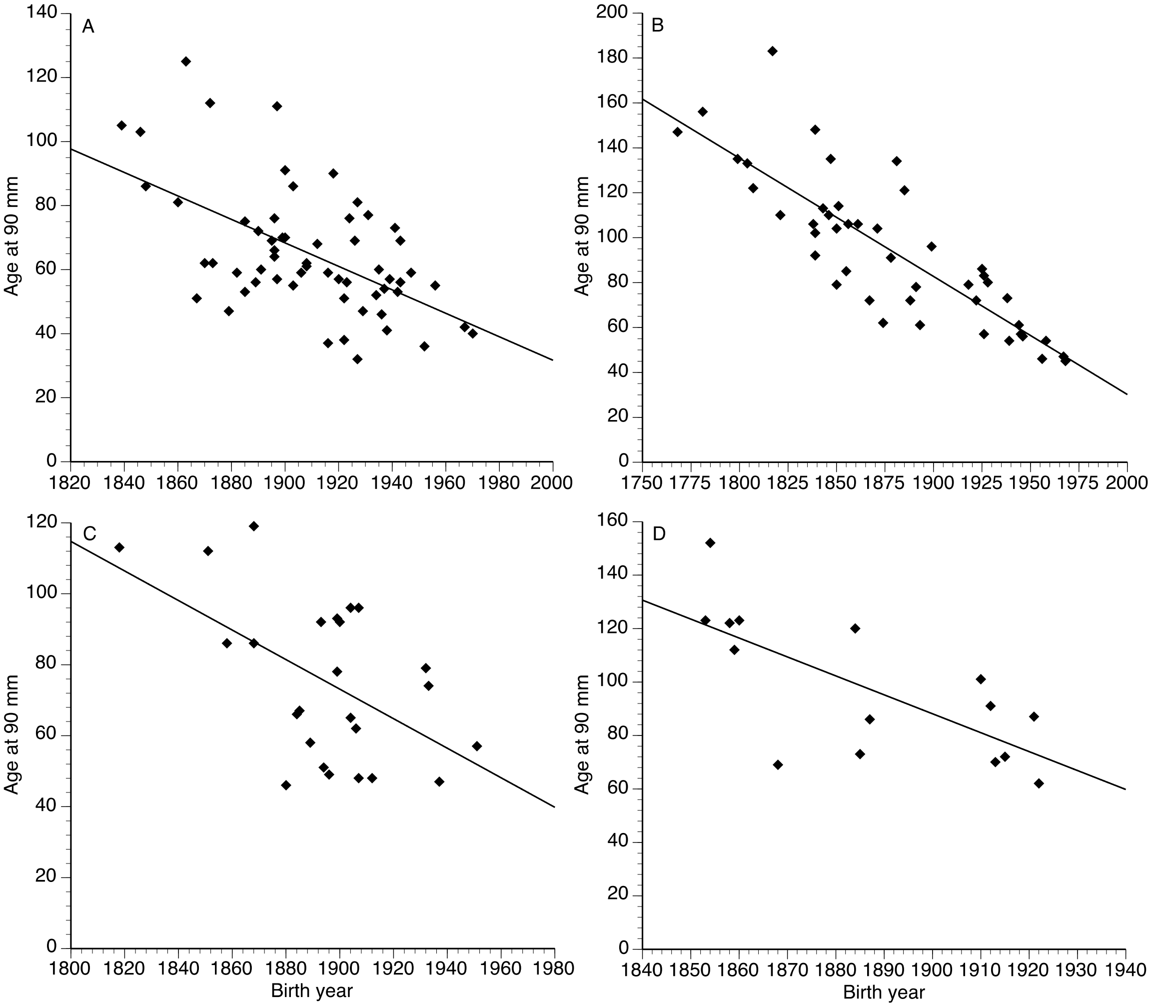

Figure 16. Birth year versus age at 90 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

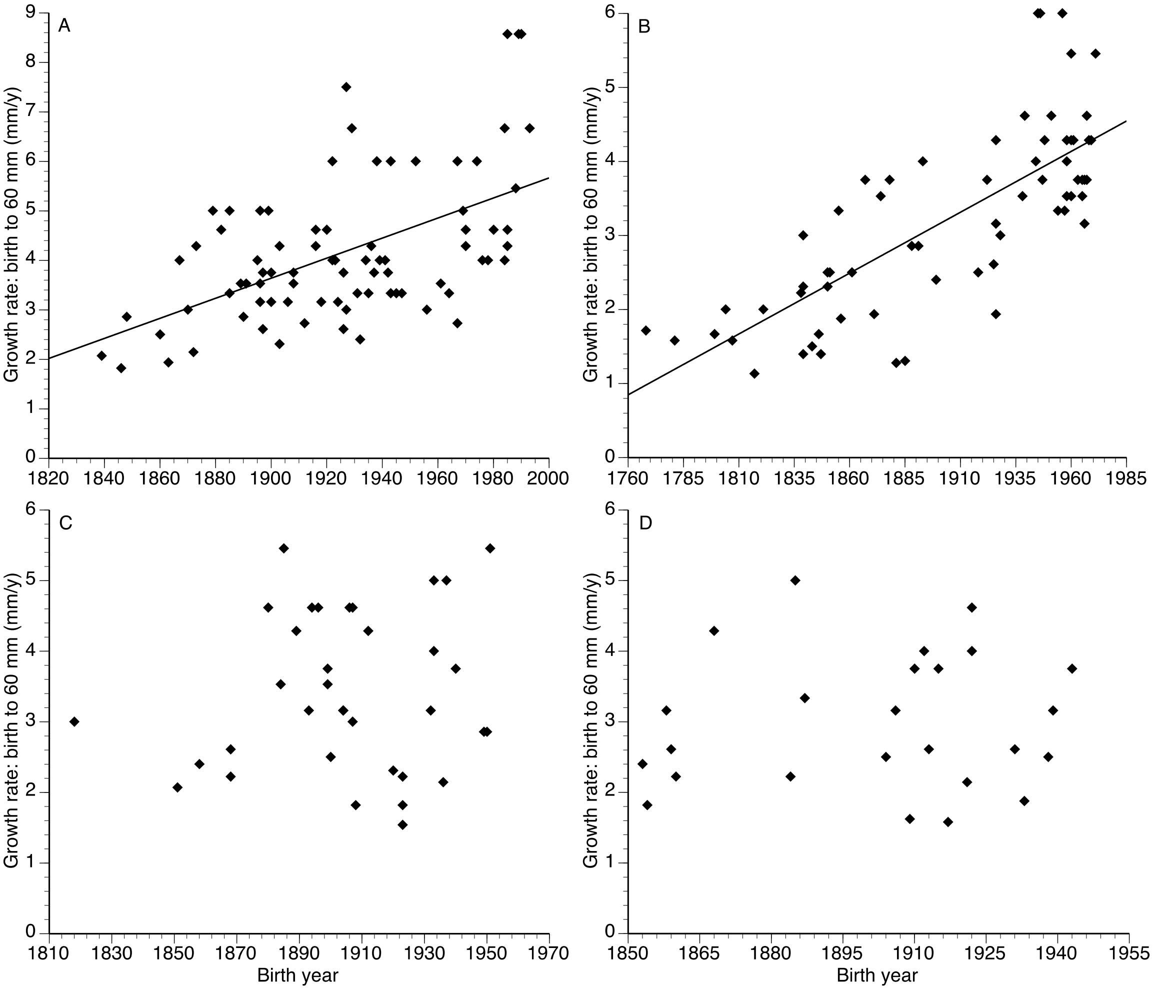

Figure 17. Plots of birth year versus average growth rate for birth to 60 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

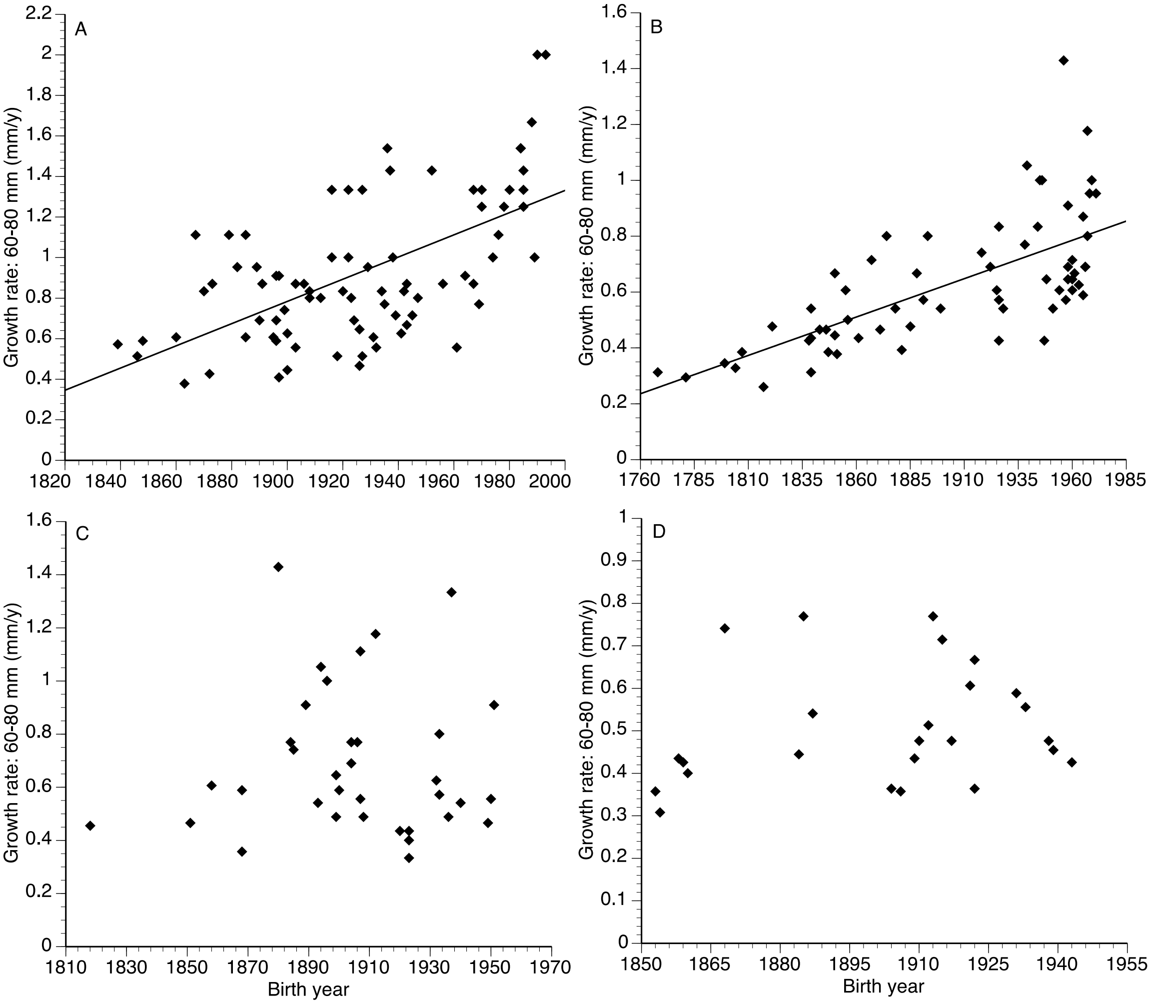

Figure 18. Plots of birth year versus average growth rate from 60 to 80 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

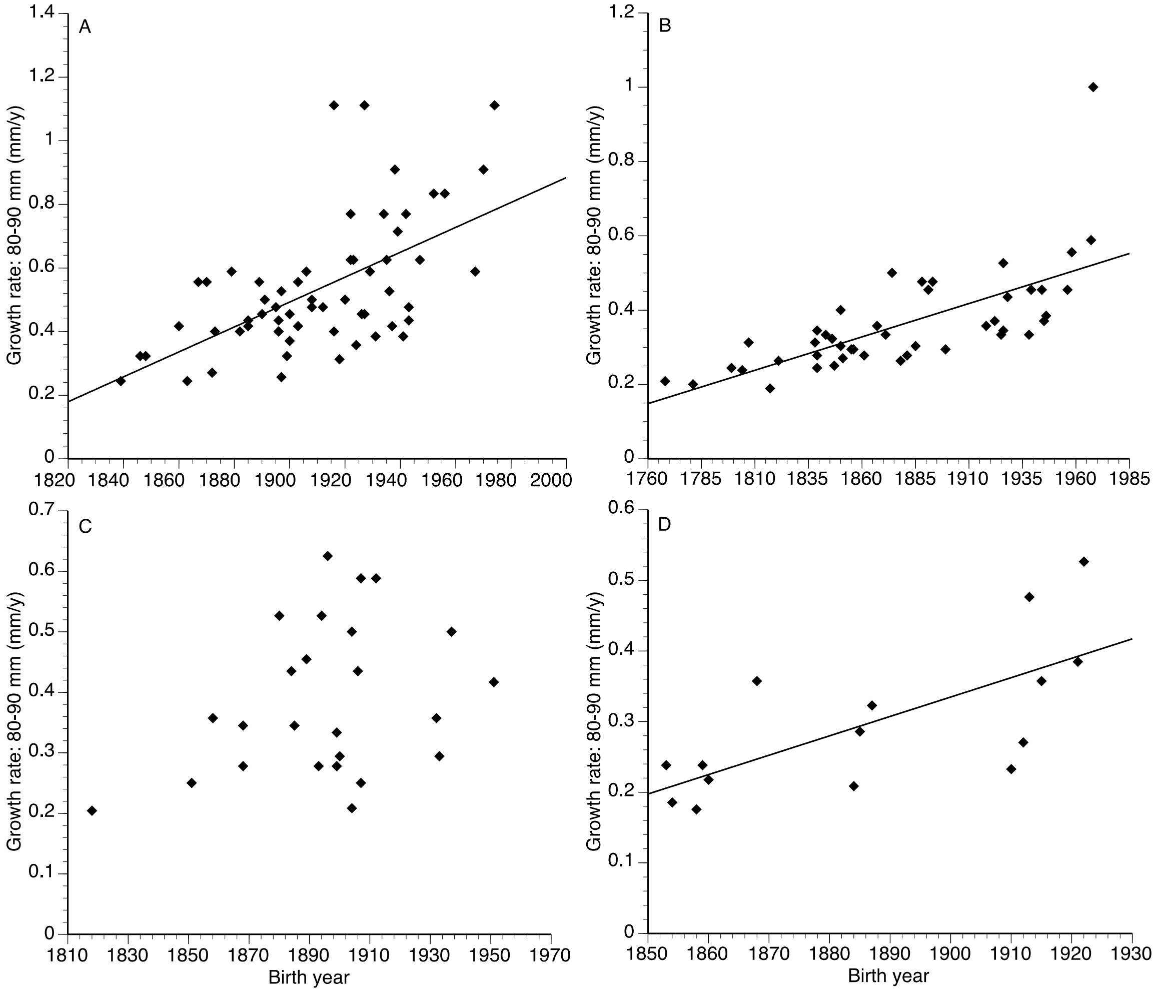

Figure 19. Plots of birth year versus average growth rate from 80 to 90 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

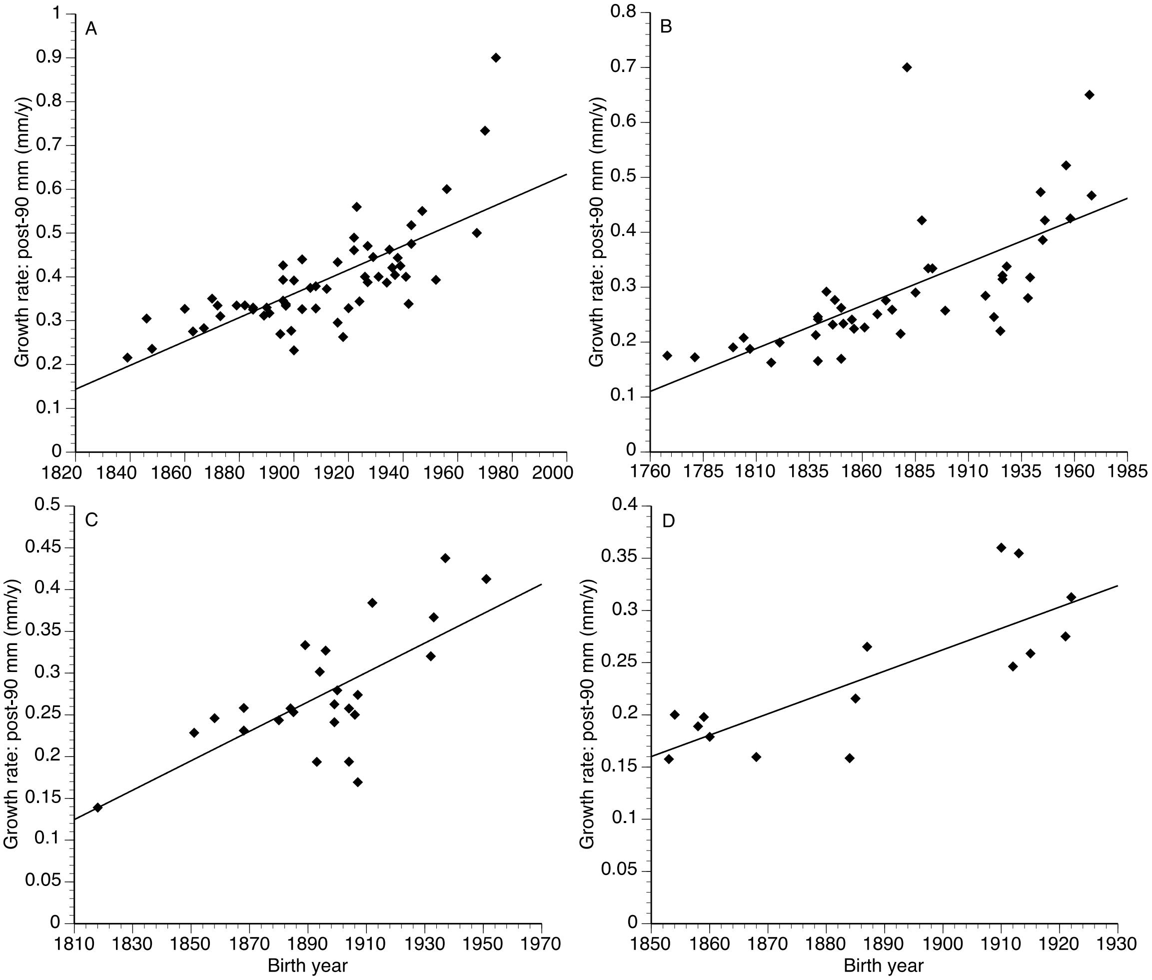

Figure 20. Plots of birth year versus average growth rate post-90 mm for (A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England.

Regression lines indicate significant correlations ($P \leq 0.05$).

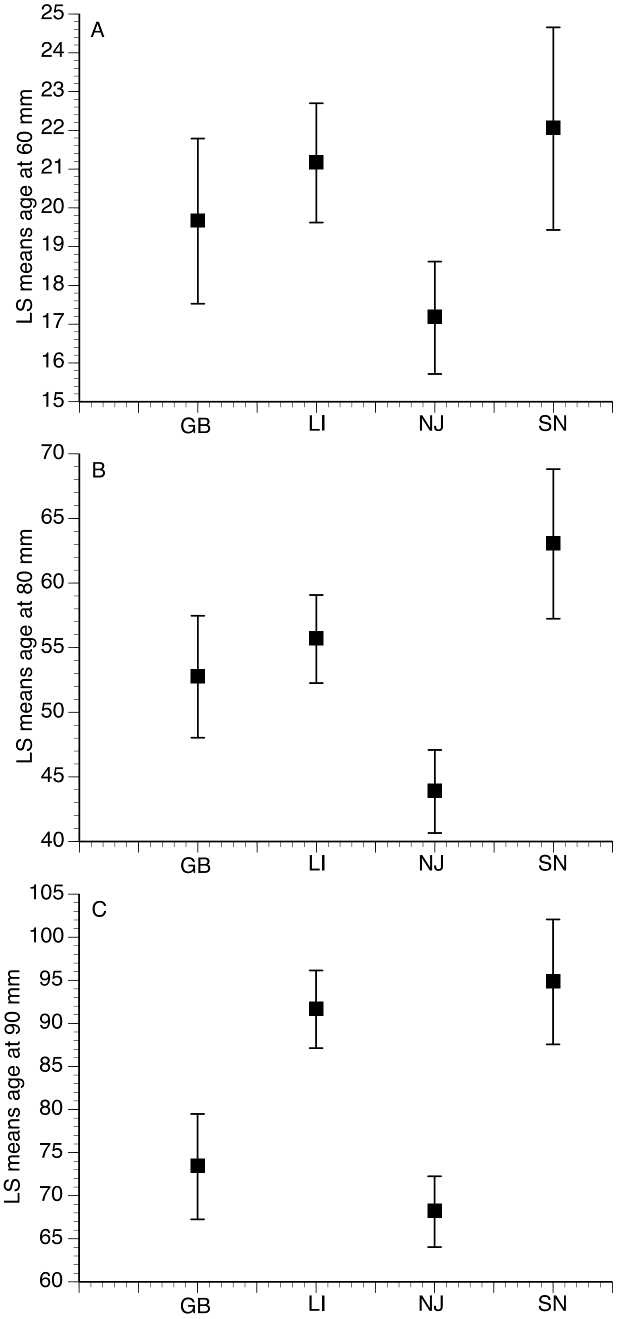

Figure 21. Plots of the least square means values and associated 95% confidence intervals for each site.

Georges Bank (GB), Long Island (LI), New Jersey (NJ), and Southern New England (SN), for (A) age at 60 mm, (B) age at 80 mm, and (C) age at 90 mm. The values are not the true mean age at each size; rather they are the post-hoc least squares mean values and associated confidence limits.

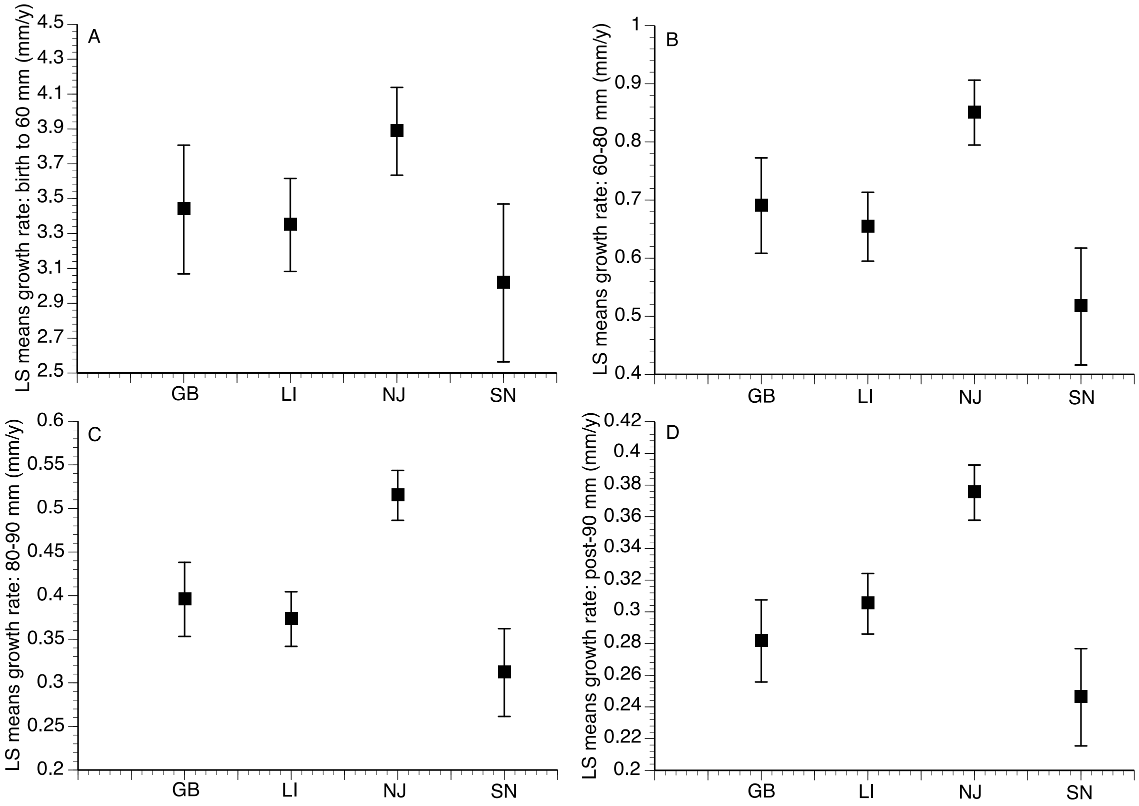

Figure 22. Plots of the least square means values and associated 95% confidence intervals for each site.

Georges Bank (GB), Long Island (LI), New Jersey (NJ), and Southern New England (SN), for average growth rates: (A) birth to 60 mm, (B) 60 to 80 mm, (C) 80 to 90 mm, and (D) post-90 mm. The values are not the mean age at each size; rather they are the post-hoc least squares mean values and associated confidence intervals.

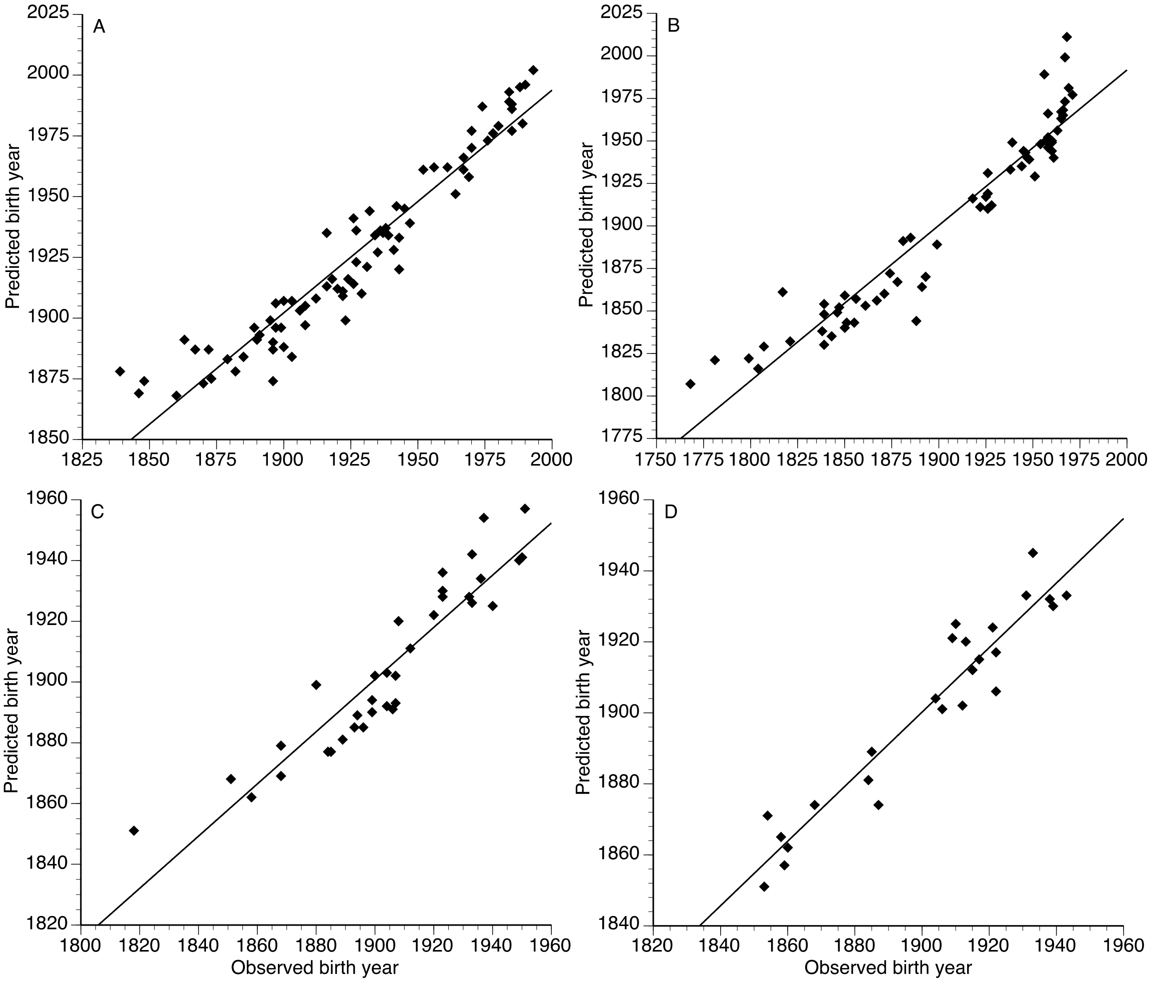

Figure 23. Plots of observed versus predicted birth year based on the best 3 variables in the five variable regression models in Table 21 for each site.

(A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England. Solid lines indicate significant regressions from multiple regression models.

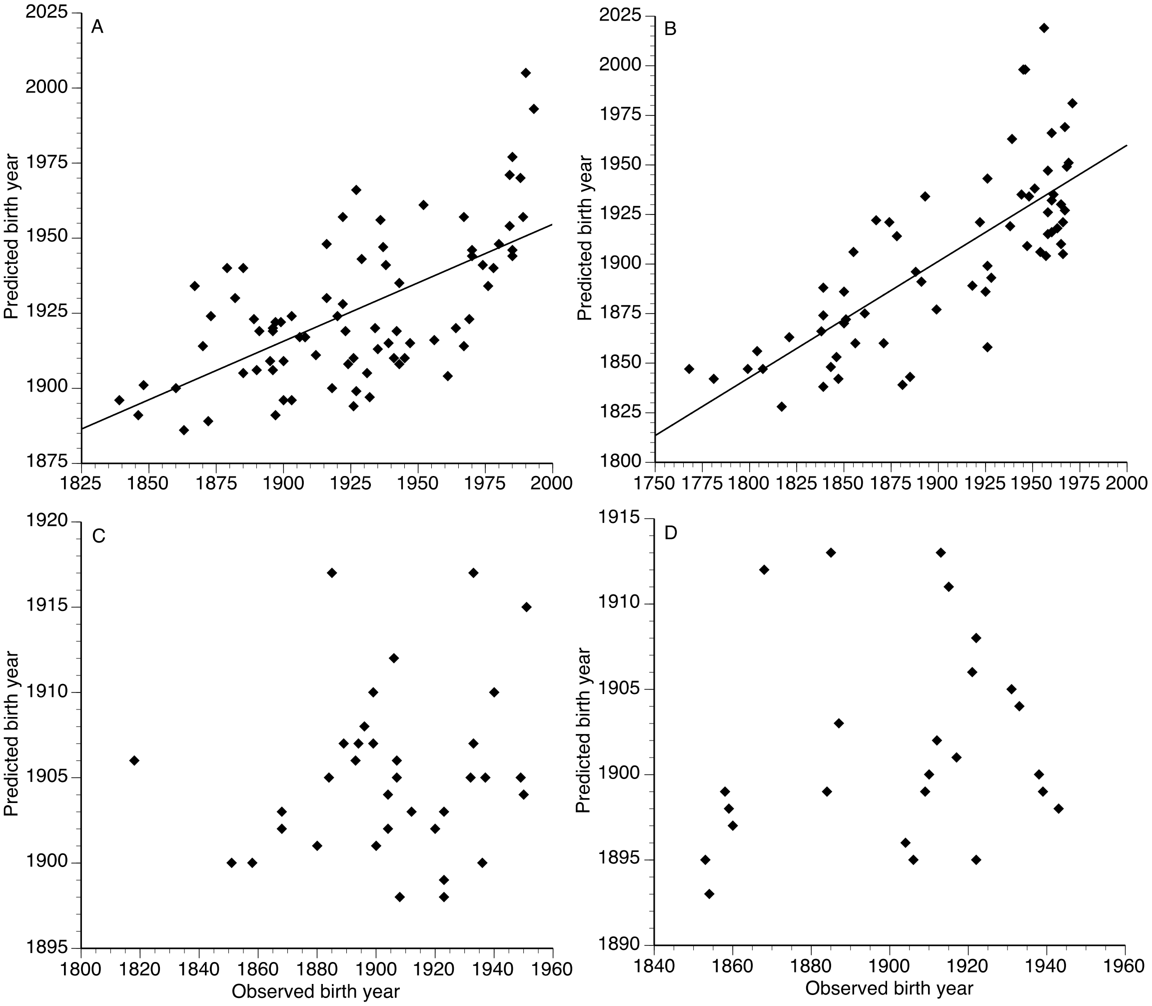

Figure 24. Plots of observed versus predicted birth year based on the regressions shown in Table 2 using only early growth rates (birth to 60 and 60-80 mm) for each site.

(A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England. Solid lines indicate significant regressions from multiple regression models.

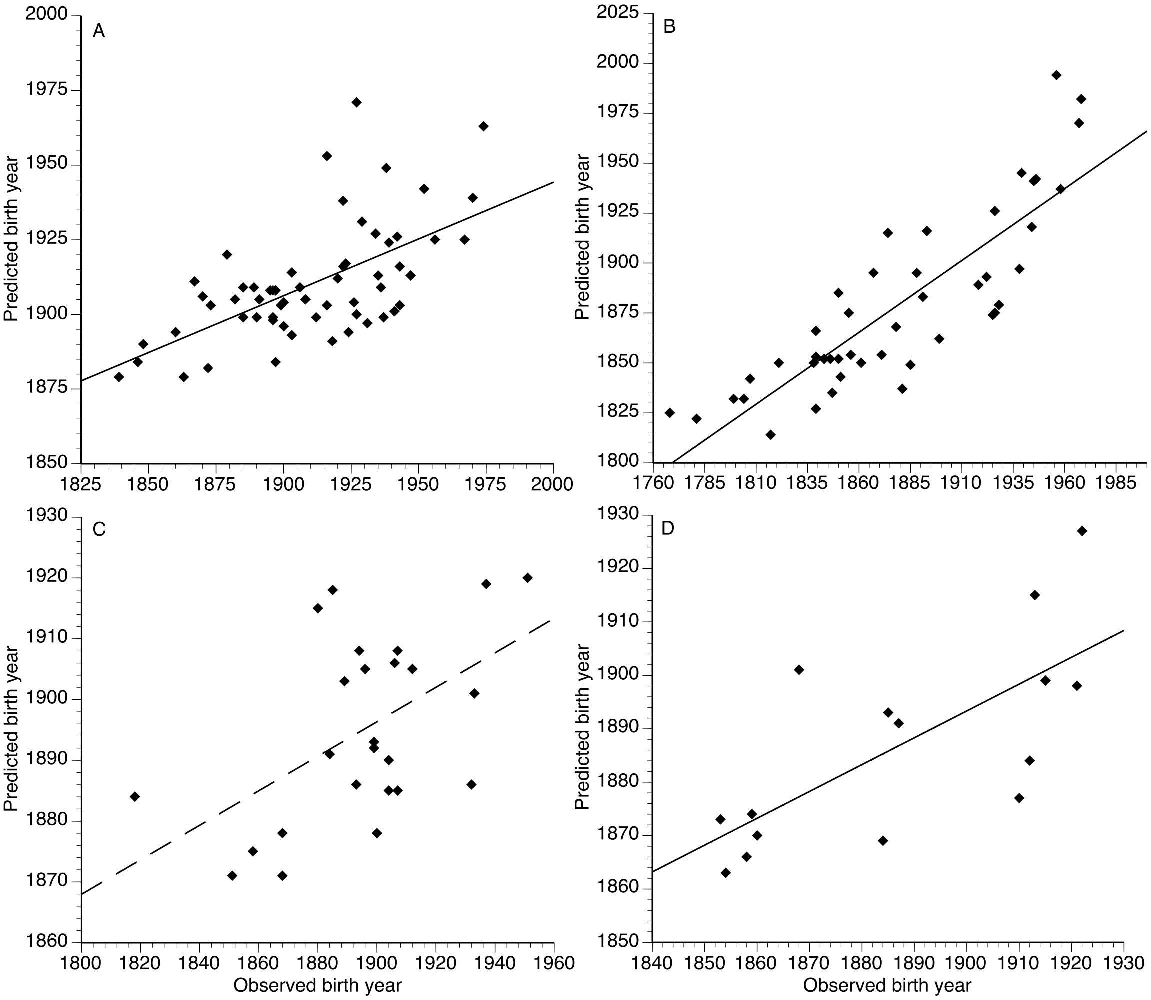

Figure 25. Plots of observed versus predicted birth year based on the 3-variable regression models in Table 2 for each site.

(A) New Jersey, (B) Long Island, (C) Georges Bank, and (D) Southern New England. Solid lines indicate significant regressions from multiple regression models. Georges Bank regression (dashed line) not significant at $\alpha = 0.05$ (Table 22).

REFERENCES

Appleyard, C. L. & J. T. DeAlteris. 2001. Modeling growth of the northern quahog, *Mercenaria mercenaria*. J. Shellfish Res. 20:1117-1125.

Ballesta-Artero, I., R. Witbaard, M. L. Carroll & J. van der Meer. 2017. Environmental factors regulating gaping activity of the bivalve Arctica islandica in northern Norway. Mar. Biol. 164(5):116; DOI 10.1007/s00227-017-3144-7, 15 pp.

Begum, S., L. Basova, O. Heilmayer, E. E. R. Philipp, D. Abele & T. Brey. 2010. Growth and energy budget models of the bivalve *Arctica islandica* at six different sites in the northeast Atlantic realm. J. Shellfish Res. 29:107-115.

Beierlein, L., O. Salvigsen, B. R. Schöne, A. Mackense, & T. Brey. 2015. The seasonal water temperature cycle in the Arctic Dicksonfjord (Svalbard) during the Holocene Climate Optimum derived from subfossil *Arctica islandica* shells. Holocene. 25: 1197-1207.

Bignami, F. & T. S. Hopkins. 2003. Salt and heat trends in the shelf of the southern Middle-Atlantic Bight. Cont. Shelf Res. 23: 647-667.

Boukal, D. S., U. Dieckmann, K. Enberg, M. Heino & C. Jørgensen. 2014. Life-history implications of the allometric scaling of growth. J. Theor. Biol. 359:199-207.

Brey, T., W. E. Arntz, D. Pauly & H. Rumohr. 1990. *Arctica* (*Cyprina*) *islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. J. Exp. Mar. Biol. Ecol. 136:217-235.

Brey, T., M. Voigt, K. Jenkins & I-Y Ahn. 2011. The bivalve *Laternula elliptica* at King George Island – a biological recorder of climate forcing in the West Antarctic Peninsula region. J. Mar. Sys. 38: 542-552.

Brandt, G., A. Wehrmann & K. W. Wirtz. 2008. Rapid invasion of *Crassosstrea gigas* into the German Wadden Sea dominated by larval supply. J. Sea Res. 59:279-296.

Butler, P. G., C. A. Richardson, J. D. Scourse, R. Witbaard, B. R. Schöne, N. M. Fraser, A. D. Wanamaker Jr., C. L. Bryant, I. Harris & I. Robertson. 2009. Accurate increment identification and the spatial extent of the common signal in five *Arctica islandica* chronologies from the Fladen Ground, northern North Sea. Paleoceanography. 24:1-18.

Butler, P. G., C. A. Richardson, J. D. Scourse, A. D. Wanamaker Jr., T. M. Shammon & J. D. Bennell. 2010. Marine climate in the Irish Sea: analysis of a 489-year marine master chronology derived from growth increments in the shell of the clam *Arctica islandica*. Quaternary Sci. Rev. 29:1614-1632.

Butler, P. G., A. D. Wanamaker Jr., J. D. Scourse, C. A. Richardson & D. J. Reynolds. 2013. Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve *Arctica islandica*. Palaeogeogr., Palaeoclimatol., Palaeoecol. 373:141-151.

Butterworth, K. G., M. K. Grieshaber & A. C. Taylor. 2004. Sulphide detoxification in the bivalve, *Arctica islandica* (L.) from two different habitats. Ophelia. 58:101-113.

Cargnelli, L. M., S. J. Griesbach, D. B. Packer & E. Weissberger. 1999a. Essential fish habitat source document: ocean quahog, *Arctica islandica*, life history and habitat characteristics. NOAA Tech. Mem. NMFS-NE-148, 12 pp.

Cargnelli, L. M., S. J. Griesbach, D. B. Packer & E. Weissberger. 1999b. Essential fish habitat source document: Atlantic surfclam, *Spisula solidissima*, life history and habitat characteristics. *NOAA Tech. Mem.* NMFS-NE-142, 13 pp.

Carlton, J. T., J. K. Thompson, L. E. Schemel & F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam, *Potamocorbula amurensis* I. Introduction and dispersal. Mar. Ecol. Prog. Ser. 66:81-94.

Castelao, R., S. Glenn & O. Schofield. 2010. Temperature, salinity, and density variability in the central Middle Atlantic Bight. J. Geophys. Res. Oceans, 115 : C10005.

Chintala, M. M. & J. P. Grassle. 2001. Comparison of recruitment frequency and growth of surfclams, *Spisula solidissima* (Dillwyn, 1817), in different inner-shelf habitats of New Jersey. J. Shellfish Res. 20:1177-1186.

Chute, A.S., R. S. McBride, S. J. Emery & E. Robillard. 2016. Annulus formation and growth of Atlantic surfclam (*Spisula solidissima*) along a latitudinal gradient in the western North Atlantic Ocean. J. Shellfish Res. 35: 729-737.

Cronin, T. M., K. Hayo, R. C. Thunell, G. S. Dwyer, C. Saenger & D. A. Willard. 2010. The Medieval Climate Anomaly and Little Ice Age in Chesapeake Bay and the North Atlantic Ocean. Palaeogeogr., Palaeoclimatol., Palaeoecol. 297:299-310.

Dahlgren, T. G., J. R. Weinberg & K. M. Halanych. 2000. Phylogeography of the ocean quahog (*Arctica islandica*): influences of paleoclimate on genetic diversity and species range. Mar. Biol. 137:487-495.

Daniel, W.W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston.

Diederich, S., G. Nehls, J. E. E. van Beusekom & K. Reise. 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? Helgol. Mar. Res. 59:97-106.

Ebert, T. A., J. D. Dixon, S. C. Schroeter, P. E. Kalvass, N. T. Richmond, W. A. Bradbury & D. A. Woodby. 1999. Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. Mar. Ecol. Prog. Ser. 190:189-209.

Ebert, T. A. & J. R. Southon. 2003. Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb ^{14}carbon. Fish. Bull. 101:915-922.

Facon, B. & P. David. 2006. Metapopulation dynamics and biological invasions: a spatially explicit model applied to a freshwater snail. Am. Nat. 168:769-783.

Flores, L., B. Ernst & A. M. Parma. 2010. Growth pattern of the sea urchin, *Loxechinus albus* (Molina, 1782) in southern Chile: evaluation of growth models. Mar. Biol. 157:967-977.

Flye-Sainte-Marie, J., F. Jean, C. Paillard, C., S. Ford, E. N. Powell, E. Hofmann, E. & J. Klinck. 2007. Ecophysiological dynamic model of individual growth of *Ruditapes philippinarum*. Aquaculture 266:130-143.

Foster, L. C., A. A. Finch, N. A. Finch & C. Andersson. 2009. Strontium distribution in the shell of the aragonite bivalve *Arctica islandica.* Geochem., Geophy., Geosy. 10:1-14.

Fréchette. M. & G. Daigle. 2002. Growth, survival and fluctuating asymmetry of Iceland scallops in a test of density-dependent growth in a natural bed. J. Exp. Mar. Biol. Ecol. 270: 73-91.

Freitas, V., J. F. M. F Cardoso, S. Santos, J. Campos, J. Drent, S. Saraiva, J. I. J. Witte, S. A. L. M. Kooijman & H. W. van der Veer. 2009. Reconstruction of food conditions for northeast Atlantic bivalve species based on dynamic energy budgets. J. Sea Res. 62: 75-82.

Freund, R.J. & R. C. Littell. 2000. SAS® system for regression. Third edition, SAS Institute Inc., Cary, North Carolina.

Funder, S. & A. Weidick. 1991. Holocene boreal molluscs in Greenland - palaeoceanographic implications. Palaeogeogr., Palaeoclimatol., Palaeoecol. 85:123–135.

Goodwin, N. B., A. Grant, A. L. Perry, N. X. Dulvy & J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. Can. J. Fish. Aquat. Sci. 63:494-509.

Gilkinson, K. D., D. C. Gordon Jr., K. G. MacIsaac, D. L. McKeown, E. C. R. Kenchington, C. Bourbonnais & W. P. Voss. 2005. Immediate impacts and recovery trajectories of macrofaunal communities following hydraulic clam dredging on Banquereau, eastern Canada. ICES J. Mar. Sci. 62:925-947.

Hancock, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-v. Réun. 164:113-131.

Hanna, E., Jónsson & J. E. Box. 2004. An analysis of Icelandic climate since the nineteenth century. Int. J. Climatol. 24: 1193-1210.

Harding, J. M., S. E. King, E. N. Powell & R. Mann. 2008. Decadal trends in age structure and recruitment patterns of ocean quahogs, *Arctica islandica* from the Mid-Atlantic Bight in relation to water temperature. J. Shellfish Res. 27:667-690.

Hennen, D. R. 2015. How should we harvest an animal that can live for centuries? N. Am. J. Fish. Manage. 35:512-527.

Hodgson, A. N., W .J. F. le Quesne, S. J. Hawkins & J. D. Bishop. 2007. Factors affecting fertilization success in two species of patellid limpet (Mollusca: Gastropoda) and development of fertilization kinetics models. Mar. Biol. 150:415-426.

Hofmann, E. E., E. N. Powell, J. M. Klinck & E. A. Wilson. 1992. Modeling oyster populations. III. Critical feeding periods, growth and reproduction. J. Shellfish Res. 11:399-416.

Hofmann, E. E., J. M. Klinck, J. N. Kraeuter, E. N. Powell, R. E. Grizzle, S. C. Buckner & V. M. Bricel. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. J. Shellfish Res. 25: 417-444.

Honkoop, P. J. C., J. van der Meer, J. J. Beukema & D. Kwast. 1998. Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*? Mar. Ecol. Prog. Ser. 164:229-235.

Hulme, M. & P. D. Jones. 1994. Global climate change in the instrumental period. Environ. Pollut. 83: 23-36.

Jones, D. S. 1980. Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. Paleobiology 6:331-340.

Karatayev, A. Y., L. E. Burlakova, S. E. Mastitsky & D. K. Padilla. 2011. Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, at different spatial scales. J. Shellfish Res. 30:923-931.

Karkach, A. S. 2006. Trajectories and models of individual growth. Demogr. Res. 15:347-400.

Kilada, R. W., S. E. Campana & D. Roddick. 2007. Validated age, growth, and mortality estimates of the ocean quahogs (*Arctica islandica*) in the western Atlantic. ICES J. Mar. Sci. 64:31-38.

Kimura, D. K. & S. Chikani. 1987. Mixtures of empirical distributions: an iterative application of the age-length key. *Biometrics* 43:23-35.

Kraeuter, J. N., S. Buckner & E. N. Powell. 2005. A note on a spawner-recruit relationship for a heavily exploited bivalve: the case of northern quahog (hard clams), *Mercenaria mercenaria* in Great South Bay New York. J. Shellfish Res. 24:1043-1052.

Lentz, S. J. 2017. Seasonal warming of the Middle Atlantic Bight Cold Pool. J. Geophys. Res. Oceans, 122: 941-954.

Lewis, C. V. W., J. R. Weinberg & C. S. Davis. 2001. Population structure and recruitment of the bivalve *Arctica islandica* (Linnaeus, 1767) on Georges Bank from 1980–1999. J. Shellfish Res. 20:1135–1144.

Lofmann, G. & B. R. Schöne. 2013. Climate signatures on decadal to interdecadal time scales as obtained from mollusk shells (*Arctica islandica*) from Iceland. Palaeogeogr., Palaeoclimatol., Palaeoecol. 373: 152-162.

Lucey, S. M. & J. A. Nye. 2010. Shifting species assemblages in the northeast US continental shelf large marine ecosystem. Mar. Ecol. Prog. Ser. 415: 23-33.

Luttikhuizen, P. C., P. J. C. Honkoop & J. Drent. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. J. Exp. Mar. Biol. Ecol. 396:156-161.

Lutz, R. A., R. Mann, J. G. Goodsell & M. Castagna. 1982. Larval and early post-larval development of *Arctica islandica.* J. Mar. Biol. Assoc. U. K. 62:745-769.

MacDonald, P. D. M. & T. J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36:987-1001.

Mangel, M., J. Brodziak & G. DiNardo. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. Fish Fisheries 11:89-104.

Mann, R. 1982. The seasonal cycle of gonadal development in *Arctica islandica* from the southern New England shelf. Fish. Bull. 80: 315-326.

Mann, R. 1985. Seasonal changes in the depth distribution of bivalve larvae on the southern New England shelf. J. Shellfish Res. 5:57-64.

Mann, M. E., Z. Zhang, S. Rutherford, R. S. Bradley, M. K. Hughes, D. Shindell, C. Ammann, G. Foluvegi & F. Ni. 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. Science. 326:1256-1260.

Marali, S. & B. R. Schöne. 2015. Oceanographic control on shell growth of *Arctica islandica* (Bivalvia) in surface waters of Northeast Iceland - implications for paleoclimate reconstructions. Palaeogeogr., Palaeoclimatol., Palaeoecol. 420: 138-149.

Marsh, R., B. Petrie, C. R. Weidman, R. R. Dickson, J. W. Loder, C. G. Hannah, K. Frank & K. Drinkwater. 1999. The 1882 tilefish kill – a cold event in shelf waters off the north-eastern United States? Fish. Oceanogr. 8: 39-49.

McCuaig, J. M. & R. H. Green. 1983. Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. Can. J. Fish. Aquat. Sci. 40:436-442.

Merrill, A. S. & J. W. Ropes. 1969. The general distribution of the surf clam and ocean quahog. Proc. Natl. Shellfish. Assoc. 59:40-45.

Mette, M. J., A. D. Wanamaker Jr., M. L. Carroll, W. G. Ambrose Jr. & M. J. Retelle. 2016. Linking large-scale climate variability with *Arctica islandica* shell growth and geochemistry in northern Norway. Limnol. Oceanogr. 61: 748-764.

Mohn, R. 1994. A comparison of three methods to convert catch at length data into catch at age. Int Comm Conserv Atl Tuna 42:110-119.

Moore, G. W. K., J. Halfar, H. Majeed, W. Adey & A. Kronz. 2017. Amplification of the Atlantic Multidecadal Oscillation associated with the onset of the industrial-era warming. Sci. Rep. 7:40861.

Morton, B. 2011. The biology and functional morphology of *Arctica islandica* (Bivalvia: Arcticidae): a gerontophilic living fossil. Mar. Biol. Res. 7:540-553.

Munroe, D. M., E. N. Powell, R. Mann, J. M. Klinck & E. E. Hofmann. 2013. Underestimation of primary productivity on continental shelves: evidence from maximum size of extant surfclam (*Spisula solidissima*) populations. Fish. Oceanogr. 22:220-233.

Munroe, D. M., D. A. Narváez, D. Hennen, L. D. Jacobson, R. Mann, E. E. Hofmann, E. N. Powell & J. M. Klinck. 2016. Fishing and bottom water temperature as drivers of change in maximum shell length in Atlantic surfclams (*Spisula solidissima*). Estuar. Coast. Shelf Sci. 170: 112-122.

Murawski, S. A., J. W. Ropes & F. M. Serchuk. 1982. Growth of the ocean quahog, *Arctica islandica*, in the Mid-Atlantic Bight. Fish. Bull. 80:21-34.

NEFSC. 1995. Report of the 19th Northeast Regional Stock Assessment Workshop (19th SAW) Stock Assessment Committee (SARC) Consensus Summary of Assessments NEFSC Ref Doc. 95–08, 221 pp.

NEFSC, 2009. 48th Northeast Regional Stock Assessment Workshop (48th SAW) assessment report. NEFSC Ref. Doc. 09-15, 834 pp.

NEFSC. 2017a. 63rd Northeast Regional Stock Assessment Workshop (63rd SAW) Assessment Report. NEFSC Ref. Doc. 17-10, 409 pp.

NEFSC. 2017b. 61st Northeast Regional Stock Assessment Workshop (61st SAW) Assessment Report. NEFSC Ref. Doc. 17-05, 466 pp.

Noreen, E.W. 1989. Computer-intensive methods for testing hypotheses: an introduction. John Wiley and Sons, New York, 229 pp.

Nye J. A., M. R. Baker, R. Bell, A. Kenny, K. H. Kilbourne, K. D. Friedland, E. Martino, M. M. Stachura, K. S. van Houran & R. Wood. 2014. Ecosystem effects of the Atlantic Multidecadal Oscillation. J. Mar. Sys. 133: 103-116.

Oeschger, R. 1990. Long-term anaerobiosis in sublittoral marine invertebrates from the western Baltic Sea: *Halicryptus spinulosus* (Priapulida), *Astarte borealis* and *Arctica islandica* (Bivalvia). Mar. Ecol. Prog. Ser. 59:133-143.

Oeschger, R.& K. B. Storey. 1993. Impact of anoxia and hydrogen sulphide on the metabolism of Arctica islandica L. (Bivalvia). J. Exp. Mar. Bio. Ecol. 170: 213-226.

Ólafsson, E. B., C. H. Peterson & W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post- settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32:65-109.

O'Reilly, J. E. & D. A. Busch. 1984. Phytoplankton primary production on the northwestern Atlantic shelf. Rapp. P.–v. Réun. Cons. int. Explor. Mer. 183: 255-268.

Pace, S. M., E. N. Powell, R. Mann, C. M. Long & J. M. Klinck. 2017. Development of an age-frequency distribution for ocean quahogs (*Arctica islandica*) on Georges Bank. J. Shellfish Res. 36:41-53.

Pace, S. M., E. N. Powell, R. Mann & C. M. Long. Submitted. Comparison of Age-Frequency Distributions for Ocean Quahogs (Arctica islandica) on the Western Atlantic US Continental Shelf.

Pace, S. M., E. N. Powell & R. Mann. Submitted. Two-hundred year record of increasing growth rates for ocean quahogs (*Arctica islandica*) from the northwestern Atlantic Ocean. J. Exp. Mar. Biol. Ecol.

Peterson, C. H. 2002. Recruitment overfishing in a bivalve mollusc fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. Can. J. Fish. Aquat. Sci. 59:96-104.

Peterson, C. H. & H. C. Summerson. 1992. Basin-scale coherences of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. Mar. Ecol. Prog. Ser. 90:257-272.

Philipp, E. E. R. & D. Abele. 2010. Masters of longevity: lessons from long-lived bivalves -- a mini-review. Gerontology. 56:55-65.

Powell E. N. & R. Mann. 2005. Evidence of recent recruitment in the ocean quahog *Arctica islandica* in the Mid-Atlantic Bight. J. Shellfish Res. 24:517-530.

Powell, E. N. & R. J. Stanton Jr. 1985. Estimating biomass and energy flow of molluscs in paleo-communities. Paleontology. 28:1-34.

Powell, E. N., J. M. Klinck, E. E. Hofmann, E. A. Wilson-Ormond & M. S. Ellis. 1995. Modeling oyster populations. V. Declining phytoplankton stocks and the population dynamics of American oyster (*Crassostrea virginica*) populations. Fish. Res. 24:199-222.

Powell, E. N., J. M. Klinck, K. A. Ashton-Alcox & J. N. Kraeuter. 2009. Multiple stable reference points in oyster populations: biological relationships for the eastern oyster (*Crassostrea virginica*) in Delaware Bay. Fish Bull 107:109-132.

Powell, E. N., K. M. Kuykendall & P. Moreno. in press. The death assemblage as a marker for habitat and an indicator of climate change: Georges Bank, surfclams and ocean quahogs. Cont. Shelf Res.

Ragnarsson, S. A. & G. G. Thórarinsdóttir. 2002. Abundance of ocean quahog, *Arctica islandica*, assessed by underwater photography and a hydraulic dredge. J. Shellfish Res. 21:673-676.

Reynolds, D. J., C. A. Richardson, J. D. Scourse, P. G. Butler, P. Hollyman, A. Román-González, & J. R. Hall. 2017. Reconstructing North Atlantic marine climate variability using an absolutely-dated sclerochronological network. Palaeogeogr., Palaeoclimatol., Palaeoecol. 465: 333-346.

Ridgway, I. D. & C. A. Richardson. 2011. *Arctica islandica*: the longest lived non colonial animal known to science. Rev. Fish Biol. Fisheries 21:297-310.

Ridgway, I. D., C. A. Richardson, J. D. Scourse, P. G. Butler & D. J. Reynolds. 2012. The population structure and biology of the ocean quahog, *Arctica islandica*, in Belfast Lough, Northern Ireland. J. Mar. Biol. Assoc. *U. K.* 92:539-546.

Rogers-Bennett, L., D. W. Rogers & S. A. Schultz. 2007. Modeling growth and mortality of red abalone (*Haliotis rufescens*) in northern California. J. Shellfish Res. 26:719-727.

Ropes, J. W., D. S. Jones, S. A. Murawski, F. M. Serchuk & A. Jearld Jr. 1984. Documentation of annual growth lines in ocean quahogs, *Arctica islandica* Linné. Fish. Bull. 82:1-19.

Rowell, T. W., D. R. Chaisson & J. T. McLane. 1990. Size and age of sexual maturity and annual gametogenic cycle in the ocean quahog, *Arctica islandica* (Linnaeus, 1767), from coastal waters in Nova Scotia, Canada. J. Shellfish Res. 9:195-203.

Sager, G. & R. Sammler. 1983. Mathematical investigations into the longevity of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Int. Rev. Ges. Hydrobiol. 68:113-120.

Schöne, B. R., I. Kröncke, S. D. Houk, A. D. Freyre Castro, & W. Oschmann. 2003. The cornucopia of chilly winters: ocean quahog (*Arctica islandica* L., Mollusca) master chronology reveals bottom water nutrient enrichment during colder winters (North Sea). Senck. Marit. 32:165-175.

Schöne, B. R., J. Fiebig, M. Pfeiffer, R. Gleß, J. Hickson, A. L. A. Johnson, W. Dreyer & W. Oschmann. 2005a. Climate records from a bivalved Methuselah (*Arctica islandica,* Mollusca; Iceland). Palaeogeogr., Palaeoclimatol., Palaeoecol. 212:215-232.

Schöne, B. R., M. Pfeiffer, T. Pohlmann & F. Seigismund. 2005b. A seasonally resolved bottom-water temperature record for the period AD 1866– 2002 based on shells of *Arctica islandica* (Mollusca; North Sea). Int. J. Climatol. 25:947-962.

Schöne, B. R., S. D, Houk, A. D. Freyre Castro, J. Fiebig & W. Oschmann. 2005a. Daily growth rates in shells of *Arctica islandica*: assessing sub-seasonal environmental controls on a long-lived bivalve mollusk. Palaios. 20:78-92.

Schöne, B. R. 2013. *Arctica islandica* (Bivalvia): a unique paleoenvironmental archive of the northern North Atlantic Ocean. Global Planet. Change. 111:199-225.

Shepherd, S. A., J. R. Turrubiates-Morales & K. Hall. 1998. Decline of the abalone fishery at La Nativida t, México: overfishing or climate change. J. Shellfish Res. 17:839-846.

Solidoro, C., R. Pastres, D. M. Canu, M. Pellizzato & R. Rossi. 2000. Modelling the growth of *Tapes philippinarum* in northern Adriatic lagoons. Mar. Ecol. Prog. Ser. 199:137-148.

Soniat, T. M., E. E. Hofmann, J. M. Klinck & E. N. Powell. 2009. Differential modulation of eastern oyster (*Crassostrea virginica*) disease parasites by the El Niño-Southern Oscillation and the North Atlantic Oscillation. Int. J. Earth Sci. 98: 99-114.

Soniat, T. M., E. N. Powell, E. E. Hofmann & J. M. Klinck. 1998. Understanding the success and failure of oyster populations: the importance of sampled variables and sample timing. J. Shellfish Res. 17: 1149-1165.

Stari, T., K. F. Preedy, E. McKenzie, W. S. C. Gurney, M. R. Heuth, P. A. Kunzlik & D. C. Speirs. 2010. Smooth age length keys: observations and implications for data collection on North Sea haddock. Fish. Res. 105:2-12.

Steingrímsson, S. A. & G. Thórarinsdóttir. 1995. Age structure, growth and size at sexual maturity in ocean quahog, *Arctica islandica* (Mollusca: Bivalvia), off NW-Iceland. ICES document C.M. 1995/K, vol. 54, 17 pp.

Sutton, R. T. & D. L. R. Hodson. 2003. Influence of the ocean on North Atlantic climate variability 1871-1999. J. Climate. 16: 3296-3313.

Svensson, J. R. & D. J. Marshall. 2015. Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. Ecology. 96:819-827.

Tanaka, M. 1982. A new growth curve which expresses infinitive increase. Amakusa Mar. Biol. Lab. 6:167-177.

Tanaka, M. 1988. Eco-physiological meaning of parameters of ALOG growth curve. Amakusa Mar. Biol. Lab. 9:103-106.

Taylor, A. C. 1976. Burrowing behavior and anaerobiosis in the bivalve *Arctica islandica* (L.). J. Mar. Biol. Assoc. U. K. 56:95–109.

Taylor, A. C. & A. B. Brand. 1975a. Effects of hypoxia and body size on the oxygen consumption of the bivalve *Arctica islandica* (L.). J. Exp. Mar. Biol. Ecol. 19:187-196.

Taylor, A. C. & A. B. Brand. 1975b. A comparative study of the respiratory responses of the bivalves *Arctica islandica* (L.) and *Mytilus edulis* L. to declining oxygen tension. Proc. R. Soc. Lond. B Biol. Scil. 190: 445-456.

Thórarinsdóttir, G. G. & S. A. Steingrímsson. 2000. Size and age at sexual maturity and sex ratio in ocean quahog, *Arctica islandica* (Linnaeus, 1767), off northwest Iceland. J. Shellfish Res. 19:943-947.

Thórarinsdóttir, G. G. & L. D. Jacobson. 2005. Fishery biology and biological reference points for management of ocean quahogs (*Arctica islandica*) off Iceland. Fish. Res. 75:97-106.

Thórarinsdóttir G. G., L. D. Jacobson, S. A. Ragnarsson, E. G. Garcia & K. Gunnarsson. 2010. Capture efficiency and size selectivity of hydraulic clam dredges used in fishing for ocean quahogs (*Arctica islandica*): simultaneous estimation in the SELECT model. ICES J. Mar. Sci. 67:345-354.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol Rev. Camb. Philos. Soc. 25:1-45.

Titschock, J., M. Zuschin, C. Spötl & C. Baal. 2010. The giant oyster *Hyotissa hyotis* from the northern Red Sea as a decadal-scale archive for seasonal environmental fluctuations in coral reef habitats. Coral Reefs. 29:1061-1075.

Troost, K. 2010. Causes and effects of a highly successful marine invasion: case - study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. J. Sea Res. 64:145-165.

Ungvari, Z., D. Sosnowska, J. B. Mason, H. Gruber, S. W. Lee, T. S. Schwartz, M. K. Brown, N. J. Storm, K. Fortney, J. Sowa, A. B. Byrne, T. Kurz, E. Levy, W. E. Sonntag, S. N. Austad, A. Csiszar & J. Ridgway. 2013. Resistance to genotoxic stresses in *Arctica islandica*, the longest living noncolonial animal: is extreme longivity associated with a multistress resistance phenotype? *J*. Gerontol. A. Biol. Sci. Med. Sci. 68:521-529.

Urban, H. J. 2002. Modeling growth of different developmental stages in bivalves. Mar. Ecol. Prog. Ser. 238:109-114.

van der Meer, J., J. J. Beukema & R. Dekker. 2003. Large spatial variability in lifetime egg production in an intertidal Baltic tellin (*Macoma balthica*) populations. Helg. Mar. Sci. 56:274-278.

Wanamaker Jr., A. D., J. Heinemeier, J. D. Scourse, C. A. Richardson, P. G. Butler, J. Eríksson & K. L. Knudsen. 2008. Very long-lived mollusks confirm 17th century AD tephrabased radiocarbon reservoir ages for North Icelandic shelf waters. Radiocarbon. 50:399–412.

Wanamaker, Jr., A. D., K. J. Kreutz, B. R. Schöne, K. A. Maasch, A. J. Pershing, H. W. Borns, D. S. Introne, & S. Feindel. 2009. A late Holocene paleo-productivity record in the western Gulf of Maine, USA, inferred from growth histories of the long-lived ocean quahog (*Arctica islandica*). Int. J. Earth Sci. 98:19-29.

Weinberg, J. R. 2005. Bathymetric shift in the distribution of Atlantic surfclams: response to warmer ocean. ICES J. Mar. Sci. 62:1444-1453.

Winter, J. 1978. Filter feeding and food utilization in *Arctica islandica* L. and *Modiolus modiolus* L. at different food concentrations. In: J. H. Steel, editor, Marine food chains, Oliver and Boyd, Edinburgh, pp. 196–206.

Wisshak, M., M. L. Correa, S. Gofas, C. Salas, M. Taviani, J. Jakobsen & A. Freiwald. 2009. Shell architecture, element composition, and stable isotope signature of the giant deep-sea oyster, *Neopycnodonte zibrowii* sp. n. from the NE Atlantic. Deep Sea Res. *Pt I* 56:374-407.

Witbaard, R. 1996. Growth variations in *Arctica islandica* L. (Mollusca): a reflection of hydrography-related food supply. ICES J. Mar. Sci. 53:981-987.

Witbaard, R., G. C. A. Duineveld, & P. A. W. J. de Wilde. 1999. Geographical differences in growth rates of *Arctica islandica* (Mollusca: Bivalvia) from the North Sea and adjacent waters. J. Mar. Biol. Assoc. U. K. 79:907-915.

Witbaard, R. & M. J. N. Bergman. 2003. The distribution and population structure of the bivalve *Arctica islandica* L. in the North Sea: what possible factors are involved? J. Sea Res. 50:11-25.

Zhang, X., D. Haidvogel, D. Munroe, E. N. Powell, J. Klinck, R. Mann & F. S. Castruccio. 2015. Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: model development, larval dispersal and metapopulation connectivity. Estuar. Coast. Shelf Sci. 153:38-53.

Zhang, X., D. Munroe, D. Haidvogel, & E. N. Powell. 2016. Atlantic surfclam connectivity within the Middle Atlantic Bight: mechanisms underlying variation in larval transport and settlement. Estuar. Coast. Shelf. Sci. 173:65-78.

Zolotarev, V. 1996. The Black Sea ecosystem changes related to the introduction of new mollusc species. P. S. Z. N. I: Mar. Ecol. 17:227-236.